

Sources of small-scale variation in the invertebrate communities of headwater streams

ROBIN LECRAW* AND ROBERT MACKERETH[†]

*Department of Zoology, University of British Columbia, Vancouver, BC, Canada

[†]Center for Northern Forest Ecosystem Research, Ontario Ministry of Natural Resources, Thunder Bay, ON, Canada

SUMMARY

1. Our objective was to investigate the associations between benthic macro-invertebrate communities and environmental factors described at three spatial scales: local, reach and catchment. Differences in these associations, because of local topography, were determined by categorising sites into those having a large or small 'reach contributing area' (RCA), which is the lateral area of land contributing surface and subsurface flow of water, nutrients, organic and inorganic materials to a stream reach independent of catchment size and upstream contributions, and created by local topography.
2. Twenty-three sites were sampled in the Lake Nipigon Forest in north-western Ontario. Local variables included hydrological metrics and stream morphology characteristics. Terrestrial reach and catchment variables included forest characteristics, topography and geomorphology. Invertebrates were identified and classified into functional feeding guilds. Canonical correspondence analysis and redundancy analysis were used to determine which variables contributed most to macro-invertebrate community structure and how the RCA influenced those associations.
3. Overall, local-scale variables explained most variation in taxonomic and functional community structure (51.6 and 59.1%). Catchment-scale variables explained more variation in the community (43.9 and 43.5%) than reach-scale variables. In sites with a large RCA, the reach-scale variables accounted for almost 10% more variability in taxonomic structure than the catchment-scale variables, and in sites with a small RCA, catchment-scale variables explained almost 23% more variation in feeding guild structure than reach-scale variables.
4. Topography was important at both the reach and the catchment scales. Variables at the reach scale most associated with invertebrate community tended to be related to forest cover, whereas important variables at the catchment scale were related to topography, wetlands and lakes.
5. The difference in associations between invertebrate communities and environmental factors based on RCA indicates the influence of local topography on the linkage between aquatic habitats and the surrounding terrestrial environment. Understanding how these linkages affect aquatic communities can help to develop more effective predictive models of invertebrate community and more prescriptive conservation and management strategies for small streams.

Keywords: community structure, functional group, redundancy analysis, spatial scale, topography

Correspondence: Robert Mackereth, Center for Northern Forest Ecosystem Research, Ontario Ministry of Natural Resources, 955 Oliver rd., Thunder Bay, ON P7B 5E1, Canada. E-mail: rob.mackereth@ontario.ca

Introduction

Understanding how the structure of the habitat in small streams and the associated biotic communities are related to the surrounding landscape is essential for the conservation of stream ecosystems. Landscape controls on stream habitat have been described as a hierarchy of spatial scales (Frissell *et al.*, 1986; Poff, 1997). The largest spatial scale (often the ecoregion or catchment scale) constrains the possible conditions at smaller spatial scales through, for example, the climatic or geological characteristics of the region. The characteristics of smaller spatial scales (for example, stream system or river valley), in turn, constrain possible conditions at even lower scales in the hierarchy: stream reach, pool/riffle and microhabitat (Frissell *et al.*, 1986).

The community of macro-invertebrates inhabiting the stream can be related to the stream habitat by two ways. The small-scale stream habitat can be thought of as a template related to specific traits represented in the biotic community; therefore, the community will contain organisms possessing a suite of the appropriate traits (Townsend & Hildrew, 1994). In the second approach, each level of the landscape hierarchy described earlier acts as a 'filter', allowing only those organisms with the appropriate traits to pass through. The community will then be composed of organisms with traits allowing them to 'pass' through all the filters of hierarchical conditions (Poff, 1997).

In the hierarchical model proposed by Poff (1997), in which each spatial scale acts as a filter for species traits, the first condition given for the application of the theory is an understanding of the degree to which each nested spatial scale is functionally linked to the next. The connectivity between the stream and the surrounding landscape is determined primarily by topography. The 'process domains' concept (Montgomery, 1999) suggests that topography at the scale of the stream reach will determine stream conditions because of the impact of scouring through flood disturbance and interactions with the lateral floodplain. In other words, the functioning of the 'filter' from the intermediate spatial scale to the stream habitat will be determined by the local topography.

A great deal of research has been focused on determining the relationship between the benthic macro-invertebrate community and the hierarchical function of the surrounding landscape. In small

streams, local habitat characteristics have been shown to be the dominant factors structuring invertebrate communities (Corkum, 1992; Brosse, Arbuckle & Townsend, 2003; Sandin & Johnson, 2004; Johnson *et al.*, 2007). Some studies, however, have shown greater importance of variables at the intermediate (reach) scale (Sponseller, Benfield & Valett, 2001; Feld & Hering, 2007), and large-scale (catchment) variables have been shown to be the most important factor distinguishing between invertebrate communities over large regional areas (Corkum, 1989). In addition to the spatial scope of the study, the type of invertebrate data assessed can influence the apparent relationship between the community and the landscape. Heino *et al.* (2007) found that large-scale factors had a greater influence on taxonomic structure and local-scale factors had a greater influence on functional structure.

To examine the effect of the hierarchy of three spatial scales on the invertebrate community, we have related the invertebrate community, as assessed taxonomically and using functional feeding groups, to the local stream habitat and to two 'landscape' scales: the intermediate 'reach' scale and the large 'catchment' scale. To test the hypothesis that the local topography will influence the connectivity of the stream to larger spatial scales, as proposed by the process domains concept (Montgomery, 1999), we explored differences in the 'reach contributing area' (RCA). We define the RCA as the area of land adjacent to a stream that provides lateral surface and subsurface contributions of water, nutrients, organic and inorganic material to a chosen reach of the stream and is independent of stream size and upstream contributions (Theobald *et al.*, 2006). Large RCAs focus surface and subsurface flows from a large terrestrial area through sloping topography converging at a stream reach ('topographic convergence'; Montgomery, 1999), which may therefore generate greater fluxes of ground water and nutrients into certain stream reaches. As a result, stream reaches with larger RCAs have the potential for stronger linkages to lateral landscape factors and to have different in-stream habitat characteristics. If this is the case, macro-invertebrate communities would then be expected to differ between stream sites with large and small RCAs and to have different associations with reach and catchment-scale variables.

The purpose of this study was to examine factors influencing invertebrate community structure and to

evaluate the relative strength of association between the community and the environmental variables measured at different spatial scales. We focused on three main objectives. First, to determine which variables at the local, reach and catchment scales are most strongly associated with variation in the structure of the benthic invertebrate community. Secondly, to determine whether the composition of benthic invertebrate taxa or feeding guilds differs between stream reaches with small and large RCAs. Thirdly, to estimate differences in the contribution of each spatial scale in explaining variation in the benthic macro-invertebrate community between stream reaches with small and large RCAs.

