

Variability and convergence in benthic communities along the longitudinal gradients of four physically similar Rocky Mountain streams

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SUMMARY

1. High-gradient mountain streams are ideal for studying longitudinal biological patterns, although the degree of similarity in the biological gradient among physically similar streams in a region is poorly known. Our first objective was to evaluate variability in benthic communities along four streams in the central Rocky Mountains of Colorado. We analysed the relative influence of longitudinal position versus reach-scale physical variables on community structure and measured community similarity at comparable longitudinal positions on the four streams.
2. Our second objective was to evaluate the relative utility of taxonomically versus functionally defined communities to characterise assemblage structure: are taxonomic patterns more predictable along the gradient than are patterns of ecologically important species traits?
3. Redundancy analyses (RDA), including measures of both reach-scale environmental variables (substratum properties, periphytic cover, local channel slope) and longitudinal position (altitude, stream size), confirmed that the longitudinal position of a site was most important in determining taxonomic composition. Functional community structure was also influenced by longitudinal position, but reach-scale variables (especially periphyton and median particle size) were of greater importance.
4. Redundancy analyses explained 29.3% of total taxonomic variance and 26.0% of functional variance, indicating that defining assemblages functionally provides no greater understanding of community patterns given several known environmental variables. Strict longitudinal limits of taxa, the presumably identical regional species pool across our sites, and/or trade-offs among different types of species traits probably explain this result.
5. Redundancy analyses did suggest, however, that traits related to longer life (semivoltinism, long-lived adults, and slow larval development) were more common downstream, while long-distance dispersal ability and high fecundity were associated with higher altitude and its associated harsher conditions.
6. When sampling sites were grouped into three ecological zones defined by altitude, mean community similarity (measured both taxonomically and functionally) was lowest across streams at the highest altitude. This pattern could be driven by increased insularity of alpine-zone streams, resulting from a combination of harsh terrestrial environment, lack of hydrological connectivity, and limited species ranges along the longitudinal continuum.

Keywords: alpine streams, benthic insects, community similarity, functional groups, longitudinal continuum, mountain streams, species traits

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Introduction

The identification and explanation of spatial gradients of biotic organisation have long been key objectives in the field of stream ecology (Illies & Botosaneanu, 1963; Hynes, 1970). The river continuum concept (Vannote *et al.*, 1980) provides a widely cited framework for explaining longitudinal changes in community structure and function. Although environmental gradients in lateral (river–floodplain; Junk, Bayley & Sparks, 1989) and vertical (surface–groundwater; Stanford & Ward, 1988) dimensions within stream systems are also ecologically important, the longitudinal gradient produces broader environmental patterns and itself influences graded changes in the other two, finer-scaled, spatial dimensions (Stanford *et al.*, 1996). The longitudinal dimension is therefore appropriate for examining coarse-scaled ecological patterns, including the distributional ranges of individual species and the turnover of entire assemblages.

Mountain streams are well suited for examining longitudinal gradients because of the rapid change in major abiotic conditions (e.g. temperature, oxygen availability, stream size and associated hydraulic conditions) with altitude. Altitude is therefore a surrogate, composite variable that represents many spatially correlated environmental factors. Accordingly, sharp gradients in local biotic assemblage structure have been documented in several mountain streams (e.g. Allan, 1975; Minshall, Petersen & Nimz, 1985; Ward, 1986; Bruns, Hale & Minshall, 1987).

These studies have increased our understanding of the physical processes controlling biotic distribution in streams. In most cases, however, ideas about the general nature of mountain streams in a region has been based on data gathered from a single study stream. Longitudinal studies that have included two or more streams in an area have focused primarily on contrasting streams having distinctly different geomorphological and/or chemical characteristics (e.g. Slack, Nauman & Tilley, 1979; Graça, Fonseca & Castro, 1989; Kownacki, 1991). The unspoken assumption has therefore been that, because similar environmental gradients tend to be accompanied by similar biotic gradients (cf. Huston, 1994), physically similar streams in a region ought to have similar longitudinal biological patterns. Although comparisons of longitudinal patterns and processes have been made across broad spatial scales (e.g. Minshall *et al.*, 1983),

studies that directly test the hypothesis of similar longitudinal patterns within a small region are lacking. The degree to which this assumption holds can provide insight into the natural range of variability among mountain streams and along their longitudinal profiles.

Apparent patterns of community structure can vary depending on the method used to define community structure (Rahel, 1990; Poff & Allan, 1995). Communities defined taxonomically contain the most detailed information on structure; however, this method has limitations for comparisons across broad spatial scales or along steep gradients, where species pools may differ between sites or stochastic colonisation events may lead to the establishment of different taxa at different sites. Vannote *et al.* (1980) suggested using a trophic categorisation of taxa (based on Cummins, 1973) in order to generalise the river continuum concept to compare streams across broad spatial scales. Functional characterisation of benthic invertebrate communities through the use of multiple ecologically relevant descriptors of taxa has recently seen resurgence in both theoretical (e.g. Townsend & Hildrew, 1994; Poff, 1997; Richards *et al.*, 1997; Dolédec, Olivier & Statzner, 2000; Usseglio-Polatera *et al.*, 2000) and applied (e.g. Barbour *et al.*, 1992; Charvet *et al.*, 2000; Statzner *et al.*, 2001) stream ecology. Over evolutionary time, the habitat template upon which a stream community has developed is expected to have selected for certain functional traits that are suited for survival there (Poff & Ward, 1990; Townsend & Hildrew, 1994); thus, in the search for a more predictive community ecology, a functional classification of the community may be more helpful than one defined taxonomically.

For this study, our main question was whether longitudinal position (and associated environmental variables) is the most important explanatory variable of insect community structure among four physically similar Rocky Mountain headwater streams. We measured community structure at the reach scale, and we used a multivariate approach to examine the influence on the biota of longitudinal position relative to several specific, reach-scale habitat variables. We also measured the average community similarity between sites occupying similar longitudinal positions on different streams. Because previous studies in mountain streams have shown longitudinal position to be a primary influence on community structure, we

predicted that communities would change similarly along the gradients of the four streams, despite any inter-stream differences in reach-scale habitat. It therefore follows that mean community similarity should be high among streams sharing a similar longitudinal position.

Another question was whether functional or taxonomic classification of assemblages provide more insight for elucidating pattern among reaches of the four study streams. We classified all benthic insects according to a set of ecologically relevant traits and assessed whether a 'functional taxonomy' was a more consistent match to a given set of important habitat characteristics. Functional classification typically has been used in comparisons of sites across large spatial extents in order to address the problem of sites having different species pools (e.g. Richards *et al.*, 1997; Statzner *et al.*, 2001). Across the small spatial extent of our study, the species pool may be constant and thus all species may have the opportunity to colonise any site. Assemblage patterns would then presumably be determined only by the filters through which they must pass to become locally established (cf. Keddy, 1992; Poff, 1997). Given this scenario, functional classification of communities would yield no more insight than would taxonomic classification. Conversely, defining communities functionally may provide more explanatory power in the event of species-specific differences within functional groups driven by stochastic colonisation events and/or variation in dispersal abilities among species (cf. Drake, 1991). Even within our small study area, rugged topography and rapid changes in even large-scale environmental filters (e.g. climate, dominant vegetation type) may lead to a greater degree of isolation between sites than would be expected for lower-altitude streams. Such isolation may strengthen the influence of stochastic historical events on the current community structure. We therefore hypothesised that functional classification would provide more insight regarding community-habitat relationships than would taxonomic classification.

