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Effects of broad-scale geological changes on patterns in macroinvertebrate assemblages

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Abstract. Understanding the broad-scale factors that influence biological communities has long been a goal of community ecology. We used benthic macroinvertebrate data to identify broad geographical patterns in macroinvertebrate community composition and specifically to examine the influence of the Precambrian Shield on stream abiotic and biotic conditions. The Precambrian Shield is a geological feature that encompasses most of northern North America. Geology differs between Shield and off-Shield areas, creating distinctly different physical and chemical conditions in aquatic systems. We focused our regional-scale study on south-central Ontario, where both Shield and off-Shield conditions are found in adjacent areas. We used constrained and unconstrained multivariate analyses to examine patterns in biotic, abiotic, and spatial variables. Our results showed that, in low-order lotic systems, macroinvertebrate communities differ between Shield and off-Shield streams. Shield streams have higher dissolved O_2, velocity, and discharge, larger amounts of woody debris, and greater canopy cover than off-Shield streams. In contrast, off-Shield streams have higher conductivity, alkalinity, pH, turbidity, and water temperature, and frequently are surrounded by meadow, cultivated, or pastured land. In general, macroinvertebrate communities at off-Shield sites had a greater proportion of taxa preferring pool or depositional habitats, whereas macroinvertebrate communities at Shield sites contained taxa typically associated with riffles or erosional habitats. Analysis of spatial location indicated that the Shield/off-Shield distinction probably is the result of a combination of intertwined abiotic and spatial factors.

Key words: macroinvertebrate communities, Precambrian Shield, Ontario, multivariate analysis.

Community ecologists have highlighted a need to understand better the relative roles of regional and local processes in determining species composition. Ricklefs (1987) suggested that to broaden concepts of the regulation of community structure, we must unite the effects of local and regional processes in community theory. Many studies (Jackson and Harvey 1989, Tonn et al. 1990, Wiley et al. 1997, Angermeier and Winston 1998, Vinson and Hawkins 1998, Wang et al. 2003, Allan 2004, Hoeinghaus et al. 2007) have incorporated these ideas into various examinations of aquatic communities in an attempt to disentangle regional and local effects, particularly with regard to managerial decisions.

Much of northern North America is a vast network of lake and river systems as a consequence of the last glaciation. Several investigators have examined broad-scale patterns to understand better the regional factors structuring lake fish communities. Jackson and Harvey (1989) found that regional patterns in Ontario fish communities reflect broad-scale factors, such as postglacial colonization and extrinsically regulated environmental conditions (e.g., lake thermal regimes), whereas variation within regions is explained by local-scale geomorphic and chemical characteristics of individual lakes. Mandrak (1995) further examined these patterns and found that postglacial dispersal and climatic processes structure regional patterns of fish species richness in Ontario lakes.

Fish community structure seems to be highly dependent on historical pathways of dispersal in the years following the glacial retreat, but there is good

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reason to think that different mechanisms may be responsible for the distribution and community composition of macroinvertebrates. In particular, dispersal mechanisms of most macroinvertebrates (e.g., an aerial dispersal stage) differ from those of fishes and, therefore, macroinvertebrates may be less constrained by waterways for post-glacial dispersal. As suggested by Hynes (1970) and later reviewed by Vinson and Hawkins (1998), many factors can affect the distribution and community composition of aquatic macroinvertebrates. The most notable factors include dispersal ability (Mackay 1992, Bohonak and Jenkins 2003), water chemistry (McKillop and Harrison 1972, Minshall and Minshall 1978, Huryn et al. 1995), physical habitat features (Allan 1975, Erman and Erman 1984, Bourassa and Morin 1995), disturbance (Wallace 1990, Huryn et al. 1995) and, at a local scale, competition and predation (McAuliffe 1984, Holomuzki and Short 1988, Burdon and Harding 2008).

Geology is one broad-scale feature of a landscape that can profoundly affect the physical and chemical attributes of aquatic systems (Johnson et al. 1997, Dow et al. 2006), which can, in turn, affect the biological communities of those systems (Esselman et al. 2006, Kratzer et al. 2006). The Precambrian Canadian Shield (referred to herein as the Shield) is a large-scale and well-known attribute of the North American landscape. The Shield encompasses a broad area covering much of Canada, with extensions into the northern US in the Midwest, New York, and New England. In this expansive area, ancient Precambrian metamorphic and igneous bedrock lies at, or close to, the surface and is covered by only a thin layer of nutrient-poor soil. In south-central Ontario, Shield geology is in sharp contrast to the younger, primarily sedimentary bedrock of southern Ontario and most of remaining North America. The weathering characteristics of these 2 geological types differ sharply. Shield rock weathers because of freeze/thaw fracturing, whereas off-Shield sedimentary rock often weathers via chemical dissolution by water. Thus, the physical and chemical attributes of aquatic systems on the Shield are likely to be quite different from off-Shield systems. For example, extremely low conductivities and a propensity for acidification resulting from poor buffering capacity against the threat of acid precipitation have been widely reported in Shield systems (Ricker 1934, Beamish and Harvey 1972, Schindler et al. 1980, Hall and Ide 1987, Kelso et al. 1990, Bowman et al. 2006). Recently, researchers have noted changes to zooplankton and crayfish communities because of declining Ca levels in Shield systems caused by recovery from acidification (Jeziorski et al. 2008, Edwards et al. 2009). In addition to differences in water chemistry on- and off-Shield, the more immediate proximity of Shield bedrock to the surface may affect the physical structure of aquatic systems, particularly during development of classical pool–riffle morphology of streams (Wohl and Legleiter 2003), but this effect is less well studied. The prevalence of bedrock outcroppings on the Shield suggests that the substrate of Shield streams will be dominated by coarser materials, e.g., bedrock and boulders, and that systems with areas of exposed bedrock will have poorly developed classical pool–riffle relationships simply because the rock resists eroding into pools. The slow erosional rates of Shield bedrock will translate chemically to waters with low conductivity, low Ca levels, and poor buffering capacity against acid inputs.