Methods

Study area

Streams were studied in the Nipigon Bay catchment on the North shore of Lake Superior, approximately 100 km east of Thunder Bay, Ontario. Sites were located in seven subcatchments (Jackfish, Jackpine, Gravel, Cypress, Ozone, Dublin and Recover) which are in the Lake St Joseph Plains and Superior Highlands Plains ecoregions (Wickware & Rubec, 1989). Both ecoregions are dominated by granitic bedrock covered with shallow sandy to loamy moraine. Forest cover is dominated by black spruce [*Picea mariana* (Miller)] with some white spruce [*Picea glauca* (Moench)], balsam fir [*Abies balsamea* (L.)], jack pine [*Pinus banksiana* (Lamb.)], white birch [*Betula papyrifera* (Marshall)] and trembling aspen [*Populus tremuloides* (Michx.)]. The main land use in the area is forestry.

Site selection

All sites were selected on stream sections with approximately a 100 ha catchment area. Using the Ontario provincial 20 m resolution digital elevation model (DEM) (Ontario Ministry of Natural Resources 2005), a model was constructed using a geographic information system (GIS) to delineate RCAs, excluding contributions from upstream, for all the streams of interest. A flow direction layer was generated from the DEM and, for each 20 × 20 m grid cell on the stream, the furthest extent of the terrestrial area on each side of the stream in which all flow directions

converge on the stream cell was delineated as the RCA (ArcGIS, ArcMap version 9.2, ESRI Inc., Redlands, CA, U.S.A.). Sites were selected having an RCA of <800 m² (or 0.08 ha) for the 'small RCA' class and >10 ha for the 'large RCA' class. If sites were located on the same stream, the large RCA site was at least 200 m downstream of the small RCA, to reduce confounding effects of large upstream lateral inputs persisting into the small RCA sites. Local topography was confirmed visually before accepting a study site. Twenty-three sites were selected in unharvested areas of which 12 had small RCAs and 11 had large RCAs.

In-stream habitat

Study reaches were 10 m in length, which allowed us to study immediate local effects of large lateral inputs. Stream habitat variables were all measured during summer stream baseflow conditions in July 2008. The gradient of each reach was measured with a clinometer. Canopy cover was measured with a densiometer from the middle of the channel at the top and bottom of each reach. Stream wetted width, bankfull width, bank height and maximum depth were measured at the top, middle and bottom of each reach. Detritus and woody debris were recorded in the categories absent (0), present (1) or abundant (2) at three transects for a total score out of 6. The substratum was quantified by measuring the median axis of 50 particles selected at random along the entire length of the reach. Substratum particles were sorted into classes based on a modified Wentworth scale (Wentworth, 1922): bedrock (>999 mm), boulder (301–999 mm), cobble (51–300 mm), pebble (21–50 mm), gravel (1–20 mm), sand and silt. The variable '% fine sediment' was calculated as the percentage of the substratum composed of sand or silt. Discharge was measured at one transect in each reach using a Flo-Mate Model 2000 portable flow meter (Marsh-McBirney, Inc, Frederick, MD, U.S.A.). Temperature, pH, dissolved oxygen (DO), conductivity and total dissolved solids were measured with a YSI 600 QS probe (YSI incorporated, Yellow Springs, OH, U.S.A.). Water samples were collected for total nitrogen and total phosphorus analysis, which was performed at the Lakehead University Environmental Laboratory. All forms of nitrogen were digested and reduced to nitrate, which was then measured colorimetrically at 540 nm (Joncas & Walford, 2008a), and all forms of

phosphorus were digested and reduced to a phosphomolybdic blue complex and measured colorimetrically at 880 nm (Joncas & Walford, 2008b). Colorimetric analysis was performed using a SanPlus Autoanalyzer (Skalar Analytical B.V., Breda, the Netherlands).

To estimate the abundance of algae, periphyton samples were collected by scraping a known surface area of a rock from the stream or, in the absence of large-substratum particles, a sample of substratum equivalent to the same surface area was collected. Samples were rinsed into an opaque container and frozen following the USEPA rapid bio-assessment protocols (Barbour *et al.*, 1999). Periphyton samples were later thawed and filtered through glass fibre filters with a 0.7- μm pore size for chlorophyll *a*, and ash-free dry mass analysis following the USDA Forest Service protocols (Davis *et al.*, 2001).

Riparian scale assessment

The transition from riparian zone to upland was determined as a distinct change from riparian wetland vegetation to upland species such as mountain maple [*Acer spicatum* (Lam.)] or white birch common to well-drained soils, or a distinct change in slope. Width and slope of the zone were measured on both banks at the upstream and downstream ends of each reach. Tree density within the RCA was measured using the point-centred quarter method (Barbour, Burk & Pitts, 1987) along 50–100 m transects perpendicular to the stream beginning at the riparian-upland border. Total tree density and relative density of each tree species were calculated and summarised as the proportion hardwood (white birch, trembling aspen, and mountain maple).

Catchment-scale assessment

Variables at the catchment scale were calculated using a GIS to analyse information in the Natural Resources and Values Information System fundamental layers (Ontario Ministry of Natural Resources 2009). Variables included catchment size, historically harvested area, proportion of geological landforms, the area of lakes and wetlands within the catchment and the coefficient of variation in elevation (CV elevation) of points within the catchment taken from the DEM. Where the geological landform is defined

as 'bedrock' it is defined as a bedrock form (knob, ridge or plain) either exposed or overlain by a thin drift veneer, usually of glacial till ground moraine <1-m deep (Gartner, Mollard & Roed, 1981). The CV elevation was calculated by dividing the standard deviation by the mean altitude of each 20 \times 20 m DEM grid cell in the catchment. These metrics were also calculated for the reach scale by calculating values within each RCA.

Invertebrate assessment

Three replicate invertebrate collections were taken at each sampling reach. In order of preference, samples were collected from riffles, snags or runs while sampling in pools was avoided. Samples were collected from the stream bed by scrubbing the substratum in a 30 \times 30 cm quadrat while holding a D-net with 500- μm mesh at the downstream edge of the quadrat. Three samples of 0.09 m² covered an average of 2.2% of the streambed in a 10-m reach of stream. Invertebrates were preserved in 75% ethanol and were sorted and identified under a microscope. Invertebrates were identified to genus where possible but Chironomidae and Simuliidae were left at the family level and non-insect taxa were identified to order. Invertebrate taxa were assigned to functional feeding guilds according to Merritt & Cummins (1996) based on generic level classification. To summarise the feeding guild structure, the abundance, percentage of total abundance and number of taxa were calculated for each of the five feeding guilds (gatherers, scrapers, shredders, filterers and predators).