Methods

Study sites

Study sites were located along four Colorado Rocky Mountain streams: the South St Vrain Creek (SSV),

Glacier Creek (GLC), the South Fork Cache la Poudre River (SFP), and the Mummy Pass Creek-Hague Creek-Poudre River system of the main stem Cache la Poudre River (PDR). All of these streams are located in the headwaters of the northern major tributaries of the South Platte River basin (Fig. 1) in the Southern Rockies ecoregion (Omernik, 1987) of Colorado U.S.A. Stream hydrographs are snowmelt-driven (Poff & Ward, 1989) and the bedrock material is primarily granitic. The four streams originate at similar altitudes (3430–3560 m a.s.l.) and have roughly similar drainage densities in their headwaters; they are therefore of comparable size at similar altitudes along the gradient.

We chose a series of five sample sites along each stream (four on SSV because of a diversion above the lowest potential site) so that sites were as similar between streams as possible with respect to altitude and size (Table 1). Size was characterised by link order (Shreve, 1966), i.e. the sum of first-order tributaries contributing to a stream at a particular location. Sample sites are henceforth referred to using the three-letter stream code followed by link order number (as in Table 1). Another estimator of stream size at a location is the area of the contributing catchment, which we estimated for each site using USGS 1 : 24 000 topographic maps and a Numonics Digitablen magnetic digitiser. Link order was positively correlated to catchment area ($r = 0.9$).

Streams in this region of steep topography pass through several vegetation-defined ecological zones over a remarkably short distance and thus experience great landscape variation compared with more lowland streams. We delineated three ecological zones defined by the dominant terrestrial vegetation type: alpine, >3300 m; spruce-fir, 3050–3300 m; and lodgepole pine, 2440–3050 m (Peattie, 1936). The four study streams have an average slope of 6–8%; thus, they pass through each of these three major vegetation zones within a stream distance of <4 km. Each stream had at least one sample site located in each zone, and the stream distance between highest and lowest altitude sample sites on any stream did not exceed 10 km (see Fig. 1).

Individual sample reaches ranged in length from 10 to 25 m and had slopes of <10% (with a single exception, Table 2). We restricted our analysis to riffle units so that sites were hydrologically as comparable as possible. In order to avoid the potential influence of

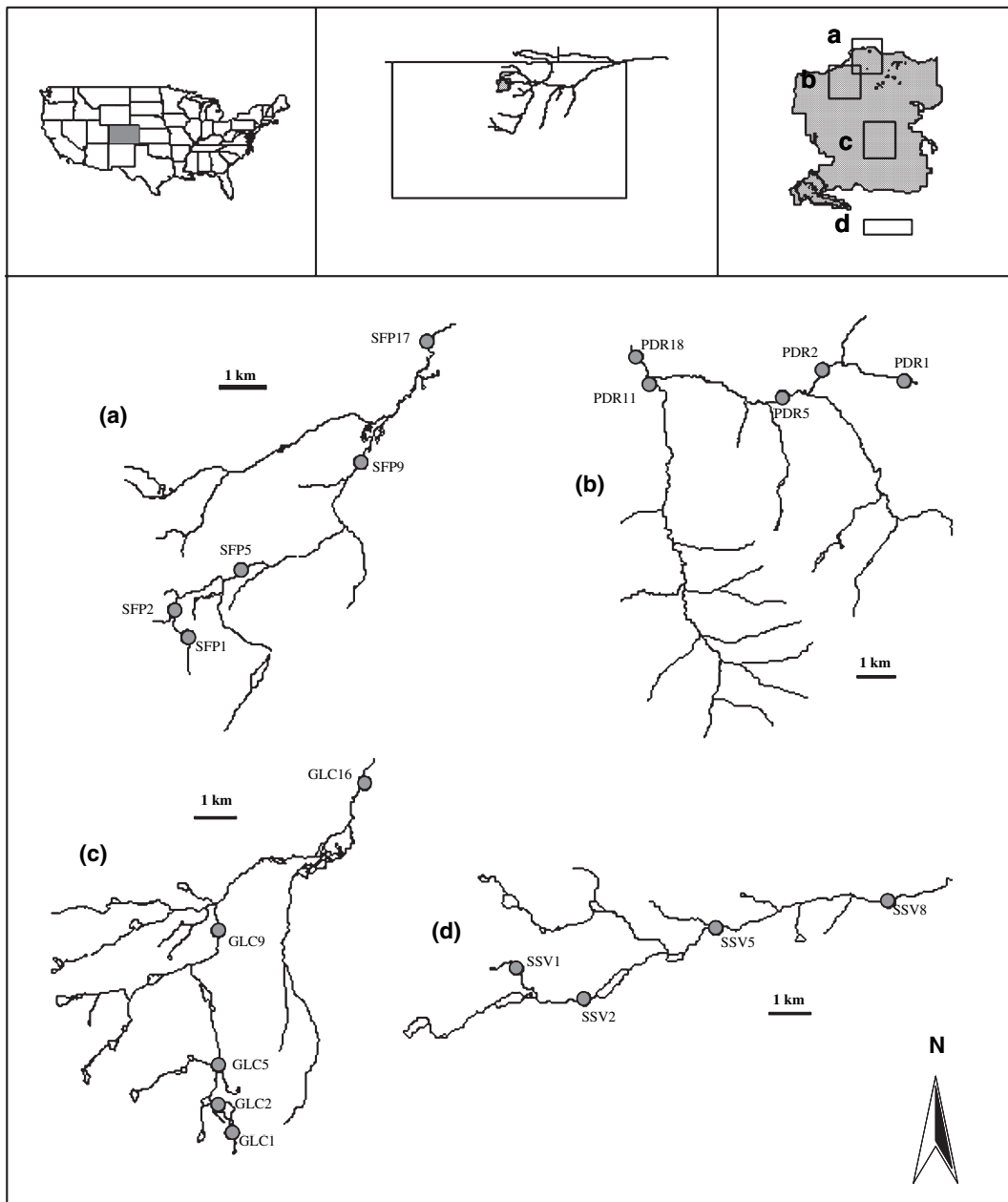


Fig. 1 Locations of study streams and sample sites. Upper left inset locates Colorado in the central United States. Upper middle inset locates Rocky Mountain National Park in the S. Platte River headwaters. Upper right inset shows specific locations of the four study streams. (a) Sites located along the Mummy Pass Creek-Hague Creek-Poudre River tributary system of the Cache la Poudre river. (b) South Fork Cache la Poudre River sites. (c) Glacier Creek sites. (d) South St Vrain Creek sites. Refer to Table 1 for site notations.

lakes on stream communities, each riffle was at least 1 km downstream of any major lake outlet. In addition, all sites had minimal human impact and there were no artificial impoundments along the study reaches. All streams had headwaters in roadless, protected areas (Rocky Mountain National Park and the Indian Peaks Wilderness Area). Glacier Creek

(GLC) and PDR sites were fully contained within these areas, while the lower two sites on both the SFP and SSV were located in areas of interspersed patches of private and federal land.

Each riffle was sampled during a 3 h period between 09.00 and 17.00 hours between 4 August and 19 August 1999, a time of year of stable baseflow

Table 1 Location, ecological zone and altitude of each sample riffle. Site alphanumeric indicates stream name and link order (Shreve, 1966). Refer to Fig. 1 for map.

Stream	Site	Veg. zone	Altitude (m)
Glacier Creek	GLC1*	Alpine	3416
	GLC2	Spruce/fir	3245
	GLC5*	Spruce/fir	3123
	GLC9*	Lodgepole	2968
	GLC16	Lodgepole	2611
S. Fork Poudre	SFP1*	Alpine	3416
	SFP2	Alpine	3379
	SFP5*	Spruce/fir	3264
	SFP9*	Lodgepole	2757
	SFP17	Lodgepole	2721
S. St Vrain	SSV1*	Alpine	3404
	SSV2	Spruce/fir	3221
	SSV5*	Spruce/fir	3099
	SSV8*	Lodgepole	2855
Poudre-main fork tribs	PDR1*	Alpine	3416
	PDR2	Spruce/fir	3257
	PDR5*	Spruce/fir	3096
	PDR11*	Lodgepole	2980
	PDR18	Lodgepole	2965

*Sites chosen for community similarity comparisons among ecological zones.

following a peak snowmelt runoff in late June/early July. Such single-sample, 'snapshot' studies are often used to examine community response to environ-

mental gradients across multiple sites (Richards *et al.*, 1997), particularly those in remote areas.