Aquatic systems of the Canadian Shield have been the subject of some research (Giberson and Mackay 1991, Jackson and Harvey 1995, Yan et al. 1996, Jeziorski et al. 2008, Edwards et al. 2009), but many of these studies were focused exclusively on lentic systems or involved only fish communities. Broad-scale patterns of lotic macroinvertebrate assemblages have been the focus of some recent studies, particularly with regard to differences attributed to ecoregions (Hawkins et al. 2000 and references therein, Van Sickle and Hughes 2000, Waite et al. 2000, Kratzer et al. 2006), but these patterns have yet to be examined in relation to the Canadian Shield. We examined abiotic and biotic patterns across southern and central Ontario to address 2 main objectives. First, we identified broad geographical patterns in macroinvertebrate community composition. We predicted that abiotic factors associated with the Shield vs off-Shield contrast would affect biotic composition in lotic systems in south-central Ontario. We identified the abiotic variables that characterized Shield and off-Shield systems and asked whether differences between macroinvertebrate communities were related to differences in those factors. We expected to observe significant differences in physical habitat and water chemistry between Shield and off-Shield streams. We also expected to find significant changes in macroinvertebrate community composition associated with abiotic changes. For example, we expected to find O_2-sensitive or acid-tolerant species prevalent in Shield systems because of steeper physical gradients (i.e., slope) and more erosional habitats, whereas we expected Ca-sensitive species to be less common because of the poor buffering capacity of the Shield geology.

Methods

In the 1970s, the Ontario Ministry of Natural Resources (OMNR) began a sampling program called the Aquatic Habitat Inventory Survey (AHIS). The purpose of this survey was to provide a record of fish and macroinvertebrate communities in lotic and lentic systems across the province. Field crews from local and regional OMNR offices sampled streams and rivers following protocols outlined in the AHIS manual (AHIS 1979, 1987). The geographical extent of this data set allows for broad-scale analysis of historical macroinvertebrate communities in a large number of lotic systems in Ontario.

The AHIS method involved extensive qualitative sampling designed to collect most of the species present at a site. Sampling occurred in as many different habitats as possible and was done with a variety of equipment, including dip nets, Surber samplers, bottom dredges, and drift nets. The sampling and processing protocol was designed to retain invertebrates exceeding a standard sieve size of 59 μm (AHIS 1979, 1987). The AHIS did not call for a rigidly standardized sampling procedure but emphasized exhaustive sampling that yielded a similar sampling effort at all sites. All invertebrate specimens collected at each site were preserved for identification, unless a large number of crayfish or large clams (>20) were collected, in which case a subsample of ≥ 10 individuals was retained (AHIS 1979).

We used a subset of all AHIS records to examine patterns in macroinvertebrate community composition. We retained all 1st- to 3rd-order stream sites (determined from 1:50,000 topographic maps) from 6 OMNR districts covering a wide area of south-central Ontario to yield 125 sites (Fig. 1). We restricted the analysis to small systems to ensure that any differences in community composition were not caused by effects of stream order and that sampled stream size did not differ systematically among districts. In addition, we restricted this analysis to south-central Ontario to minimize differences in climate patterns among sites, particularly between Shield and off-Shield locations. We mapped sites from both data sets onto a geographical information system (GIS) layer of bedrock geology to determine whether they were on the Canadian Shield (Fig. 1) before classifying them.

After collection, all macroinvertebrate samples were identified to the lowest possible taxonomic level, which, in many cases, was to genus or species. Identifications were completed by qualified personnel in the Ontario Ministry of Natural Resources. For our analysis, we scaled all identifications to family to account for possible misidentifications at lower taxonomic levels and to account for groups identified to only levels above species or genus. We converted original records from abundance to presence/absence to ameliorate the potential disparity in sampling effort among sites and districts. The final data set consisted of a 125 site × 121 invertebrate taxa (families) presence/absence matrix.

Records for 58 of the 125 sites included in our analysis contained extensive abiotic data collected at the same time as the macroinvertebrate sampling. This information included physical–chemical data, such as water temperature (T), dissolved O_2 (DO), pH, turbidity (Turb), alkalinity (Alk), specific conductance (Cond), amount of in-stream cover represented as organic debris (OD; included accumulations of leaves, twigs, and algae), woody debris (WD), in-stream rock cover, undercut banks (UCBank), width, depth, velocity, and discharge. In addition, the original data set also included % composition or categorical variables, including substrate size (categories: rock, boulder, rubble, gravel, sand, silt, clay, muck, marl, and detritus), % canopy cover of stream, degree of gradient (i.e., channel slope; categorized as low, medium, or high), bank stability (a measure of bank erosion, bank slumping, and amount of trees and other vegetation), and the surrounding landscape type assessed laterally to 50 m from the sampling reach (categories: cultivated, firm pasture, meadow, upland hardwood, upland conifer, swamp hardwood, swamp conifer, shrub marsh, and open marsh). Variables within a set of categories or their percentages are not independent (Jackson 1997), so we used correspondence analysis (CA) to summarize the variation within each group of variables (i.e., substrate, canopy cover, channel slope, bank stability, and landscape type) into ≥ 1 correspondence analysis axes and used their resulting site score as a new variable. These summary variables included 2 substrate axes (S1, S2), 1 canopy-cover axis (Cov), 1 channel-slope axis (G), 1 bank-stability axis (BS), and 4 axes summarizing landscape composition (L1, L2, L3, L4) (Table 1).

For these analyses, the 1st data set (A) included 125 sites with macroinvertebrate presence/absence of 121 taxa collected from 1972–1977, and the 2nd data set (B) included the 58-site subset with macroinvertebrate presence/absence of 109 taxa plus corresponding environmental information represented in 23 abiotic variables. We used data set A to assess broad-scale patterns in macroinvertebrate community composition because this data set included more sites and covered a greater spatial extent. We used data set B to examine the relationship between macroinvertebrate community composition and the abiotic environment.