Analysis

Environmental data were divided into the three spatial scales, and collinear variables were excluded (variance inflation factor > 10). The final variables used in the analysis are listed in Table 1. Stream width, riparian width and chlorophyll *a* were $\log_{10}(x + 1)$ transformed to improve normality. Invertebrate data were used to build two matrices, one based on taxonomic structure and one based on functional feeding groups. The taxonomic data were analysed at the family level (to reduce the number of taxa occurring in only one site), as there is evidence that family-level classification is as effective as generic or species levels for determining community

Table 1 Means (1 SD) of all environmental variables for all sites, and for each RCA class. Abbreviations given are found in ordination diagrams

Variable	Abbreviations	All sites	RCA size class	
			Large	Small
Local				
Stream gradient (degrees)	Gradient	2.65 (2.97)	1.83 (1.73)	3.47 (3.16)
% Canopy cover	Canopy C	78.17 (21.64)	71.75 (27.79)	84.59 (10.44)
Log ₁₀ stream width (m)	log10strm	1.40 (0.72)	1.31 (0.56)	1.49 (0.87)
Water temp (°C)	Temp	13.33 (3.14)	13.10 (3.43)	13.56 (2.91)
Dissolved oxygen (mg L ⁻¹)	DO	9.12 (2.20)	8.98 (2.12)	9.27 (2.35)
Total woody debris (count)	Total wo	4.00 (1.58)	4.40 (1.40)	3.60 (1.68)
Total detritus (abundance scale)	Total de	3.60 (1.90)	4.07 (2.02)	3.13 (1.73)
% Fine substratum	finesub	43.27 (39.04)	55.47 (40.75)	31.07 (34.31)
Water velocity (m s ⁻¹)	velocity	0.10 (0.05)	0.10 (0.06)	0.09 (0.04)
Total nitrogen (mg L ⁻¹)	Total N	0.46 (0.15)	0.52 (0.17)	0.41 (0.12)
Log ₁₀ chlorophyll <i>a</i> (mg m ⁻²)	log10chla	2.17 (3.17)	1.97 (2.57)	2.36 (3.75)
Reach				
Size of RCA (m ²)*	rca	1.14E5 (1.47E5)	2.27E (1.32E5)	853 (521)
Tree density (per ha)	tree den	4760 (2888)	3935 (3325)	5586 (2184)
Log ₁₀ riparian width (m)	log10Rip	10.75 (13.88)	11.63 (5.79)	9.88 (19.07)
Proportion hardwood	prophard	0.36 (0.26)	0.36 (0.28)	0.36 (0.25)
% of rca harvested within 20 years	rca20har	22.72 (45.87)	37.20 (58.60)	8.24 (21.78)
% of rca harvested within 10 years	rca10har	18.98 (45.48)	33.65 (59.53)	4.32 (16.73)
% of rca bedrock	rcaBedr	84.99 (33.29)	89.97 (22.97)	80.00 (41.40)
Coefficient of variation of elevation in the rca	rcaCV elev	0.02 (0.03)	0.04 (0.03)	0.01 (0.01)
Catchment				
Catchment size (sq m)	eshed_sqm	9.41E5 (2.55E5)	1.02E6 (3.05E6)	8.62E5 (1.68E5)
% of catchment bedrock	% Bedrock	94.60 (13.68)	92.92 (15.33)	96.28 (12.10)
% of catchment harvested within 20 years	harv20	7.84 (13.54)	9.53 (15.01)	6.15 (12.18)
% of catchment harvested within 10 years	harv10	2.95 (7.70)	5.12 (10.40)	0.78 (2.11)
% of catchment lakes	%lake	0.88 (1.52)	0.92 (1.47)	0.83 (1.62)
% of catchment wetlands	%wetland	1.12 (2.17)	0.62 (1.28)	1.62 (2.76)
Coefficient of variation for elevation in catchment	CV elev	0.05 (0.03)	0.05 (0.04)	0.05 (0.03)

RCA, reach contributing area.

*Scientific notation presented as $1.14 \times 10^5 = 1.14E5$

gradients in multivariate analysis (Furse *et al.*, 1984; Bowman & Bailey, 1997).

Canonical correspondence analysis (CCA) and redundancy analysis (RDA) ordinations were performed to determine how much of the variation in both the taxonomic and the functional feeding group sets of invertebrate community data could be explained by variables at each of the three spatial scales. Data were analysed including (i) all sites, (ii) only the small RCA sites and (iii) only the large RCA sites. Each of the three site groupings, combined with all three spatial scales and two data sets resulted in a total of 18 ordinations. CCA was used for the taxonomic invertebrate data, and RDA was used for the feeding guild metric data. Further partitioning of the variance explained uniquely by each spatial scale through partial ordinations was not possible, because

of constraints of sample size and the number of environmental variables needed for partial correspondence analysis. All ordinations were performed in CANOCO 4.5 (Biometris, Wageningen, the Netherlands) using interspecies relationships and biplot scaling. In CCA, the taxonomic data were $\log_{10}(x + 1)$ transformed and rare species downweighted. In RDA, the feeding guild metrics were divided by standard deviation, centred and not transformed.

Multiple response permutation procedure (MRPP) and non-metric multidimensional scaling (NMDS) were used to determine whether there was a difference in stream habitat characteristics and invertebrate communities between RCA classes. All NMDS ordinations and MRPP analysis were performed using the Bray–Curtis distance measure. NMDS ordinations were run using ‘slow and thorough’ autopilot

including 250 runs in six dimensions (PC-ORD; MjM Software, Gleneden Beach, OR, U.S.A.). The NMDS algorithm used in PC-ORD is based on methods found in Mather (1976) and Kruskal (1964).

To determine the relative importance of the reach and catchment-scale variables to explain variance in invertebrate communities, ordinations were performed for invertebrate data and combined reach and catchment-scale variables for both small RCA sites and large RCA sites. Analyses were performed on both taxonomic and feeding guild data for a total of four ordinations.