Sampling

Benthic insects. We used a D-frame kicknet (mesh size 150 μm) to sample benthic insects across all potential microhabitats in each sample riffle. Total sampling time for a site ranged from 2 to 5 min, depending on the spatial extent and microhabitat diversity of the riffle; times were recorded to the nearest 30 s to provide an estimate of insect density (individuals/time) for each site. Samples were sieved in the field, preserved in 75% ethanol, and insects were identified in the lab to the lowest practical taxonomic level. Densities were untransformed for subsequent analyses.

We identified nine major functional categories from which we assigned specific traits to the taxa collected, using literature sources (Merritt & Cummins, 1996 and references therein) or expert opinion (B. C. Kondratieff, Colorado State University Dept. of Bioagricultural Sciences and Pest Management). The nine chosen categories (Table 3) encompassed a variety of biological and ecological functions that were expected to respond to differences in a variety of habitat parameters, such as temperature, flow regime,

Table 2 Physical variables, and taxonomic and functional (trait) richness for each sample site. For site notations, refer to Table 1. See text for detailed descriptions of variables.

Site	Slope (m m^{-1})	D50 (cm)	% Embeddedness	Relative periphytic growth	Hydraulic radius (m)	Taxonomic richness	Trait richness
GLC1	0.08	19.0	0.64	3	0.13	18	22
GLC2	0.22	17.5	0.60	2	0.15	23	22
GLC5	0.05	15.0	0.50	3	0.28	38	23
GLC9	0.02	16.0	0.54	2	0.38	34	24
GLC16	0.02	4.1	0.00	1	0.23	38	25
SFP1	0.05	4.7	0.14	1	0.12	22	22
SFP2	0.05	11.6	0.44	2	0.08	28	22
SFP5	0.08	9.0	0.28	2	0.13	31	22
SFP9	0.02	6.9	0.26	1	0.20	33	22
SFP17	0.02	17.8	0.50	2	0.22	33	24
SSV1	0.07	17.8	0.48	2	0.19	22	24
SSV2	0.03	6.6	0.18	2	0.21	33	22
SSV5	0.05	17.5	0.60	2	0.33	35	25
SSV8	0.03	7.0	0.14	1	0.29	40	25
PDR1	0.08	5.4	0.34	1	0.06	13	22
PDR2	0.05	3.6	0.00	1	0.12	26	22
PDR5	0.03	9.9	0.34	1	0.19	26	22
PDR11	0.04	8.4	0.18	1	0.23	38	25
PDR18	0.04	6.0	0.04	1	0.36	38	25

Table 3 List and description of categories and traits used for a functional classification of communities

Category	Notation in Fig. 3	Description
Voltinism	volt1	Semivoltine (<1 generation year ⁻¹)
	volt2	Univoltine (1 generation year ⁻¹)
	volt3	Multivoltine (>1 generation year ⁻¹)
Development	dv11	Fast seasonal
	dv12	Slow seasonal
	dv13	non-seasonal
Size at larval maturity	size1	Small
	size2	Medium
	size3	Large
Female adult life span	life1	Short (<1 month)
	life2	Long (>1 month)
Adult dispersal	disp1	Low (<1 km before laying eggs)
	disp2	High (>1 km before laying eggs)
Female fecundity	fec1	100 eggs per cycle
	fec2	1000 eggs per cycle
Larval attachment	atch1	None (free-ranging)
	atch2	Some (sessile, sedentary)
Rheophily	rheo1	Depositional only
	rheo2	Depositional + erosional
	rheo3	Erosional only
Trophic group	gather	Collector-gatherer
	filter	Collector-filterer
	scrape	Scraper
	shred	Shredder-detritivore
	pred	Predator

food supply, or various aspects of habitat heterogeneity. They included life history characteristics (life cycle pattern, voltinism, adult life span, female fecundity, size at larval maturity), aspects of resistance/resilience to changing environmental conditions (ability to attach to the substratum, dispersal distance of adults), ecological traits (trophic group) and general habitat preference (rheophily; i.e. the type of flow environment preferred).

Each taxon was assigned a single trait value from each of the nine categories. 'Fuzzy coding' was not practical for our dataset because alpine insects in this region have not been studied well enough to code them reliably; therefore, we assigned each taxon trait values based on predominant values from the literature. Traits were assigned at the subfamily level for Chironomidae, at the family level for other Diptera and Coleoptera, and at the genus level for all other insects. These levels of taxonomic resolution have been demonstrated to provide accurate description of

biological traits at the reach scale (Dolédec *et al.*, 2000).

Physical variables. We quantified several reach-scale habitat variables for each sample site after collecting the biota. These included median particle size and percent embeddedness of the substratum, relative periphytic cover, a measure of stream size, and slope of the reach.

Median particle size of the bed (D50, or the 50th percentile particle size) was determined by sampling 50 substratum particles (defined as any inorganic bed material) throughout the riffle. These 50 were selected using the random-walk method of walking throughout the riffle and randomly choosing a single particle at the location of each step (Gordon, McMahon & Finlayson, 1992). The secondary (B) axis lengths were measured to the nearest centimetre for all particles greater than about 1.5 cm in diameter. Smaller particles were categorised as either sand or gravel, and later given values of 0.05 or 0.8 cm, respectively, average values for each category according to the Wentworth scale (as cited in Allan, 1995). Few particles in this study represented these small categories. Percent embeddedness was determined at the same time by recording the proportion of particles out of the random 50 that were surrounded by tightly packed finer bed material. Such embeddedness of larger particles is thought to decrease biological productivity because the whole surface area of the particle is not available as a substratum for the biota (Gordon *et al.*, 1992).

Relative periphytic cover was a categorical measure recorded as an estimate of primary producer biomass on the particles of the streambed, including filamentous and attached algae and moss. Periphyton contributes to both benthic food resources and to habitat complexity (Allan, 1995). Its growth was recorded as either level 1 (no growth to very little, in the form of attached diatoms), level 2 (intermediate level of growth, either consisting primarily of low-lying forms or sparse or patchy distribution of long filaments) or level 3 (high level of growth, with large amounts of filamentous algae or moss occurring throughout the riffle).

The cross-sectional area of each riffle unit was measured by calculating depth at either 60 cm increments across the stream or at zones of conspicuous changes in depth laterally across the stream. The areas of all sections were summed to get the total

cross-sectional area. These measurements were used to approximate the wetted perimeter of the riffle (at a cross-section, the distance along the bed and banks). We then calculated hydraulic radius, a more general measure of the stream size, as cross-sectional area divided by wetted perimeter (Gordon *et al.*, 1992). Finally, average slope of each sample riffle was estimated using a hand-held clinometer.

Analyses

Multivariate analyses. We used redundancy analyses (RDA) to analyse relationships between both taxonomic and functional community structure and physical variables. This is a constrained analysis – essentially, a multivariate version of multiple regression. It assumes that species respond linearly to environmental gradients. Although species have often been noted to respond unimodally, rather than linearly, along long environmental gradients (e.g. Whittaker, 1967), the small spatial extent, the short gradient and the physical similarity of sites in the current study suggest that even taxonomic ‘species’ are more likely to respond linearly. Functional ‘species’ (i.e. traits) are likely to respond linearly along even extensive gradients. RDAs were performed using the software package CANOCO (ter Braak & Smilauer, 1998).