Statistical analyses

We used CA to examine the general patterns in regional macroinvertebrate community composition

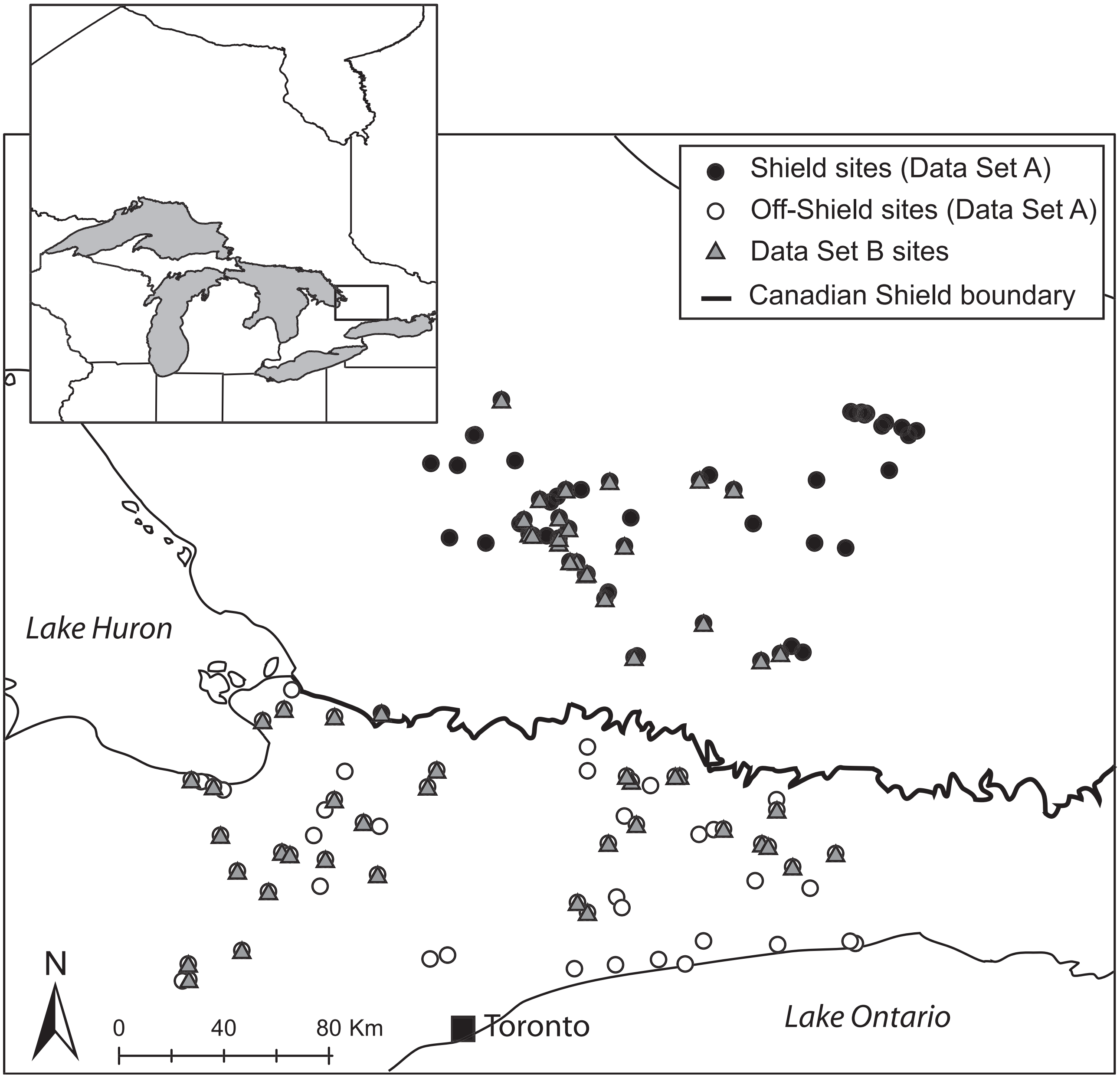

FIG. 1. Map depicting bedrock geology and sampling sites in south-central Ontario. The heavy dark lines depict the Precambrian Shield boundary in this area of the province.

in data set A. CA is a multivariate indirect gradient analysis well suited to analyzing presence/absence data (Jackson and Harvey 1989). We used discriminant analysis to elucidate patterns in environmental variation between Shield and off-Shield systems. This analysis summarized covariation among the abiotic variables in data set B to test whether environmental characteristics differed between Shield and off-Shield sites. We used both CA and Canonical Correspondence Analysis (CCA) with data set B to determine the relationship between biotic and abiotic variables and to elucidate which environmental variables best explained macroinvertebrate community patterns across south-central Ontario. We used CCA with a single predictor categorical variable (Shield/off-Shield) to test whether differences in macroinvertebrate community composition existed between Shield and off-Shield streams. We used a permutation test (n = 9999) to determine if the resulting constrained axis was significant, i.e., were communities from the 2 regions significantly different?

TABLE 1. Compositional abiotic variables analyzed using correspondence analysis (CA) and their interpretations based on ordination scores. The first 2 CA axes were used for substrate composition (summarizing 39.1% of the variation), the first 4 were used for landscape composition (72.4%), and the 1st axis was used for each of canopy cover (59.4%), gradient (62.2%), and bank stability (40.5%).

Variable	Abbreviation	CA score	Description
Substrate composition	S1	High	Rock, boulder, and rubble
		Low	Clay, sand, marl, and muck
	S2	High	Sand, clay
		Low	Marl, muck
Canopy cover	Cov	High	Dense canopy cover
		Low	Open canopy cover
Gradient	G	High	Medium stream gradient
		Low	Low stream gradient
Bank stability	BS	High	Unstable banks
		Low	Stable banks
Landscape composition	L1	High	Cultivated, meadow, and pasture
		Low	Shrub marsh and open marsh
	L2	High	Open marsh
		Low	Shrub marsh
	L3	High	Cultivated, shrub marsh, and open marsh
		Low	Swamp hardwood and swamp conifer
	L4	High	Swamp hardwood and cultivated
		Low	Upland conifer and upland hardwood

Last, we used partial CCA to examine the relative influence of spatial position in the landscape on observed biotic and abiotic patterns (Borcard et al. 1992). We used Shield/off-Shield as a conditional variable to remove the variation attributable to the large-scale spatial location from the biological data set before constraining it by the abiotic variables. This technique effectively controlled for differences between Shield and off-Shield in the interpretation of the patterns in invertebrate communities and environmental variables.

All statistical analyses were done with the vegan package (Oksanen et al. 2009) in R (version 2.10.1; R Development Core Team, Vienna, Austria).