Results

Environmental characteristics

The stream sites studied covered a wide variety of conditions. Stream width was fairly uniform and averaged 1.5 m. Streams were slow flowing with an average velocity of 0.1 m s^{-1} . The most variable factors were gradient, substratum and chlorophyll *a* (see Table 1 for summary statistics). Stream gradient ranged from 0 to 12° , substratum ranged from 0% fines (high gradient sites dominated by boulder and cobble) to 100% fines (low gradient sites dominated by silt and sand) and chlorophyll *a* ranged from 0.1 to 15.0 mg m^{-2} . Stream gradient was omitted from ordination analyses because of significant negative collinearity with both % fine substratum ($R^2 = 0.400$, $P < 0.001$) and riparian width ($R^2 = 0.154$, $P = 0.032$). Stream temperature ranged from 8.2 to 16.5°C and DO from 5.37 to 12.66 mg L^{-1} , although the means were relatively constant across RCA classes. Other factors were less variable overall but had greater differences between site groupings, such as more canopy cover at small RCA sites (85%) than at large RCA sites (72%). More than three quarters of sites had at least 75% canopy cover.

The RCAs of sites were dichotomous by design and ranged from 0.04 to 0.20 ha in the small size class and from 6.36 to 45.92 ha in the large-size class. Width of the riparian zone was also highly variable ranging from 1 to 24 m. Total tree density in the RCA ranged from 971 to 13 330 trees per ha and tended to be greater in large RCAs. The proportion of hardwood ranged from 0 to 0.90 but the mean was fairly constant among RCA classes. RCA geology was dominated by bedrock; 17 out of 23 sites had 100% bedrock cover in

the RCA. Historical harvesting in the past 10 and 20 years averaged 19 and 23% of RCA area, respectively, and was higher in large RCA sites. For five of the eight reach-scale variables, variance was significantly greater at large than small RCA sites, including RCA size [Levene statistic (LS) = 42.7, $P < 0.001$], proportion of RCA harvested in the past 20 years (rca20harv, LS = 7.6, $P = 0.01$), proportion of RCA harvested in the past 10 years (rca10harv, LS = 12.2, $P = 0.002$), percentage bedrock (LS = 4.5, $P = 0.044$), and the coefficient of variation in elevation (CV elev, LS = 34.1, $P < 0.001$).

Catchment size ranged from 45.9 to 146.7 ha and means did not differ among RCA classes (MANOVA, $P > 0.1$). The catchments were dominated by bedrock with 19 of the 23 sites having more than 95% bedrock cover. Catchments had between 0 and 39% of their area harvested in the past 10 years and 0 to 49% harvested in the past 20 years. Catchment areas were covered up to 5% with lakes and up to 10% with wetlands. Wetlands were significantly negatively correlated with CV altitude in the catchment ($R^2 = 0.16$, $P = 0.03$). The mean topographic relief was fairly constant among RCA classes, ranging from 2 to 13% with a mean of 5%.

Invertebrate community

A total of 18 435 invertebrates were collected and identified (Appendix 1). After removing taxa occurring at only one site, 30 taxa (at the family level classification) were included in the analyses. The family Chironomidae was dominant at almost all sites, comprising 63% of all individuals. Because of the lack of taxonomic resolution in the chironomids, and wide variation in life strategies, they were omitted from the feeding guild analyses. The Simuliidae (black flies) were the next most dominant taxon comprising approximately 14% of all individuals. The communities were dominated by the filter feeders (29–49%) and gatherers (21–48%).

Invertebrate–environment relationships

CCA and RDA ordinations both indicated that variation in invertebrate community structure was most strongly associated with local and catchment-scale variables. CCA analysis showed that variables at the local, reach and catchment scales explained 51.6, 40.3

and 43.9% of among-site variation in invertebrate taxonomic composition, respectively. Ordinations based on local and catchment-scale variables showed significant relationships between environmental and invertebrate data sets (Monte Carlo randomisation test, $P = 0.002$ and $P = 0.036$ respectively). RDA analysis showed a similar pattern with local, reach and catchment-scale variables explaining 59.1, 37.5 and 43.5% of among-site variation in feeding guild composition, respectively. Only the ordination based on local variables showed a significant relationship between the environmental and invertebrate data sets ($P = 0.048$).

Patterns in the relationships among invertebrate data and environmental variables were similar in both CCA analysis of the taxonomic data set and RDA analysis of the functional data set. The results presented here will focus on the functional data set, as the hierarchical landscape controls and process domains concept would be expected to act on shared species traits, or functional groups. An RDA ordination of feeding guilds and local-scale habitat variables showed two roughly orthogonal gradients of local habitat characteristics; a depositional gradient (from fine substratum and low velocity, to coarse substratum and greater velocity) and a temperature gradient (from warmer water with low DO to colder water with high oxygen). Sites with a greater proportion of filter feeders were those with high velocity, and sites dominated by gatherers and shredders tended to be associated with fine substratum and higher water temperature (Fig. 1a). An ordination of feeding guilds and reach-scale variables again showed two roughly orthogonal gradients of reach-scale variables. Sites with a high abundance of shredders had a greater tree density, contrasting with sites with high abundances of gatherers and filterers which were associated with a greater proportion of the RCA having been harvested in the past 10 years. The second gradient separated sites with a high abundance of scrapers, which were associated with greater topographic relief (CV elev), from sites with a greater abundance of filterers, which were associated with a higher proportion of bedrock in the RCA (Fig. 1b). In the third RDA ordination of feeding guild structure and catchment-scale variables, the gradients separated sites with high abundances of shredders, scrapers and predators (which were associated with greater topographic relief within the catchment) from sites with high abundances of filter