Physical variables initially included in the analyses included the five major riffle-scale environmental variables measured in the field, as well as altitude (longitudinal position) of the sites (Tables 1 and 2). A high degree of collinearity among environmental variables in multivariate analysis may bias the results (ter Braak & Smilauer, 1998); therefore, we excluded variables that were highly correlated ($r > 0.8$) for final RDAs.

In order to facilitate comparisons between RDA results for taxonomic and functional community structure, as well as to avoid statistical biases, we included only the commonest taxa in the analyses. We had 19 sites, 25 traits and >80 total taxa collected. To reduce the number of taxa, we excluded any taxon with <3% abundance across all sample sites *or* that occurred in only one of the four basins. Densities (individuals/time) of the resulting 28 common taxa were used directly in the taxonomic RDA. For the functional RDA, we retained the same 28 taxa in order to allow us to compare results directly to the taxonomic RDA. We

multiplied the species \times traits matrix (28 species \times 25 possible traits) by the species density \times sites matrix (28 species \times 19 sites) to arrive at a traits \times sites matrix (25 traits \times 19 sites), which we used, untransformed, as input to RDA along with the physical variables.

Community similarity within longitudinal zones. To investigate the degree of between-stream community similarity specifically in reference to position along the longitudinal continuum, we chose one representative site from each of the four streams within each of the three major longitudinally described ecological zones, for a total of 12 sampling units. Sites were chosen within each zone that were as similar in altitude (between streams) as possible (see Table 1). Within each zone, we calculated mean community similarity by averaging across similarities for all six possible pairs of sites using Gower’s similarity coefficient (Gower, 1971; Legendre & Legendre, 1998). Gower’s coefficient calculates partial similarities given abundance data of all individual taxa (or traits) between two sites, and then averages all of the partial similarities to yield a single similarity coefficient for the pair of sites. Values range from zero (no similarity) to one (exact similarity). We used an asymmetrical version (i.e. one that does not include double-zeroes in the calculations) because we used abundance data (individuals/time) of *all* collected insect taxa as input, and we thought it important to minimise effects of the many rare species.

Pairwise similarity matrices for both taxonomic and functional similarity were computed using R Package software (Casgrain & Legendre, 2001). We report mean similarity along with standard errors (based on the six replicate pairwise calculations per zone) for each of the three zones and for taxonomically and functionally defined communities separately. Although many similarity coefficients are sensitive to species richness, Gower’s coefficient avoids this pitfall by averaging across partial similarities. Therefore, values can be compared between zones that may vary in total taxonomic and/or functional richness.

Results

Benthic insects

Total taxonomic richness varied widely among the sample riffles (Table 2), ranging from 13 taxa at PDR1

(in the alpine zone) to 40 at SSV8 (in the lodgepole zone). General patterns of richness and species turnover along the longitudinal gradient were expected given results of previous studies in this region (e.g. Allan, 1975; Ward, 1986). Specifically, there was a significant negative relationship between altitude and taxonomic richness. Refer to Appendix for the complete list of taxa.

Total functional group (trait) richness varied much less across sites and along the longitudinal gradient than did taxonomic richness. At least 22 of 25 traits (in Table 3) were found at all sites, and several sites had representatives of all 25 traits (Table 2). Although the variation was small, the lower-altitude sites still tended to have more traits represented than higher sites.

Physical variables

Local habitat variables measured in the field typically varied widely among sites (Table 2). Hydraulic radius varied predictably along the longitudinal continuum, increasing with decreasing altitude. Reach slope also tended to be slightly greater at upstream sites (although the correlation was not strong, $r = 0.37$). The other variables, including particle embeddedness, D50 and periphytic growth, were not influenced by longitudinal position. Particle embeddedness was strongly correlated with D50 ($r = 0.93$); therefore, we excluded embeddedness from the multivariate analyses. Other environmental factors did not covary significantly.

Multivariate analyses

The taxonomic RDA (Fig. 2) for the commonest 28 taxa indicated that altitude (longitudinal position) was the most important predictor of community structure. RDA axes 1–4 explain a total of 29.3% of the variance in the taxonomic species data, with axis 1 explaining 23.0%. All explanatory environmental variables were essentially equally associated with both axes 1 and 2, with altitude, stream size (hydraulic radius) and periphytic cover being the most important. Sites within basins generally arrayed themselves by link order along the altitude vector (i.e. from lower right to upper left in Fig. 2a), and distinct groups of sites were thus also associated with altitudinally defined ecological zones (illustrated by symbol shape and fill in Fig. 2a). Reach-scale variables were

orthogonal to the longitudinal gradient, helping explain differences among sites within longitudinal zones. A species plot shows that species were the most widely distributed along the altitude gradient (Fig. 2b), with a greater spread in species variation occurring at the higher-altitude end of the gradient.

For the functional RDA (Fig. 3), axes 1–4 explain a total of 26.9% of the total variation in traits among sites, with axis 1 explaining 23.4%. In contrast to the taxonomic analysis, the reach-scale variables of median particle size (correlated with embeddedness) and periphytic cover were the most important predictors of functional trait composition of the benthic communities (Fig. 3a). The longitudinal variables of altitude and stream size (hydraulic radius) were less important and were, interestingly, orthogonal to one another (cf. Fig. 2a). Accordingly, sites did not fall out as predictably in order of their occurrence along the longitudinal gradient (Fig. 3a). Many individual traits did, however, vary in the direction of the most important environmental variables (Fig. 3b). For example, traits associated with the high-altitude/high-periphyton/large particle size end of the gradient included long-distance dispersal, high fecundity and erosional-only rheophilic preference, and the low end of the gradient was associated with semivoltinism, long adult life spans and slow seasonal development.

Community similarity within longitudinal zones

Taxonomic community similarity compared among the three ecological zones revealed significant mean differences (ANOVA: $F = 7.33$; $P = 0.006$; Fig. 4a). Mean similarity (Gower's coefficient = 0.51) was significantly lower in the alpine zone than in the spruce-fir zone (Gower's = 0.63; Tukey's *post hoc* test $P = 0.022$) and the lodgepole pine zone (Gower's = 0.65; $P = 0.008$). There was no difference in mean similarity between the spruce-fir and lodgepole zones, however ($P = 0.866$).

Functional community similarity was also significantly different between altitudinal zones (ANOVA: $F = 6.24$; $P = 0.011$; Fig. 4b). Mean similarity was again significantly lower in the alpine zone (0.56) than in the lowest-altitude lodgepole pine zone (Gower's = 0.80; Tukey's *post hoc* test $P = 0.011$) and lower with marginal significance in the alpine zone than in the spruce-fir zone (Gower's = 0.74; $P = 0.053$). No matter the method of definition (taxonomic