Results

Data set A: regional community composition

CA axis 1 for data set A summarized a gradient of taxa that tend to prefer slow-moving waters (positive values) over fast-flowing waters (negative values) (Fig. 2A; see Appendix 1 for taxon codes). Nearly all families of Trichoptera, Plecoptera, and Ephemeroptera had negative values, whereas nearly all families of Hemiptera, Gastropoda, Amphipoda, Hirudinea, and Isopoda had positive values. Generalist taxa (e.g., Chironomidae, Baetidae) tended to be weakly negative or positive, a result indicating that they were well represented across most sites or that they lacked affinity for particular conditions. The composition of gastropods underwent a transition along the axis from pulmonate snails (e.g., Planorbidae, Physidae, Lymnaeidae), which had strong positive values on axis 1, to prosobranch snails (e.g., Bithyniidae, Viviparidae), which had weakly positive to negative values. Hirudinidae (Hirudinea) and all families of Amphipoda and Isopoda had strongly positive values on axis 1. Prosobranch snails and most taxa of Odonata, Hirudinea, Hydrachnida, Oligochaeta, Nematomorpha, Tricladida, and Unionidae were strongly associated with the far negative end of CA axis 2. When the first 2 axes were examined simultaneously, 3 families of Odonata (Macromiidae, Gomphidae, and Calopterygidae) and 2 families of Diptera (Ceratopogonidae, and Empididae) were strongly associated with each other.

We coded each site according to the bedrock geology to examine patterns of community composition in relation to the Canadian Shield (Fig. 2B). The result was a strong pattern along the first 2 CA axes. Shield sites occurred predominantly on the negative ends of both axes, and off-Shield sites occurred primarily on the positive ends of both axes. This pattern indicated that macroinvertebrate composition at a site differed strongly between Shield and off-Shield sites.

Data set B: community composition and abiotic environment

Linear discriminant analysis revealed that specific conductance and alkalinity were most important for distinguishing between Shield and off-Shield sites (Table 2). We used a jackknife (i.e., cross-validated; Olden and Jackson 2001) approach to classify indi-

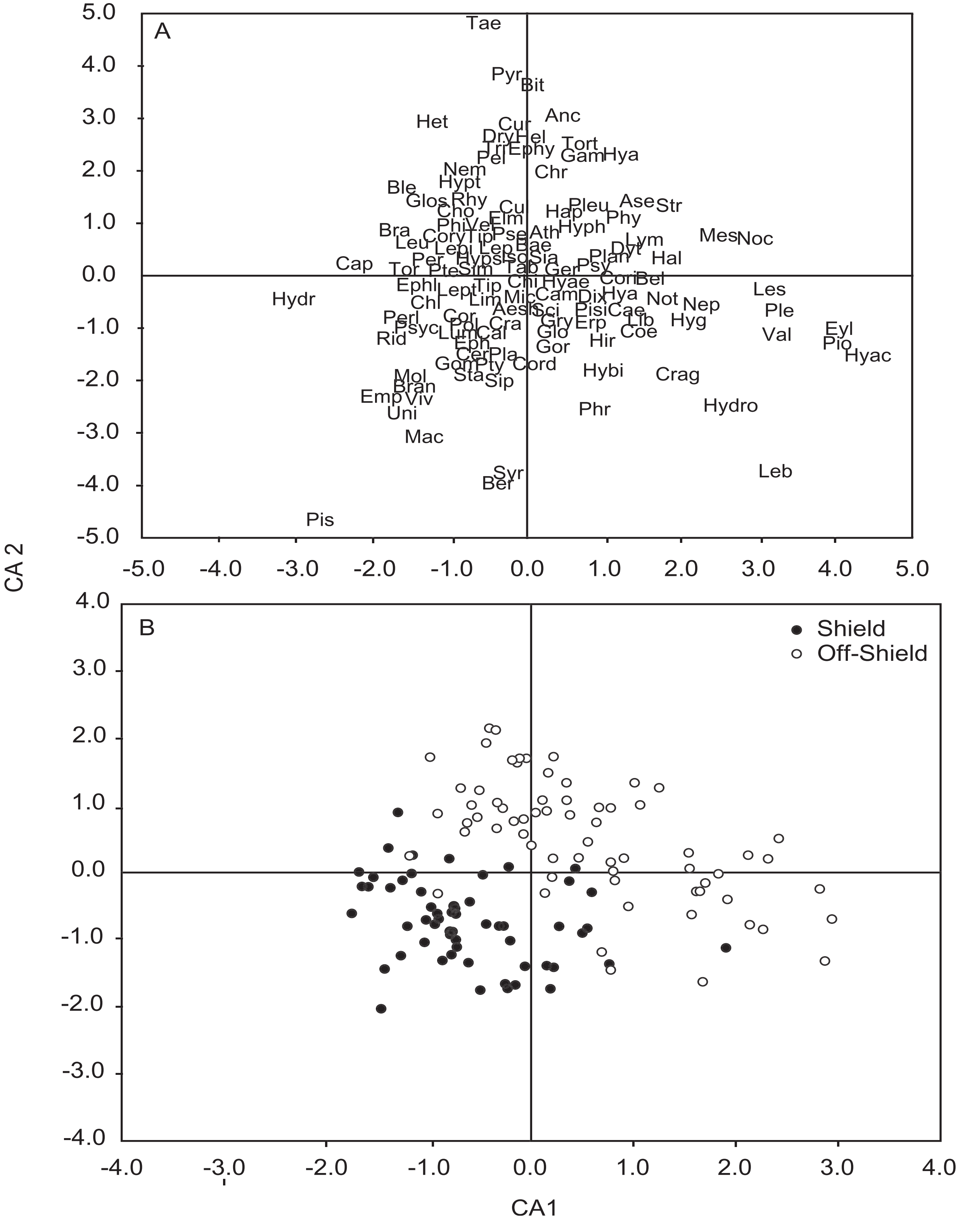

FIG. 2. The ordination resulting from a Correspondence Analysis (CA) of 121 macroinvertebrate taxa (A) and 125 study sites (B) located either on or off the Precambrian Shield. The first 2 CA axes explained 11% of the variability of invertebrate community composition. See Appendix 1 for taxon abbreviations. Labels are centered over the point for each taxon.

TABLE 2. Results from linear discriminant analysis of data set B environmental data from Shield and off-Shield sites. Variables with strong negative scores were associated with off-Shield sites, whereas variables with strong positive scores were associated with Shield sites. Linear discriminant analysis correctly classified 95.8% of Shield sites and 94% of off-Shield sites based on their environmental conditions. See Table 1 for abbreviations of compositional abiotic variables (S1, S2, L1, L2, L3, L4).