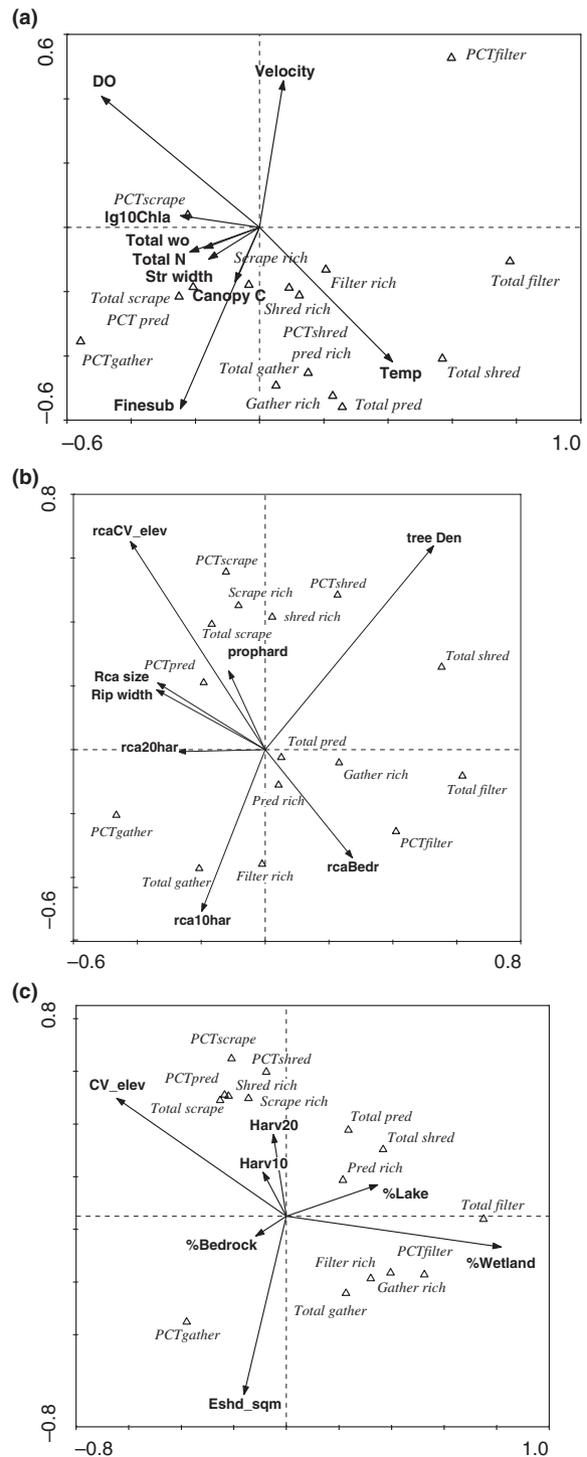


Fig. 1 Redundancy analysis ordinations (axes 1 and 2) of invertebrate feeding guilds (points) and environmental variables (vectors) at (a) local scale, (b) reach scale, and (c) catchment scale for all sites. Feeding guild abbreviations are PCT, percent; rich, richness; total, abundance; gather, gatherer; filter, filter feeder; shred, shredder; scrape, scraper; pred, predator. Environmental abbreviations are given in Table 1.

feeders (which were associated with a greater proportion of wetlands in the catchment). Sites with greater abundances of gatherers also tended to be associated with larger catchment size (Fig. 1c).

RCA effects

There was a weak but significant difference in local stream characteristics between sites with large and small RCAs (MRPP, $A = 0.033$, $P = 0.030$). An NMDS ordination of sites based on local stream characteristics summarised 78.9% of the variability among sites (64.7 and 14.2% in each axis, stress 15.2; Fig. 2). The NMDS ordination showed a separation between sites with large and small RCA along the horizontal axis, and showed that sites were most strongly separated along a gradient associated with substratum particle size. High proportions of silt, woody debris and detritus were most strongly correlated with the negative end of the axis, associated with large RCA sites, and high proportions of coarse substrata (boulder, cobble and pebble) were most strongly correlated with the positive end of the axis, associated with small RCA sites. Higher stream gradients were also positively correlated with the positive end of the horizontal axis, showing a trend for small RCA sites to be steeper and dominated by coarse substrata (erosional) while large RCA sites tended to have a shallower

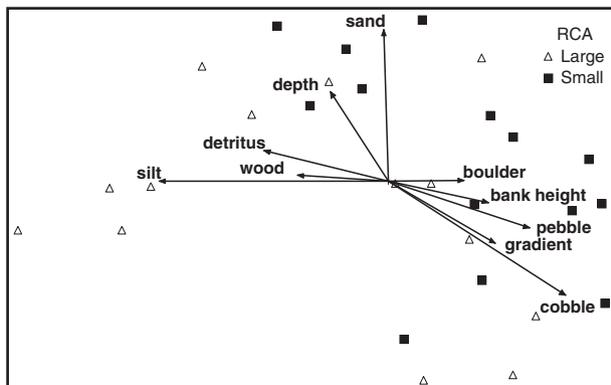


Fig. 2 Non-metric multidimensional scaling ordination of all sites based on the Bray-Curtis distance measure of local habitat characteristics. Large reach contributing area (RCA) sites are shown as triangles, Small RCA sites are shown as squares and the environmental variables are shown as vectors pointing in the direction of greatest correlation with the axes with a minimum cut-off of 0.25. (Axes capture 64.7 and 14.2% of variation in stream habitat characteristics, stress = 15.2).

gradient and were dominated by fine substrata and detritus (depositional).

There was also a weak but significant difference in the composition of invertebrate communities between RCA groups (MRPP, $A = 0.013$, $P = 0.009$). An NMDS ordination of all sites based on invertebrate taxa captured 53.2% of among-site variation in invertebrate taxonomic structure (40.6 and 12.6% in each axis, stress 18.2; Fig. 3). There was a slight separation of invertebrate communities along the vertical axis between sites with large and small RCAs. Sites at the top end of the axis tended to have small RCAs and were dominated by filter feeding taxa, including Simuliidae, and predaceous taxa including Rhyacophilidae, Dytiscidae, Tabanidae and Empididae. Sites at the bottom end of the axis tended to have large RCAs and were dominated by gatherer and shredder taxa from the Ephemeroptera (Leptophlebiidae), Plecoptera (Leuctridae) and Lepidoptera (Pyralidae). Small RCA sites had a higher proportion of Simuliidae and Plecoptera and a lower proportion of Oligochaeta and Nematoda (Fig. 4a,b). These taxa reflect differences in the dominant feeding guilds, with large RCA sites dominated by gatherers, compared to a larger proportion of filter feeders in the small RCA sites (Fig. 4c,d).

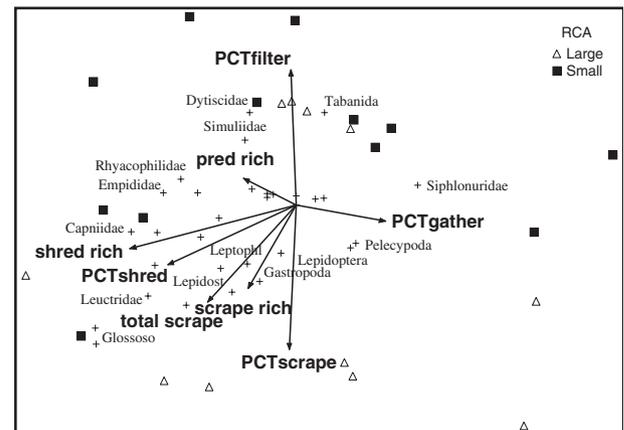


Fig. 3 Non-metric multidimensional scaling ordination of all sites based on the Bray-Curtis distance measure of invertebrate taxonomic data. Triangles indicate large reach contributing area (RCA) sites, squares indicate small RCA sites. Crosses indicate invertebrate taxa and vectors indicate the correlation of feeding guild metrics with the axes (cut-off at a minimum correlation of $r^2 = 0.20$). (Axes capture 40.6 and 12.6% of variation in invertebrate community stress = 18.2). Feeding guild abbreviations found in Fig. 1.