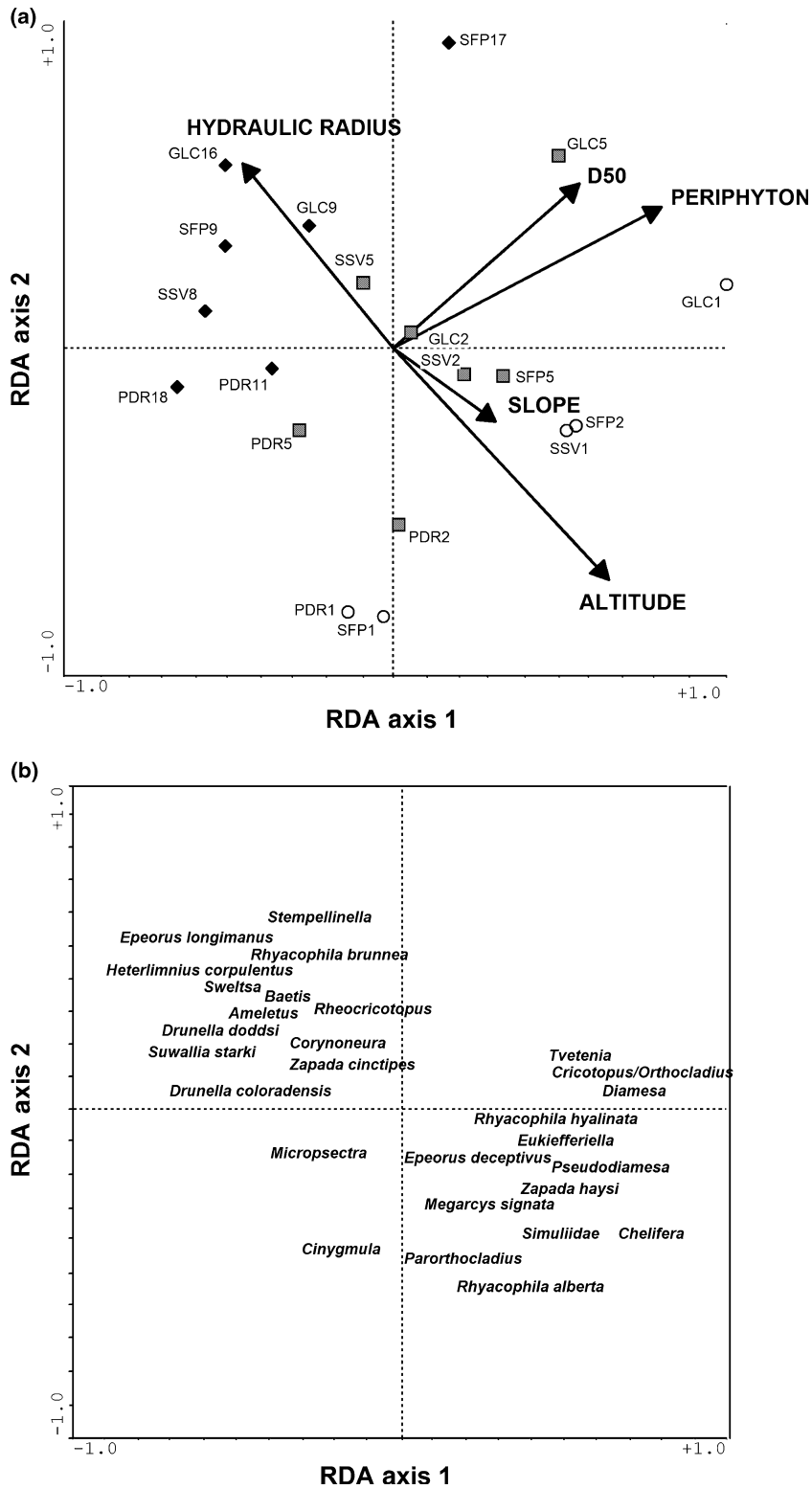


Fig. 2 Biplot of the first and second RDA axes for the taxonomic communities. (a) Sites (○ = sites located in the alpine zone; ■ = sites in the spruce-fir zone; ◆ = sites in the lodgepole pine zone) plus environmental variables (arrows) (b) Taxa plotted according to axes 1 and 2 scores. Eigenvalues for all RDA axes: axis 1 = 0.230; axis 2 = 0.044; axis 3 = 0.010; axis 4 = 0.009.

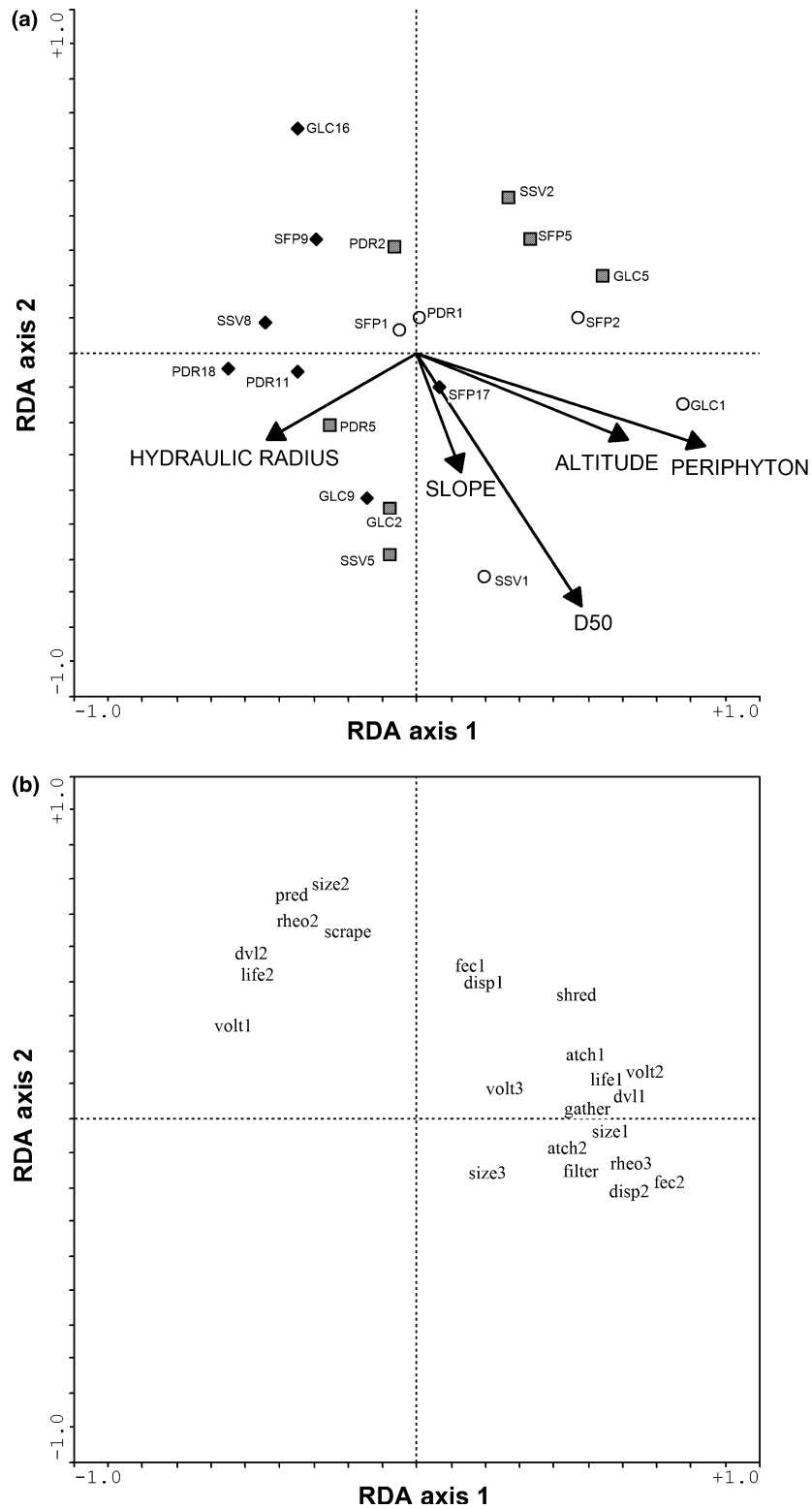


Fig. 3 Biplot of the first and second RDA axes for the functionally defined communities. (a) Sites (symbol shape and fill according to Fig 2a) plus environmental variables (arrows). (b) Individual traits plotted according to axes 1 and 2 scores (refer to Table 3 for abbreviations). Eigenvalues for all RDA axes: axis 1 = 0.234; axis 2 = 0.019; axis 3 = 0.014; axis 4 = 0.002.