Variables	Coefficients of linear discriminants
Alkalinity	−1.4159
Bank stability	0.2658
Specific conductance	−1.2002
Canopy cover	0.3314
Depth	0.2459
Discharge	−0.0327
Dissolved O_2	−0.1893
Gradient	−0.2012
L1	0.1352
L2	−0.0126
L3	−0.1551
L4	−0.2857
Organic debris	0.0634
pH	−0.0366
Rocks	0.0065
S1	0.0447
S2	−0.3296
Temperature	−0.1234
Turbidity	−0.2954
Undercut banks	−0.1653
Velocity	0.3934
Woody debris	0.0013
Width	−0.0513

vidual sites as Shield or off-Shield based on their environmental characteristics. Twenty-three Shield sites (95.8%) and 32 off-Shield sites (94%) were correctly classified in this analysis. In general, off-Shield sites had higher conductivity and alkalinity values, whereas Shield sites had higher water velocity, more dense canopy cover, unstable banks, and greater stream depths.

Relationships found in the unconstrained CA on data set B were consistent with those for data set A, a result indicating that sites in data set B were a representative subset of the broader set (Appendix 2). When the abiotic variables were used to constrain the invertebrate community data in a CCA of data set B, 47.3% of the overall variation was explained by the resulting CCA axes (Fig. 3A). On CCA axis 1, sites with negative scores were associated with higher DO concentrations, higher velocity, greater amounts of woody debris, a denser canopy, and higher % sand and % clay substrate. Taxa associated with the negative side of CCA axis 1 were most families of Trichoptera, Plecoptera, Ephemeroptera, Lepidoptera, Viviparidae (a prosobranch gastropod), Unionidae, and Torrenticolidae (a hydrachnid). Sites at the positive end of the axis were more alkaline, with higher specific conductance, turbidity, and warmer thermal conditions. In addition, these sites had increased amounts of meadow, cultivated, or pastured riparian areas, and larger substrates. Associated taxa included most families of Zygoptera, slow-water Hemiptera, most gastropods, amphipods, Hirudinea, the remaining Hydrachnida families, and Isopoda. CCA axis 2 also showed similar patterns, with higher values of pH, specific conductance, alkalinity, and meadow, cultivated, or pastured landscapes associated with sites and species positioned toward the negative end of the axis. Associated taxa included predominantly shredder and scraper families of Trichoptera, Plecoptera, and Coleoptera; skater families of Hemiptera; pulmonate gastropods; Amphipoda; and Isopoda. Sites toward the positive end of CCA axis 2 were associated with greater stream depth, width, discharge, unstable banks, and more instream woody debris. Taxa associated with the positive end of CCA axis 2 were most odonate families, Ephemeroptera preferring depositional habitats, prosobranch gastropods, and most families of Hirudinea, Bivalvia, Lepidoptera, Hydrachnida, and Oligochaeta.

The single CCA axis produced by constraining the macroinvertebrate community data location (Shield/off-Shield) was highly significant ($p < 0.0001$). This result indicated that sites could be grouped by geological location with confidence based on their macroinvertebrate community composition.

We used partial CCA to assess the relative influence of spatial location and environment on the patterns observed among individual sites. Environmental information alone explained 44.8%, location (Shield/off-Shield; i.e., regional differences in space) alone explained 2.5%, and the covariation between space and environment explained 2.6% of the total variation. When the effect of Shield/off-Shield location was partialled out of these data, the ability of abiotic variables to separate Shield/off-Shield sites was reduced. Some Shield sites were grouped in the ordination plot, but scores of Shield and off-Shield overlapped strongly (Fig. 3B). Abiotic variables with negative scores on CCA axis 1 were DO, pH, % sand and clay substrates, and velocity. Among the abiotic variables with positive scores, the importance of conductivity and alkalinity decreased and depth and water temperature increased. Patterns on the spatially conditioned CCA axis 2 were similar to those on the unconditioned CCA axis 2. pH and % pasture or