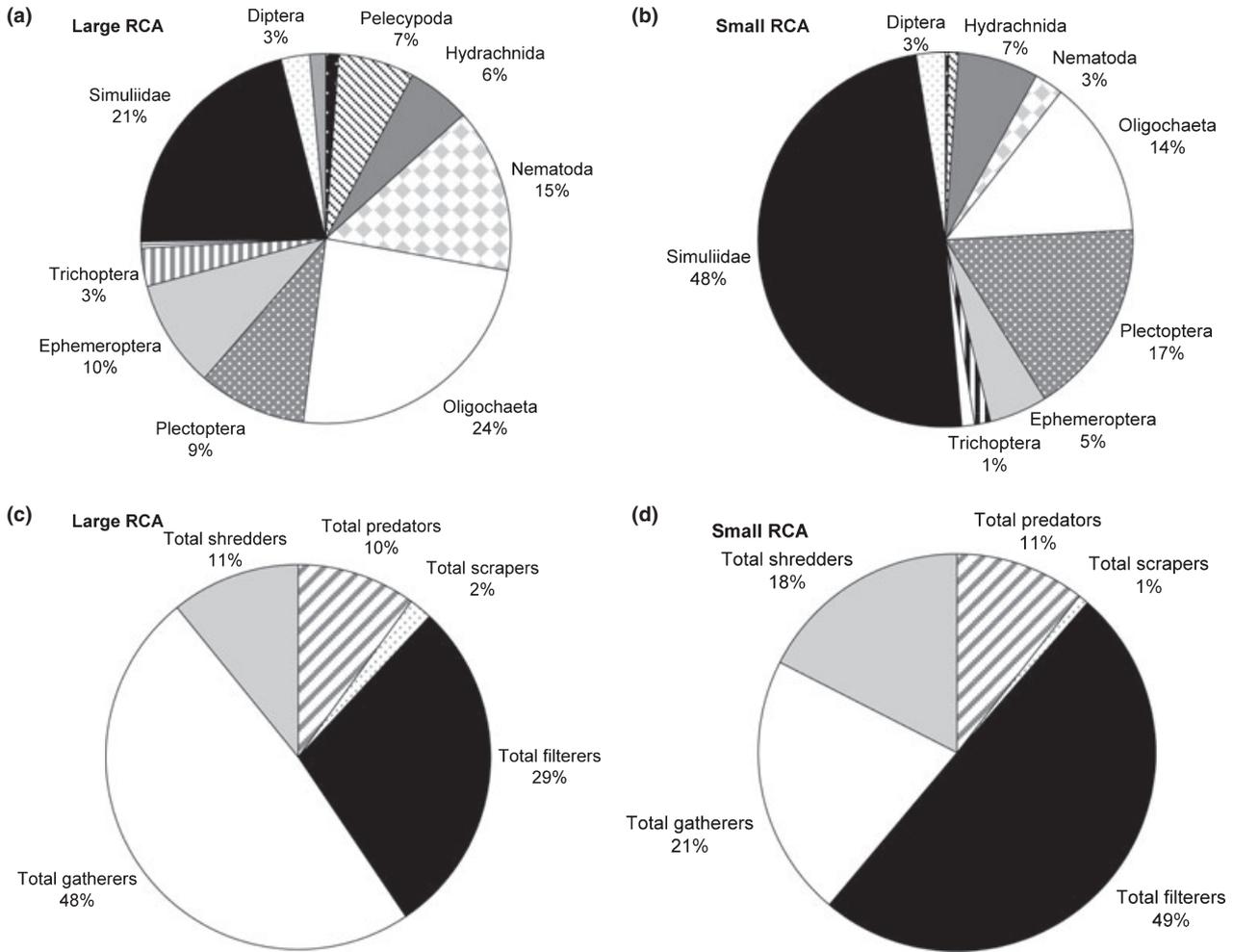


Fig. 4 Average proportion of invertebrate orders in sites with (a) large reach contributing areas (RCAs) and (b) small RCAs and proportion of feeding guilds in sites with (c) large RCAs and (d) small RCAs. Chironimidae have been omitted from figure to prevent dominance from obscuring other relevant patterns.

Local-scale variables explained the most among-site variation in invertebrate community in terms of both taxonomy and feeding guilds. Reach and catchment-scale variables explained approximately equal proportions of the variation in the invertebrate taxonomic composition within small RCA sites, but for sites with large RCAs the reach scale explained almost 10% more variation in invertebrate taxonomic composition than the catchment-scale variables (Fig. 5a). The reach and catchment scales had approximately equal power in explaining variations in feeding guilds in large RCA sites but, at sites with small RCAs, the catchment scale explained almost 23% more among-site variation in feeding guild composition than the reach-scale variables (Fig. 5b).

Combining the reach and catchment-scale variables in a single RDA ordination allowed us to determine which 'landscape' variables were contributing to variance in functional feeding groups. In sites with a small RCA, three of the four variables most strongly correlated with among-site variability in feeding guild structure were from the catchment scale. Tree density (reach scale) was associated mostly with the sites dominated by gatherers, percentage bedrock in the catchment was most closely associated with sites dominated by shredders and percentage of the catchment harvested in the past 10 years was associated with sites dominated by filterer feeders. Catchment size was negatively correlated with tree density and, therefore, gatherers and predators were more often