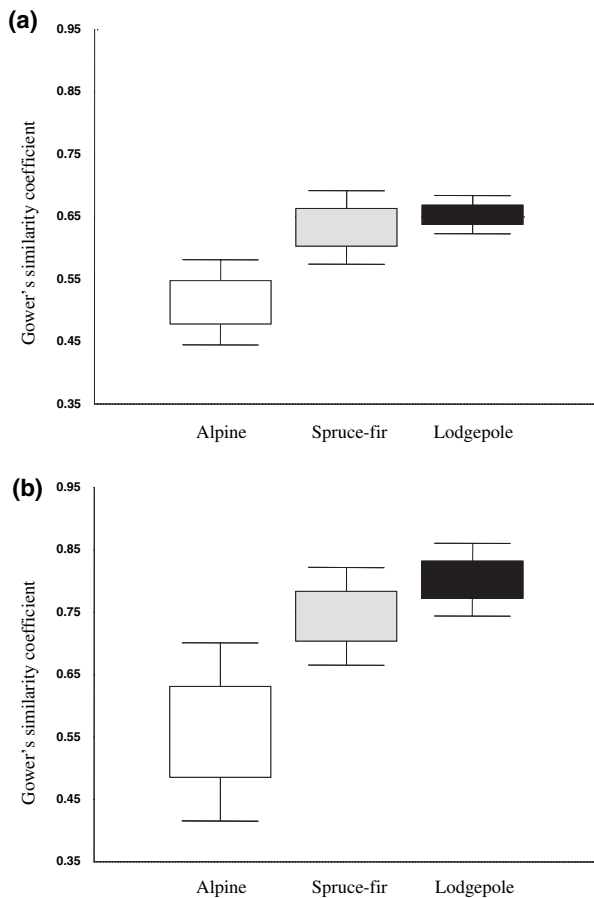


Fig. 4 Box-whisker plots representing mean, standard error (box edges) and $1.96 \times$ standard error (whiskers) Gower's pairwise community similarity values for each longitudinal zone (box colours follow shading scheme used in Fig. 2 and 3). (a) similarity based on taxonomy; (b) similarity based on functional traits.

or functional) the pattern of community similarity among altitudinal zones was similar. Alpine average similarity was lower than average similarity of communities at lower altitudes.

Discussion

In support of our first hypothesis, the longitudinal gradients of these four physically similar Rocky Mountain streams are accompanied by a relatively predictable spatial arrangement of taxa. This finding reinforces previous work suggesting that longitudinal location is among the most important factors with respect to the distribution of benthic invertebrates in high-gradient mountain streams (Allan, 1975; Minshall *et al.*, 1985; Ward, 1986). More variation in

taxonomic community structure can be explained by altitude than by reach-scale physical habitat, although reach-scale variation may become important for explaining between-stream differences within narrow altitudinal bands. Reach-scale variables have been shown to be more important than longitudinal position in low-altitude (and much lower-gradient) streams (e.g. Corkum, 1990; Richards *et al.*, 1997), a finding that supports our demonstration that factors at the reach scale matter most in discerning biotic differences among sites of similar altitude and stream size.

Our second hypothesis was that a functional characterisation of communities would provide more insight regarding community-habitat relationships than would taxonomy (*sensu* Poff & Allan, 1995). We reasoned that, even across the relatively small spatial extent of our study, the steep gradient of change in important habitat characteristics along with the probable increased isolation between streams because of rugged topography would lead to the development of different suites of taxa even at physically similar sites. In such a case, species-specific replacements within functional groups are likely, presumably making functional classification more consistent than taxonomic. However, we found no support for this hypothesis, as the amount of variation explained by the functional RDA was slightly less than the taxonomic RDA (29.3% versus 26.3%). Given that all functional traits occurred in virtually all sites (see Table 2), it is perhaps not too surprising that the functional RDA did not perform that well.

Redundancy analyses may have explained slightly more variation in taxa than in functional groups in our small region because the species pool was similar for all sites, and along the steep longitudinal gradient taxonomic turnover is necessarily high. This taxonomic response is probably dominated by a direct response to temperature regime on individual life history cues (Ward, 1986). Functional traits are not necessarily so limited and thus are likely to respond to a combination of longitudinal and reach-scale habitat characteristics. Individual traits are also more likely to be distributed unpredictably among environmental variables because of trade-offs and alternative adaptive solutions to the same habitat (Townsend & Hildrew, 1994; see below).

Charvet *et al.* (2000) have argued that a low variation in functional structure in unimpacted streams across

long environmental gradients may have important implications for bioassessment. In their study, 'reference' sites tended to house a high diversity of species traits that was not highly variable no matter the environmental location, whereas human-disturbed sites had lower functional diversity. Charvet *et al.* (2000) suggested that such a pattern would result given high temporal stability and spatial heterogeneity of reference streams. In the current study, all stream sites had very low human impact (and hence could all be considered 'reference' sites) and, therefore, such an explanation would be consistent with the low level of pattern found in our functional group data. We did reveal a slight trend of increasing trait richness with decreasing altitude (Table 2), which may suggest a harsher environment (although not human-caused) in the alpine zone than at lower altitudes.

Despite the low level of explanatory power, RDA revealed some interesting patterns of functional traits along the altitudinal gradient, some of which may support the contention of harsher conditions at alpine sites. Several life history traits relating to longer life (semivoltinism, long-lived adult stages, and slow-seasonal larval development) were more prominent at lower altitude. Highest-altitude streams are arguably more stressful environments because of the very short emergence season, long-term snow cover, lack of riparian trees to protect from wind and solar radiation, and thus low input of organic matter (Ward, 1994; Hieber *et al.*, 2002). Short-lived adults may be more common to avoid energetic costs of the terrestrial environment, and eggs may be the preferred overwintering stage in this case, thereby selecting against slow-seasonal and semivoltine life histories (as in the Arctic: Downes, 1965). Traits conferring long-distance adult dispersal and high fecundity were also associated with higher altitudes. These are typical strategies for 'weedy' species adapted for resilience in more disturbed or stressful habitats (Townsend & Hildrew, 1994). In a longitudinal study of a glacier-fed alpine stream, Snook & Milner (2002) showed that species traits including small body size, clinger habit and short life cycles dominated in the highest-altitude sites. They suggested that these traits offered aspects of resistance/resilience to the harsh environment typical of glacial streams (cf. Milner & Petts, 1994). Although our snowmelt-fed alpine streams are more temporally stable than glacial headwaters (which are very unstable physically because of continual sediment

supply and frequent channel migration, Milner & Petts, 1994), the relatively extreme environmental characteristics of alpine streams in general (compared with lower reaches) may influence the predominance of more 'weedy' traits.

As previously mentioned, an obstacle in the use of traits to predict patterns of community organisation is the problem of trade-offs between traits suited for life in a particular habitat (Townsend & Hildrew, 1994; Usseglio-Polatera *et al.*, 2000; Snook & Milner, 2002). There may be several categories of traits that allow, for example, success in a harsh environment, but chances are slim that a single taxon will possess the entire suite. It is more likely that a taxon will possess only one or a few of them, and other unrelated traits will be carried along because of phylogenetic constraints. Blackflies (Simuliidae), for example, have high fecundity, capacity to disperse long distances, and fast seasonal development (perhaps suiting them to life at high altitude) but they retain the filter-feeding trait, which may be selectively neutral there. Blackflies were dominant in alpine sites and, therefore, the filter-feeding trait appeared to be associated with higher altitudes (against RCC predictions; Vannote *et al.*, 1980). Such patterns confound analyses based on traits and may be an important reason for the low level of variance explained when categorising communities functionally.

An important and unexpected result of our analyses that has never been reported is the trend of significantly lower community similarity among alpine stream sites than those at lower altitudes. This trend was consistent when characterising streams both taxonomically and functionally (Fig. 4). There are several potential explanations for this surprisingly strong pattern.