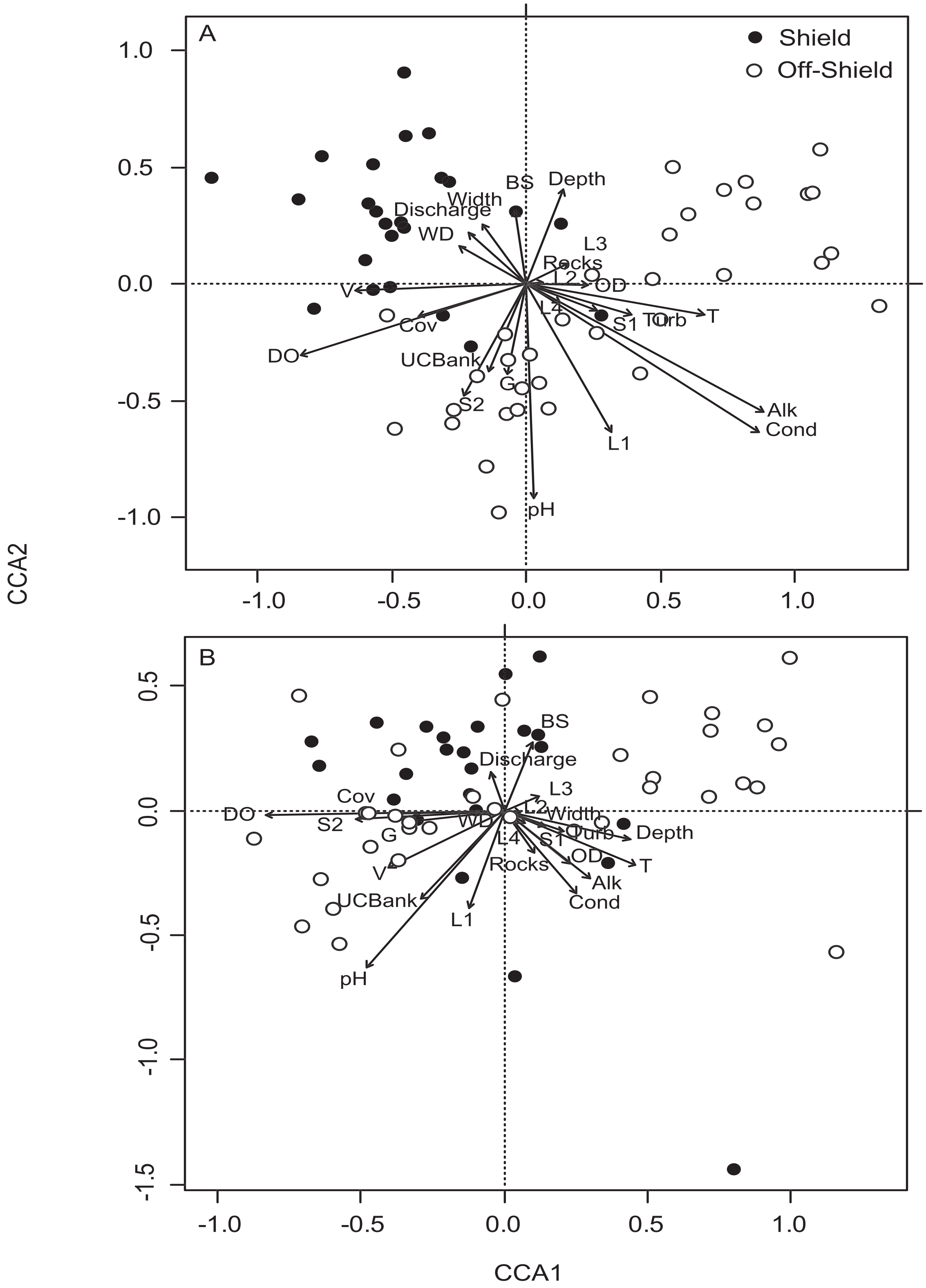

FIG. 3. A.—Ordination from a Canonical Correspondence Analysis (CCA) of 109 invertebrate taxa, 21 environmental variables, and 58 sites. Vector variables are: dissolved O_2 (DO), velocity (V), alkalinity (Alk), conductivity (Cond), turbidity (Turb), width, depth, discharge, organic debris (OD), woody debris (WD), rocks, undercut banks (UCBank), landscape variables (L1, L2, L3, and L4), substrate variables (S1, S2), gradient (G), canopy cover (Cov), and bank stability (BS). Variability explained by CCA axis 1 = 7% and CCA axis 2 = 5%. B.—The ordination from a partial CCA of invertebrate, environmental, and site data shown in Fig. 3A, with spatial information in the form of Shield/off-Shield site location partialled out of the data.

cultivated land use had strongly negative scores associated mainly with off-Shield sites, whereas bank instability and discharge were strongly associated mainly with Shield sites. However, width, depth, and woody debris had less influence on the spatially conditioned CCA axis 2, and channel slope and % sand and clay substrates were more influential on CCA axis 1.

When spatially-structured abiotic information was partialled out of the data set, the macroinvertebrate communities at Shield/off-Shield sites were less distinctly separated based on abiotic variables. This result suggested that some key abiotic differences that distinguish Shield and off-Shield sites were removed with the conditional Shield/off-Shield categorical variable.

Discussion

We showed that the Canadian Precambrian Shield, a large-scale, abrupt geological transition, influences both abiotic conditions and regional patterns in macroinvertebrate community composition in lotic systems of south-central Ontario. Our analyses accurately distinguished sites as Shield or off-Shield based on environmental characteristics alone or based on macroinvertebrate community composition data alone. Other investigators have shown that patterns in macroinvertebrate community composition can be caused by differences in physical habitat (Allan 1975, Erman and Erman 1984, Bourassa and Morin 1995) and water chemistry (McKillop and Harrison 1972, Minshall and Minshall 1978, Huryn et al. 1995), both of which differ between Shield and off-Shield sites. Previous studies in which the effect of a geological transition was examined explicitly tended to be focused on only a few taxa, such as communities or populations of gastropods (McKillop and Harrison 1972, Huryn et al. 1995). Results of other studies incorporating changes in geology between ecoregions have been mixed. For example, Waite et al. (2000) compared lotic macroinvertebrate assemblages in ecoregions in the Mid-Atlantic Highlands (USA) where geological differences between some ecoregions are similar to the differences between Shield and off-Shield locations. Waite et al. (2000) found no clear site clusters by ecoregion in a CA ordination of macroinvertebrate assemblages, but they did find that sites could be arranged consistently according to stream slope, size, and water chemistry, which are important variables distinguishing Shield from off-Shield sites. In contrast, Kratzer et al. (2006) showed that geology might be an important determinant of macroinvertebrate communities in ecoregions in the New York City drinking-water-supply watersheds, but they pointed out that the relative importances of geological variables and patterns of land use were difficult to disentangle.

Two driving variables in the distinction between Shield and off-Shield lotic systems appeared to be conductivity and alkalinity, both of which typically were much higher at off-Shield than at Shield sites. This result was expected because of the differences in weathering rates between Shield (predominantly granites and gneiss) and off-Shield (limestone) bedrock in Ontario (Chapman and Putnam 1984). These differences in weathering rates produce differences in chemical composition (e.g., increased levels of many elements, including P, and higher pH) that ultimately influence primary productivity (Dillon and Rigler 1974). Shield sites tended to have higher water velocity, steeper channel slopes, denser canopy cover, less stable banks, and greater channel depths, whereas off-Shield sites were more turbid, with more stable banks and open canopies, and were more frequently surrounded by meadow, cultivated, or pastured land. These physical differences all fit within expectations for Shield and off-Shield systems, except that unstable banks were more prevalent in Shield systems. However, the measure of bank stability was based on both slope and lack of vegetation, which could apply to systems with steep, bare, boulder or bedrock banks (i.e., steep slopes are regarded as an indicator of unstable banks, but may also be the result of granitic bedrock that resists erosion), conditions we would expect at Shield sites.

Other variables were important in distinguishing macroinvertebrate communities at Shield and off-Shield sites. For example, Shield sites were more northerly than off-Shield sites because of the geographical location of the Canadian Shield. However, restricting the geographic scope of the study area to south-central Ontario effectively reduced the influence of broad-scale climatic differences that could have confounded our analyses. Moreover, much of the spatial variation in invertebrate communities was associated with an east–west gradient that probably was caused by lake-effect climate variability and proximity of the study area to Lake Huron.