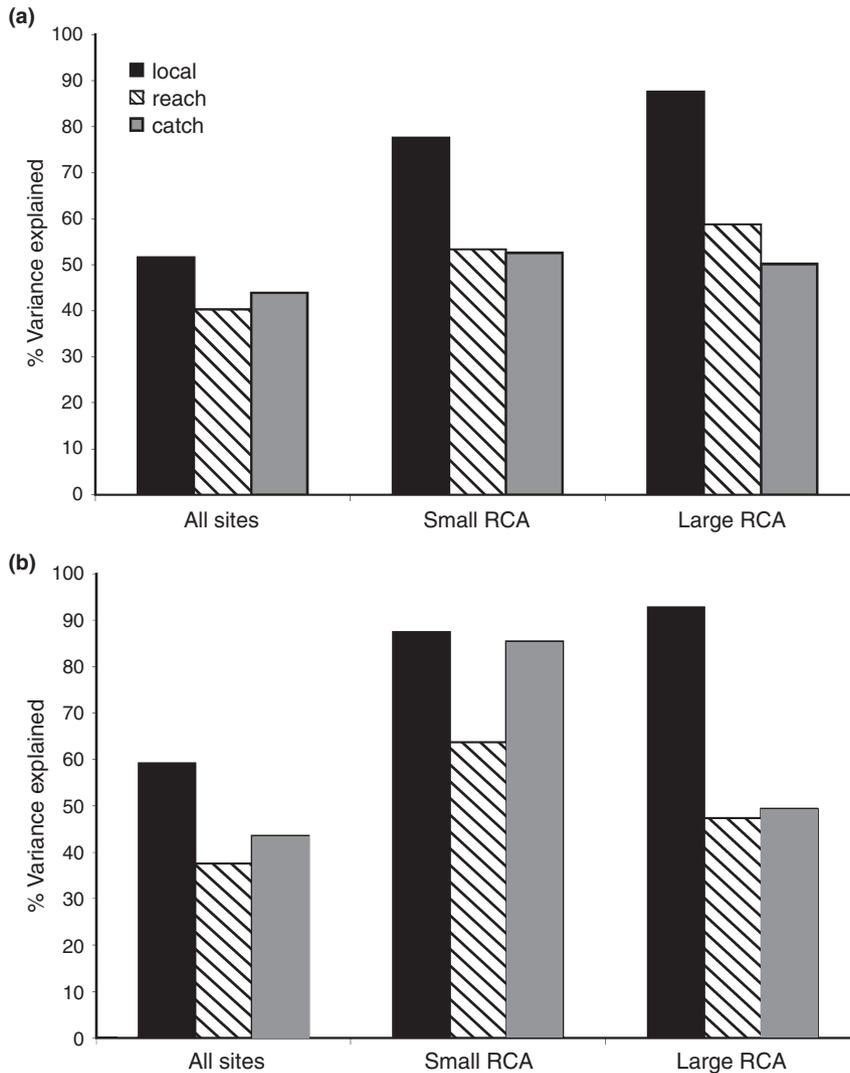


Fig. 5 Relative contributions of environmental variables at the local, reach and catchment scale to explain variance of (a) invertebrate taxonomic composition and (b) feeding guild composition from canonical correspondence analysis and redundancy analysis.

found at sites with a high density of trees (Fig. 6a). In large RCA sites, three of the four variables most correlated with variability in feeding guild structure were from the reach scale. Relief ratio in the RCA (rcaCV elev) and tree density were most associated with sites dominated by predators, scrapers and shredders. Bedrock in the RCA was associated with sites dominated by filter feeders, while the percentage of wetlands in the catchment were associated with sites dominated by gatherers (Fig. 6b).

Discussion

Spatial scale–invertebrate relationships

Studies of environmental factors at multiple spatial scales often state that patterns of invertebrate

assemblage can only be sufficiently explained by combining all spatial scales (Corkum, 1989; Brosse *et al.*, 2003; Weigel *et al.*, 2003; Heino *et al.*, 2007). In a study of nested spatial scales such as this, each scale can obviously not be considered independently. From this study, therefore, we cannot conclude mechanisms by which each scale drives community composition. These results indicate the spatial scales at which the terrestrial and aquatic environments are most closely linked and allow more accurate predictions of environmental effects on community structure. The contradictory results of previous studies investigating the importance of spatial scale (local habitat – Brosse *et al.*, 2003; Sponseller *et al.*, 2001; Johnson *et al.*, 2007; reach scale – Feld & Hering, 2007; catchment scale – Corkum, 1992; Johnson *et al.*, 2007) may reflect the spatial scope of the study, the type of community data

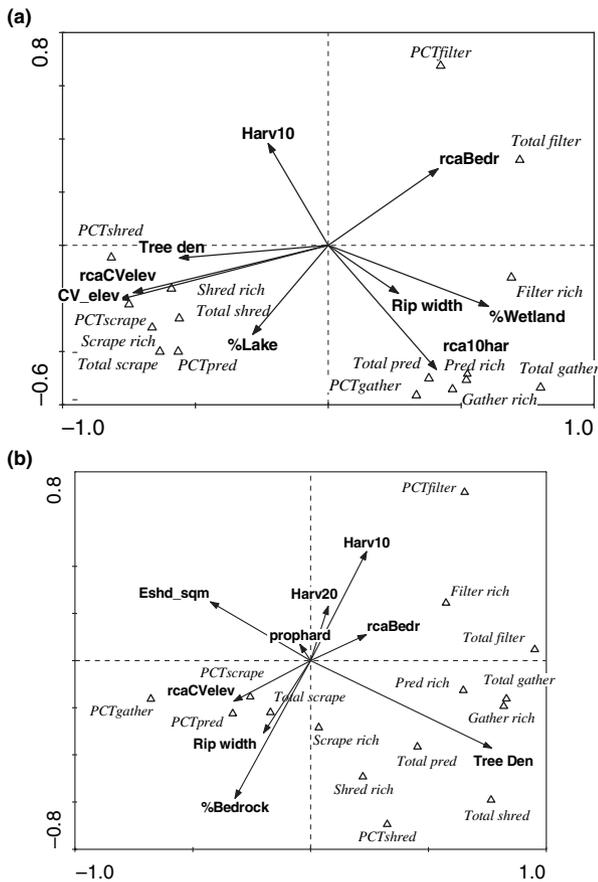


Fig. 6 Redundancy analysis ordinations of invertebrate feeding guild composition (points) and environmental variables (vectors) at the reach and catchment scale in sites with (a) large reach contributing areas (RCAs) and (b) small RCAs. Feeding guild abbreviations as in Fig. 1. Environmental abbreviations are given in Table 1.

being analysed (Weigel *et al.*, 2003) or, most pervasively, the complex interactions among spatial scales (Frissell *et al.*, 1986).

Local stream habitat variables had the strongest association with the invertebrate community, perhaps reflecting the relatively small area over which this study was conducted. The dominant feeding guilds were distributed along a depositional gradient providing either more detritus (supporting gatherers), or more suspended fine organic particles (supporting filterers) (Cummins & Klug, 1979). This gradient demonstrated the importance of certain habitat characteristics for invertebrate community structure, such as substratum and detritus (Rabeni & Minshall, 1977; Habdija *et al.*, 2004), water velocity (Corkum, 1989) and periphyton growth (McIntire, 1968). Temperature was

another local variable strongly associated with invertebrate community structure and affects metabolic rate, assimilation efficiency and life cycles (e.g. Vannote & Sweeney, 1980) which can explain the dominance of feeding guilds and the structure of communities.