First, the physical habitat of the streams may simply be more variable in alpine reaches, thereby leading to more variable communities. RDAs indicated the importance of other, local-scale variables orthogonal to altitude. Periphytic growth, stream size, and median particle size (with embeddedness) all helped explain some variation in communities within the same altitudinal zones. However, we found no difference in the range of these secondary variables in alpine sites compared with lower-altitude zones. Further, temperature data collected in 2001–2002 (D.S. Finn, unpublished data) showed minimal variation among the alpine sites (e.g. mid-July to mid-August

means range from 5.5–8 °C; average diel range 5–6.5 °C; annual low temperature reached 0 °C at all sites). We therefore have no evidence thus far to support the hypothesis of greater physical variability between higher-altitude stream sites.

A second potential explanation for the lower community similarity among alpine sites is that they are temporally less stable. The high variation around the low mean functional similarity at the alpine sites (Fig. 4b) is attributable to some pairs of alpine sites having relatively high similarity, while other pairs were very dissimilar. Such a pattern, in addition to the incomplete representation of total trait diversity, suggests that there may be high turnover and empty niche space in alpine streams. The absence of some expected traits from some sites could arise if these sites are frequently disturbed thus continually reset and recolonised (cf. Townsend, 1989). As yet, however, we have no data that demonstrate a higher temporal variability in the alpine stream sites. These streams have stable channels and perennial flow, and continual benthic collections from 2000 to 2002 have not yet demonstrated appreciable taxonomic turnover through time (D.S. Finn, unpubl. data).

A third hypothesis for the high variability of alpine stream communities involves the insularity of these streams. Physical isolation of sites combined with the effects of chance historical events can lead to large differences in community structure between sites, according to the basic tenets of island biogeography (MacArthur & Wilson, 1967) as well as neutral theory (Hubbell, 2001). Because of the distinct and narrow longitudinal ranges of many alpine insect species (Allan, 1975), often the only biological connectivity that adjacent streams have is via the flying adult stage. Even adjacent streams may be separated by steep catchment boundaries that can cause a higher degree of isolation (Ward, 1994). Theory predicts lower species richness and higher frequency of endemism on more isolated islands. Although endemism of aquatic invertebrates is unlikely to occur within single alpine streams (but is possible at broader scales: Ward, 1994), low community similarity among physically similar streams could be an indication of effects of isolation at a finer spatiotemporal scale. Even in lower-altitude, boreal headwater streams, Heino *et al.* (2003) had difficulty defining predictable invertebrate assemblage types based on local and regional habitat characteristics. Although isolating mechanisms will

operate to varying extents depending on terrestrial landscape, it may be that headwater streams in general, because of their distinct taxonomic assemblages and physically insular nature, are by nature more disparate than counterpart reaches further down the longitudinal continuum.

Molecular analyses on some stream insect species have supported the idea (cf. Begon, Harper & Townsend, 1996) that it is the winged adults, rather than the aquatic juveniles, that are the primary dispersers to new habitats (Schmidt, Hughes & Bunn, 1995; Bunn & Hughes, 1997). A study of populations of the stonefly *Yoraperla brevis* (Banks) in adjacent Montana streams found that populations were much more similar between sites within a stream than between streams (Hughes *et al.*, 1999). The authors suggested that these results could be explained by the fact that the streams were isolated by steep canyons across which the winged adults were not likely to fly. In small alpine streams, a similar effect of between-stream isolation would be expected because of high winds, steep catchment boundaries and lower air temperatures.

Our analyses have demonstrated that, although the longitudinal gradient appears to have similar effects in shaping the benthic communities of four different physically similar Rocky Mountain streams, there is also evidence that biological similarity differs at different points along the continuum. Beyond its general ecological significance, an understanding of the natural variability among unimpacted streams in a region has considerable practical application, in particular in the understanding of reference conditions for bioassessment. Lack of homogeneity of reference conditions within an ecoregion can be dealt with by stratification of collection locations with respect to their finer-scale environmental differences (Hawkins *et al.*, 2000), including position along the altitudinal gradient (Sandin & Johnson, 2000). Our study suggests that such stratification in mountain streams is justified, but that for higher-altitude sites even this technique may be insufficient to capture the broad range of natural variability. Functional classification of streams may be another, simpler approach to bioassessment because of its lower-than-expected variability among 'reference' sites; however, it is important to consider natural relative to human caused disturbance as a cause of functional variation among sites. Alpine streams in particular appear to

have the potential to be quite variable biologically, whether communities are defined taxonomically or functionally. This was an unexpected observation, the mechanisms behind which merit further research.

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Appendix Density of taxa collected at each study site, in number of individuals per minute of sampling

	GLC1	GLC2	GLC5	GLC9	GLC16	SFP1	SFP2	SFP5	SFP9	SFP17	SSV1	SSV2	SSV5	SSV8	PDR1	PDR2	PDR5	PDR11	PDR18
Ephemeroptera																			
<i>Aneides</i> spp.*		0.3	1.5	5.3	5	1.7	0.7	1.3	0.8		1.3	0.3	0.8		0.3	1	3.2		
<i>Baetis</i> spp.*	85.5	5.3	13	21.3	80.8	0.3	5	25.8	53.8	27	0.3	30	35	85.8	0.5	31.3	107	42.6	25.8
<i>Cinigmula</i> spp.*	0.5	18	9.5	7.3	27	43.6	37.4	51.8	18.3	4	5	22	8.1	24.6	0.5	43.4	25	17.8	19
<i>Epeorus deceptivus</i> (McDunnough)*		20	0.8	0.3	0.5	6.3	18	54	12	5.8		12.5			2.7	18.7	1.8	13.6	
<i>Epeorus longimanus</i> (Eaton)*				0.3	2.8			5	4.4				4.5	2.5					6.2
<i>Drunella coloradensis</i> (Dodds)*		1.3		6.3	6.3	0.3	0.3	11.3	1.4		8	1	1.3		3	4.7	0.2	1.2	
<i>Drunella doddsi</i> (Needham)*		0.3		0.3	1.5			1	0.6		0.5	1.8	17.3		0.7	8.3	0.2	3.2	
<i>Ephemerella infrequens</i> (McDunnough)				0.7	0.5	0.3		0.3	0.2		0.8		0.8				2.6	1.4	
<i>Rhithrogena robusta</i> (Dodds)					1.8														
<i>Rhithrogena hageni</i> (Eaton)				5.3				10	0.5		0.3		0.5	2				0.2	2.2
Immature <i>Rhithrogena</i> spp.																2.7	0.4	0.2	
Plecoptera																			
<i>Saetisa</i> spp.*		0.3	9.5	10.3	44.3	0.3	2.3	1.25	3.5	0.8	10	3.8	8.3		9	5.3	4	2.8	
<i>Alloperla</i> sp.																3.3			
<i>Suwallia starki</i> (Alexander & Stewart)*								10					6.8				2.4	2.2	
Immature Chloroperidae				0.3		0.3	2.3	0.3	11.3							4.7		2.8	
<i>Megarcys signata</i> (Hagen)*		7.3		0.3		4.7	4.3	19.8	2.8	14.3			0.3	6.8	1	2		2.2	
<i>Cultus aestivalis</i> (Needham & Claassen)			0.5																
<i>Kogotus modestus</i> (Banks)			0.8	1.3					2.8	0.2		2.8	1	1.3	0.7		0.2	0.4	
Immature Perlodidae		1	0.8	0.3	2.5				2.3	0.6		0.3	0.3	0.8	0.3	0.3	1.8	0.4	
<i>Zapada haysi</i> (Ricker)*		0.5	13.3	30	6.7	3.8	33.7	30.7	1.8	0.6	6.3	25	5	5	10.7	10	1.2	8	
<i>Zapada cinctipes</i> (Banks)*			2.3	2.3	2.7	1			1.8			7.8	2.5	1.8	4		0.6	2.4	
<i>Amphinemura banksi</i> (Baumann & Gaufin)										0.2								0.2	
<i>Hesperoperla pacifica</i> (Banks)			0.3	0.3					2.5	0.3	0.2	0.5	2.5	0.3			0.6	0.4	
Capniidae			0.7	0.3		0.3		0.3	2.5	24			1.3				0.4	5.6	
<i>Doddsia occidentalis</i> (Banks)																1			
<i>Taeniopterna pallidum</i> (Banks)				0.3						0.4									
<i>Paraleuctra vershina</i> (Gaufin & Ricker)															2	3.7	0.6	1.2	
Trichoptera																			
<i>Rhyacophila brunnea</i> (Banks)*			0.3	3.7	0.3		0.3		0.5	1		1.5	1		0.7			0.4	
<i>Rhyacophila hyalinata</i> (Banks)*			0.5					4.3	1			7.8			0.3				
<i>Rhyacophila alberta</i> (Banks)*											1	0.8		0.5					
<i>Rhyacophila angelita</i> (Banks)		2.5	0.3	0.3		10.7	1.3	1										0.2	0.2
<i>Rhyacophila verrula</i> (Milne)					1								0.8						
<i>Rhyacophila coloradensis</i> (Banks)		0.7	0.5					5.25											
<i>Rhyacophila hamiltoni</i> (Ross)												0.3	0.8	7.3	0.3	0.7	0.6	2	
<i>Rhyacophila pellisa</i> (Ross)			0.3				0.3		2.3	1.4					0.3	0.3	0.4	0.4	
<i>Rhyacophila</i> sp.									0.3	0.6					0.3	0.3	0.4	0.4	
<i>Arctopsyche grandis</i> (Banks)			0.3		0.5				0.5	0.2		0.3	0.8		0.3	0.3	0.4	3.2	