The interplay between geology and land use in determining the ecological condition of lotic systems has been well documented (e.g., Allan 2004, Dow et al. 2006, Kratzer et al. 2006), with the general conclusion that separating the effects of geology and land use on macroinvertebrate communities is tricky at best. Geology often plays a large role in determining land use, and this is the case in Ontario, where the nature of the Shield limits agricultural development in Shield areas. Landuse data relevant to the time period covered by our data set were not available for the geographical extent of the study area, so we were unable to include a more detailed comparison of the effects of land use on macroinvertebrate communities in Shield and off-Shield systems. A cursory analysis of current landuse data (Aquatic Landscape Inventory Software [ALIS], 2001–2003) indicated that land uses differ between Shield and off-Shield areas. Off-Shield areas tend to have more cropland, pasture, and other types of less forested land uses than Shield areas. These landuse data were compiled ~30 y after the historical surveys used in our study, but the predominant uses have not changed during this time interval for this region. We used a partial CCA to attempt to control for differences in land use. The results indicated that land use accounted for only a very small portion of the total variation in macroinvertebrate communities. When landuse information was partialled out of the data set, the distinction between Shield and off-Shield sites remained. Previous studies comparing Shield and off-Shield lentic systems also revealed patterns similar to those found in our study (Jackson and Harvey 1989). That is, Shield and off-Shield sites were distinct, regardless of the fact that the off-Shield sites encompassed a range of different habitat types and conditions.

Physical habitat often is an important variable when distinguishing macroinvertebrate communities. Substrate size was not an influential abiotic variable in the distinction between Shield and off-Shield sites, but some variability in macroinvertebrate communities could be attributed to preferences for erosional or depositional habitats. In general, more taxa that tend to prefer depositional habitats, such as Odonata, Hemiptera, Coleoptera, Hirudinea, Gastropoda, Diptera, Hydrachnida, and Isopoda, were found at off-Shield than at Shield sites. These taxa are found predominantly in slower waters and have adaptations, such as sprawling, climbing, burrowing, and diving habits, that enable them to exploit food resources primarily found in depositional habitats. In contrast, more taxa that tend to prefer erosional habitats, such as Trichoptera, Plecoptera, and Ephemeroptera, were found at Shield than at off-Shield sites. Many of these taxa are clingers, with adaptations to hold on to substrates in fast water and exploit food resources found in swifter currents. Variation exists in the types of habitat exploited by species within each invertebrate family, but this general distinction in the types of taxa associated with Shield and off-Shield systems is consistent with the physical characteristics of each system.

We addressed the effect of spatial organization of sites by using a partial CCA to tease apart the effects of location (Shield/off-Shield) and environmental conditions on the arrangement of sites according to their species composition. Spatial information accounted for only a minor percentage of the variation explained by the analysis, but it had a significant influence on the separation of Shield and off-Shield sites in the resulting biplot of the first 2 constrained axes. This difference in the community ordination suggests that some key abiotic differences that distinguish Shield and off-Shield sites were removed once the effect of spatial location was removed. Given the strong differences in conductivity and pH and the relatively minor differences in most other variables between regions, we suggest that water chemistry was the most influential determinant of differences between communities in the 2 regions.

Some taxa may be constrained to off-Shield sites by physiological limitations related to the low ionic composition or low Ca concentration in Shield waters. Ca is an essential element for all organisms for a variety of physiological and structural processes, and its concentration in aquatic systems is often dependent on substrate rock type (Webster and Patten 1979). Our analyses showed that most gastropods and other crustaceans, such as Amphipoda and Cambaridae, were strongly associated with off-Shield sites. For example, only one gastropod family (Viviparidae, a prosobranch snail that requires higher O_2 levels and permanent water) was strongly associated with Shield streams. McKillop and Harrison (1972) found a similar pattern in which densities of pulmonate snails were higher in hard water (325–885 μS/cm) and of prosobranch snails were higher in medium-to-soft water (55–86 μS/cm). They suggested that pulmonate snails may be physiologically limited from occurring in low-conductivity water, but the exact mechanism for their limitation was not specified. Nearly 45% of all freshwater gastropods are restricted to waters with Ca concentrations >25 mg/L (Thorp and Covich 1991). Ontario Ministry of the Environment data (Ministry of Environment, unpublished data) indicate that Ca levels in streams in the south-central Ontario region of the Canadian Shield range from 1.0 to 15.3 mg/L (higher values often are related to local deposits of glacial till containing carbonate rocks) and conductivity values range from 14.4 to 161 μS/cm (n = 126). In our study, conductivity ranged from 26 to 181 μS/cm at Shield sites and from 312 to 600 μS/cm at off-Shield sites. The low conductivity of Shield water could interact with biological factors to lead to indirect biotic interactions. For example, if pulmonate snails are less well adapted than prosobranch snails to low-Ca waters, then their sparse abundance in Shield waters might be the result of physiological stress or of other factors, such as competitive interactions with prosobranch snails. In addition, many fish species that occur in Shield waters are able to crack the shells of gastropods and prey upon them effectively (Scott and Crossman 1998). Pulmonate shells tend to be thinner than prosobranch shells (Dillon 2000), so pulmonate snails may be at more risk than prosobranch snails in environments with snail-predating fishes. A lack of available Ca in the water may make snails with thin shells even more vulnerable to predation. However, Dillon (2000) noted that large interspecific variation exists in Ca tolerance in freshwater gastropods, and the breadth of tolerance of the taxa in the study region is not known. The patterns of association match well with predictions based on the literature, but further support is required from experimental work to determine the role of Ca in regulating the composition of gastropods and, potentially, other taxa. For example, similar distribution patterns were observed for Amphipoda and Isopoda families, but too little information is available in the literature concerning the physical and chemical habitat preferences of these organisms to draw any further conclusions. Minshall and Minshall (1978) noted that some indirect evidence exists to suggest that *Gammarus pulex* (Amphipoda) may be affected by Ca levels. Glazier et al. (1992) found that some amphipod species were absent from systems with conductivities <25 μS/cm. At present, little direct evidence exists to support a hypothesis of Ca limitation on the distribution of benthic invertebrates, although attention to this question is increasing because of declining Ca concentrations in areas on the Canadian Shield (Jeziorski et al. 2008, Edwards et al. 2009).