Overall, reach-scale landscape variables explained less variation in invertebrate community than catchment-scale variables, but still explained more than a third of the among-site variation. The strongest variable at the reach scale was topographic relief. It has been shown in models of stream geomorphology that changes in slope and retention areas (e.g. hyporheic zones) because of variation in topographic relief can increase nutrient retention and algal biomass (Doyle & Stanley, 2006). The proportion of scrapers was most strongly correlated with chlorophyll *a* in the local RDA ordination (Fig. 1a) and topographic relief in the reach RDA ordination (Fig. 1b), which may reflect greater potential for algal growth in areas of high topographic relief.

Tree density and harvesting in the past 10 years were also important reach-scale variables, associated with more shredders and filterer/gatherers, respectively. Greater tree density potentially creates greater leaf input to the stream (Cummins & Klug, 1979), whereas more recent harvesting might increase organic inputs to the stream in runoff (Stedman, 2000) or labile (deciduous) leaf inputs from the younger forest stands (Hernandez, Merritt & Wipfli, 2005). In another study on low-order boreal streams, the opposite trend was found; gatherers and filterers relying on fine particulate organic matter were less abundant in clear-cut areas, as a result of lower leaf decomposition in those areas (Kreutzweiser *et al.*, 2008).

Topographic relief has been shown to affect stream habitat at several scales (Montgomery, 1999; Brosse *et al.*, 2003). Brosse *et al.* (2003) found that the increased relief ratio created more heterogeneity in the stream habitat which supported a greater richness of species. In our study, greater relief ratio in the catchment was not associated with greater richness in every feeding guild, although sites with greater relative abundance and richness of shredders, scrapers and predators were associated with greater topographic relief. At the other end of the gradient, a greater percentage of wetlands in the catchment were associated with sites dominated by grazers and

filterers relying on fine particulate organic material. Wetlands can accumulate and store particulate organic matter which may then be released into downstream environments through flooding.

Catchment size has long been used to predict the invertebrate community, and the associated characteristics of increasing catchment size are well understood (Vannote *et al.*, 1980). In our study, sites were chosen in first or second-order streams with a catchment range of 46–147 ha, and the size of the catchment did have an effect on invertebrate community. Gatherers tended to be associated with larger streams, which would be expected to have reduced leaf litter input from stream banks, and receive more particulate organic matter from upstream. Vannote *et al.* (1980) did predict this pattern in the River Continuum Concept, although over a much larger spatial scale in which gatherers should dominate in large rivers near the end of the continuum. The streams in this study are all headwater streams, and therefore there may be another mechanism driving the association of gatherers with slightly larger headwater streams, or it may be because of other environmental factors that covary with stream size.

Effect of RCA

Montgomery (1999) states that while catchment conditions may form a continuum over large spatial scales, at small spatial scales geomorphic and topographic controls create a mosaic of different 'process domains'. We have, indeed, found that at the scale of headwater streams, which tend to be classified as a single functional unit, topographic controls created reaches with different connections to the reach, and catchment-scale landscapes resulting in different stream conditions and biotic communities. The invertebrate community differed between small and large RCA size classes because of differences in the dominant feeding guild. Filter feeders tended to be dominant in sites with a small RCA (driven by a higher abundance of Simuliidae), while sites with large RCAs tended to be dominated by the gatherer feeding guild, driven by greater abundances of Oligochaetes and Ephemeroptera. These patterns of invertebrate assemblages seem to be associated with inherent morphological differences in the stream sites based on topographic controls. Small RCA sites were

steeper with coarser substrata, while large RCA sites had a shallower gradient and were dominated by fine substrata and detritus. This created riffle-dominated erosional habitats and run-dominated or pool-dominated depositional habitats, within the small scale of headwater streams. This type of habitat classification is usually applied to larger-scale stream systems ranging from erosional headwaters to depositional lowlands and, regardless of scale, is a fairly reliable predictor of general functional group assemblages (Vannote *et al.*, 1980; Merritt & Cummins, 1996; Montgomery, 1999).

Analysis of the relative contributions of variables at each spatial scale shows a trend for reach-scale variables to be relatively more important at large RCA sites, and catchment-scale variables to be relatively more important at small RCA sites. Studies of the link between hillslope processes and stream conditions indicate that, at a large scale, wide, flat valleys tend to be disconnected from hillslope processes because of greater buffering capacity of the riparian zone, and streams with steep valley sides will be more strongly affected by those hillslope inputs (Montgomery, 1999; McGlynn & Seibert, 2003). Our study does not agree with this pattern, which could be an effect of the scale of variation being studied, or the difference between disturbance effects and natural variability. Most studies of this nature focus on variation from headwater streams to larger downstream reaches, whereas our study is focused on variation at a much smaller scale within headwater streams. The proposal that a smaller buffering riparian zone will result in stronger effects of disturbance on steep slopes (Montgomery, 1999) is not applicable to our sites, where the stream is not hydrologically linked to the landscape beyond a short steep bank which is generally too small an area for forest harvesting disturbance to take place.

The difference in the relative importance of reach and catchment spatial scales may be explained in two ways. The first explanation is based on the process domains theory, in which topography separates stream reaches based on disturbance effects (Montgomery, 1999). Montgomery (1999) states that steep channels constrained by steep banks (a small RCA in our study) will be more affected by flood disturbance (by scouring, for example) whereas low gradient channels with extensive floodplains (a large RCA in our study) will be less affected by flooding,

as they can expand into the floodplain. Arscott, Tockner & Ward (2005) have shown how connectivity with the floodplain can affect the macro-invertebrate community of the stream reach through ground water and nutrient exchange between the floodplain and the stream waters. Both of those factors could be affected by the bedrock and topographic relief in the RCA, which are strongly associated with invertebrate community in large RCA sites in our study.

The second explanation is that, in our study system, a physical barrier to lateral inputs may exist in the small RCA sites. Sites with a small RCA were characterised by steep banks culminating in a ridge close to the stream. These ridges could block any lateral inputs (from surface runoff, soil or vegetation) from the stream channel, thereby reducing the importance of lateral variables in structuring the invertebrate community. In this case, most of the input to the stream will be from longitudinal flow which has been influenced by factors in the entire catchment, such as bedrock and historical harvesting.

Our study illustrates that the lateral topography can be a determinant of the scale at which the landscape is most closely associated with headwater streams and community structure. This conclusion has applications from management practices to landscape ecology research. We have proposed several mechanisms which may be responsible for the patterns in associations of spatial scales and stream communities. This is a starting point for future research which can test these hypotheses and determine how the RCA influences mechanistic linkages between the stream and surrounding landscape.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Summary of all invertebrate taxa collected.

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