Appendix (Continued)

	GLC1	GLC2	GLC5	GLC9	GLC16	SFP1	SFP2	SFP5	SFP9	SFP17	SSV1	SSV2	SSV5	SSV8	PDR1	PDR2	PDR5	PDR11	PDR18
Immature Limnephilidae	0.3							0.25	0.8										
<i>Brachycentrus americanus</i> (Banks)					0.8				0.2										
Hydroptilidae			0.3	0.3															
<i>Asynarchus nigriculus</i> (Banks)	1.5					1	0.7												
<i>Hesperophylax occidentalis</i> (Banks)										2.7									
<i>Psychoglypha subborealis</i> (Banks)			0.5			9.3	1.3			0.3				0.5					
<i>Psychronia costalis</i> (Banks)										0.3									
<i>Dicosmoeccus atripes</i> (Hagen)								0.8											
<i>Lepidostoma</i> sp.																			
<i>Glossosoma</i> spp.											0.5	0.3	9.3	0.3	0.3	0.2	0.2		
<i>Dolophilodes aequalis</i> (Banks)													0.5						
<i>Micrasema bacro</i> (Ross)											2	0.5							
Coleoptera																			
Elmidae																			
<i>Heterlimnius corpulentus</i>	0.5		21.3	50.8					5.6	0.3		12	31			13.6			2.2
(LeConte)*																			
Diptera																			
Chironomidae																			
Chironominae																			
Tanytarsini																			
<i>Micropsectra</i> sp.*	0.5	0.3	5	0.3	1	3.3	1.7	1.5	1	1.7	1.3	11.8	4	4.5	0.7	3	9.8		
<i>Paratanytarsus</i> sp.	0.5																		
<i>Stempellinella</i> sp.*			3.3	0.7	8.5				2.6			0.3	0.3	1.3	0.7	1.2	0.2		
Chironomini																			
<i>Phaenopsectra</i> sp.										1									
<i>Polypeditum</i> sp.												0.3							
Diamesinae																			
<i>Diamesa</i> sp.*	55.5	10	0.3	0.3	4.3	3.3	3.3	5	1.5	0.6	3	4.8	0.3	0.8	2	0.3	0.2		
<i>Pagastia</i> sp.	1.7	1.5	2	1.3		0.3					0.3	3	1.3		0.7				
<i>Pseudodiamesa</i> sp.*	16	1.7																	
<i>Symphothastia</i> sp.																			
Tanypodinae																			
<i>Thienemannimyia</i> group																			
<i>Zaurelimyia</i> sp.			0.5	0.7					0.2				1.8						
Orthocladiinae																			
<i>Chaetocladius</i> sp.	0.5		0.3	5	1	1	0.3	0.3	0.3	0.6	0.3	3.8	0.3	2	0.5	0.3	0.2	0.2	
<i>Corynoneura</i> sp.*			0.3										0.3						
<i>Cricotopus nostocicola</i> (Wirth)		0.3																	
<i>Cricotopus/Orthocladius</i> sp.*	54	12.7	11	13.3	11.3	1	23.3	22.5	11.8	1.6	26.7	2.3	16	12.8	8.5	1.7	0.7	6.2	2.4
<i>Diplocladius</i> sp.															2				

Appendix (Continued)

	GLC1	GLC2	GLC5	GLC9	GLC16	SFP1	SFP2	SFP5	SFP9	SFP17	SSV1	SSV2	SSV5	SSV8	PDR1	PDR2	PDR5	PDR11	PDR18
<i>Eukiefferiella devonica</i> (Edwards) group	0.5	1	1.3	0.3	1		0.3	0.5				2.3	1.5	1				0.2	
<i>Eukiefferiella</i> spp.*	11.5	16	5	0.3	1.3	9	4	4.8	6	0.6	0.7	1.8		1.3	0.5	1.3	3.3	0.6	3.6
<i>Heleniella</i> sp.														0.5					
<i>Heterotanytarsus</i> sp.			0.3																
<i>Heterotrissocladius</i> sp.			0.3						0.3	0.3									
<i>Hydrobaenus</i> sp.			0.3	0.3				0.3		34.7									
<i>Krenasmitia</i> sp.																			
<i>Nanocladius</i> sp.			0.3	0.7		2		3.3			0.3	3.5	0.3				1.2		0.2
<i>Parametricnemus</i> sp.																			
<i>Parochlus</i> sp.												0.3							
<i>Parorthocladius</i> sp.*	3.5	0.7	3	1.3		34.3	1	2.8	1	0.2	0.7	7	2	0.5	0.3	1	1	0.6	
<i>Rheocricotopus</i> sp.*	2	21	2.7	15		0.3	4	1	1	0.2	0.3	34.3	47.5	16.8	0.3	0.3	1.8	3.2	
<i>Thienemanniella</i> sp.			0.25	2	0.3	1.3	0.8	0.3	0.3	0.3	0.3	1.3	1.3	3.3	1	0.3	0.2	0.4	
<i>Tvetenia</i> sp.*	446	7	1.75	0.7	13.5	2	9	5.3	1.8	1.8	19	3	3	2.8	1	2.3	0.8	3.8	
Empididae																			
<i>Chelifera</i> spp.*	6	1	0.25	0.7		3.3	3.3	5.3			3			3			0.4		0.2
Tipulidae																			
<i>Dicranota</i> spp.			0.3	0.3				0.3	0.5					0.3					0.4
<i>Hexatoma</i> sp.										0.2									
<i>Tipula</i> spp.						0.7	0.3												
Simuliidae*	177	12.7	0.25	1.3	0.8	208	20.3	8	0.8	10	14.3	2.5	2.5	0.5	24.5	0.3	2	0.2	2
Deuterophlebiidae																			
<i>Deuterophlebia coloradensis</i> (Pennak)										0.2			0.3						
Blephariceridae		0.7																	
Ceratopogonidae							0.3		0.5	0.2				0.3	0.3	0.3	0.2	0.2	0.2

*Taxa used in RDA analyses. Immatures included here were not used in analyses. Refer to Table 1 for site notations.