Another potential limiting variable constraining taxa to Shield or off-Shield sites is pH. In some ways, pH is related to water-chemistry variables like Ca, but pH is of particular interest in Shield systems because of the effects of acidic precipitation in the area. In a study of Canadian Shield lakes, Lonergan and Rasmussen (1996) noted that the abundances of several macroinvertebrate taxa were significantly associated with pH after other water-chemistry variables were partialled out of the analysis. For instance, *Hyallela azteca* (Amphipoda) was an important indicator of pH variation among lakes and was found predominantly in waters with higher pH (e.g., Glazier et al. 1992 and references therein). This strong association with pH also may help explain the association of amphipod taxa with off-Shield sites in our analysis because Shield sites were generally more acidic than off-Shield sites.

Five Shield sites—North, Stoddard, Esson, Beaver, and McCue—consistently grouped with off-Shield sites in both abiotic and biotic analyses. A possible explanation for this outcome is that all of these sites are near the southern edge of the Canadian Shield, where the geology is a more complex mix of metamorphic and igneous rock than the gneiss-dominated deposits further north. For example, McCue Creek is the only Shield site on carbonate metasedimentary bedrock, and this distinction could explain why both the environmental and biological characteristics of this stream had scores in the area of overlap between Shield and off-Shield points in both the CA and CCA. Therefore, sites close to the transition area between Shield and off-Shield geology may exhibit abiotic and biotic characteristics of both areas.

The influence of the Canadian Precambrian Shield on both the physiochemical habitat and macroinvertebrate communities of lotic systems suggests that this feature is an important regional-scale landscape determinant of biological patterns in south-central Ontario. Such broad-scale environmental discontinuities probably are important determinants of biodiversity, and could enhance regional biodiversity by providing strong contrasts in environmental conditions. We do not know whether such differences in community composition are common in response to such natural discontinuities, and we acknowledge that we were unable to disentangle fully the potential effects of differences in landuse patterns between Shield and off-Shield sites that may influence macroinvertebrate communities. Regardless, macroinvertebrate community composition differed significantly between Shield and off-Shield lotic systems in our analysis. These differences may be important when considering the potential for species ranges to change in response to factors such as climate change. Some conditions, such as thermal environments, may change, but underlying physiological conditions (caused by water chemistry in this instance) may limit the potential for changes in distributions of taxa.

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Appendix 1. Invertebrate families and associated abbreviations used in the ordination figures.

Family	Abbreviation	Family	Abbreviation	Family	Abbreviation
Aeshnidae	AESH	Glossiphoniidae	GLO	Notonectidae	NOT
Ancylidae	ANC	Glossosomatidae	GLOS	Peltoperlidae	PEL
Asellidae	ASE	Gomphidae	GOM	Perlidae	PER
Atheceridae	ATH	Gordiidae	GOR	Perlodidae	PERL
Baetidae	BAE	Gyrinidae	GRY	Philopotamidae	PHI
Belostomatidae	BEL	Haliplidae	HAL	Phryganeidae	PHR
Beraeidae	BER	Haplotaxida	HAP	Physidae	PHY
Bithyniidae	BIT	Helicopsychidae	HEL	Pionidae	PIO
Blephariceridae	BLE	Heptageniidae	HEP	Piscicolidae	PIS
Brachycentridae	BRA	Heteroceridae	HET	Pisidiidae	PISI
Branchiobdellida	BRAN	Hirudinidae	HIR	Planariidae	PLA
Caenidae	CAE	Hyalellidae	HYA	Planorbidae	PLAN
Calopterygidae	CAL	Hydrachnidae	HYAC	Pleidae	PLE
Cambaridae	CAM	Hydraenidae	HYAE	Pleuroceridae	PLEU
Capniidae	CAP	Hydrobiidae	HYBI	Polycentropodidae	POL
Ceratopogonidae	CER	Hydrodromidae	HYDRO	Psephenidae	PSE
Chironomidae	CHI	Hydrophilidae	HYPH	Psychodidae	PSY
Chloroperlidae	CHL	Hydropsychidae	HYPS	Psychomyiidae	PSYC
Chordodidae	CHO	Hydroptilidae	HYPT	Pteronarcidae	PTE
Chrysomelidae	CHR	Hydryphantidae	HYDR	Ptychopteridae	PTY
Coenagrionidae	COE	Hygrobatidae	HYG	Pyralidae	PYR
Cordulegastridae	COR	Isonychiidae	ISO	Rhyacophilidae	RHY
Corduliidae	CORD	Lebertiidae	LEB	Reduviidae	RID
Corixidae	CORI	Lepidostomatidae	LEPI	Sciomyzidae	SCI
Corydalidae	CORY	Leptoceridae	LEP	Sialidae	SIA
Crambidae	CRA	Leptophlebiidae	LEPT	Simulidae	SIM
Crangonyctidae	CRAG	Lestidae	LES	Siphlonuridae	SIP
Culicidae	CUL	Leuctridae	LEU	Staphylinidae	STA
Curculionidae	CUR	Libellulidae	LIB	Stratiomyidae	STR
Dixidae	DIX	Limnephilidae	LIM	Syrphidae	SYR
Dryopidae	DRY	Lumbriculidae	LUM	Tabanidae	TAB
Dytiscidae	DYT	Lymnaeidae	LYM	Taeniopterygidae	TAE
Elmidae	ELM	Macromiidae	MAC	Tipulidae	TIP
Empididae	EMP	Mesovelidae	MES	Torrenticolidae	TOR
Ephemerellidae	EPHL	Microsporidae	MIC	Tortricidae	TORT
Ephemeridae	EPH	Molannidae	MOL	Tricorythidae	TRI
Ephydridae	EPHY	Muscidae	MUS	Unionidae	UNI
Erpobdellidae	ERP	Nemouridae	NEM	Valvatidae	VAL
Eylaidae	EYL	Nepidae	NEP	Veliidae	VEL
Gammaridae	GAM	Noctuidae	NOC	Viviparidae	VIV
Gerridae	GER				

APPENDIX 2. Ordination from a correspondence analysis (CA) of 58 study sites and 109 macroinvertebrate taxa (data set B). The first 2 CA axes explain 13.8% of the total variation.