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Variability in stream macroinvertebrates at multiple spatial scales

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SUMMARY

1. We intensively sampled 16 western Oregon streams to characterize: (1) the variability in macroinvertebrate assemblages at seven spatial scales; and (2) the change in taxon richness with increasing sampling effort. An analysis of variance (ANOVA) model calculated spatial variance components for taxon richness, total density, percent individuals of Ephemeroptera, Plecoptera and Trichoptera (EPT), percent dominance and Shannon diversity.
2. At the landscape level, ecoregion and among-streams components dominated variance for most metrics, accounting for 43–72% of total variance. However, ecoregion accounted for very little variance in total density and 36% of the variance was attributable to differences between streams. For other metrics, variance components were more evenly divided between stream and ecoregion effects.
3. Within streams, approximately 70% of variance was associated with unstructured local spatial variation and not associated with habitat type or transect position. The remaining variance was typically split about evenly between habitat and transect. Sample position within a transect (left, centre or right) accounted for virtually none of the variance for any metric.
4. New taxa per stream increased rapidly with sampling effort with the first four to eight Surber samples (500–1000 individuals counted), then increased more gradually. After counting more than 50 samples, new taxa continued to be added in stream reaches that were 80 times as long as their mean wetted width. Thus taxon richness was highly dependent on sampling effort, and comparisons between sites or streams must be normalized for sampling effort.
5. Characterization of spatial variance structure is fundamental to designing sampling programmes where spatial comparisons range from local to regional scales. Differences in metric responses across spatial scales demonstrate the importance of designing sampling strategies and analyses capable of discerning differences at the scale of interest.

Keywords: invertebrates, metrics, sampling, spatial scale, streams

Introduction

Concern for the health of ecosystems and interest in biological diversity have generated a demand for ecological information at multiple scales (Levin, 1992; Meyer, 1997). Our perceptions of physical and biolog-

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ical processes depend on the scale at which observations are made (Cooper *et al*., 1998). Stream macroinvertebrates, traditionally studied at the microscale, are particularly challenging to describe at a landscape scale (Resh, 1979; Peckarsky, Cooper & McIntosh, 1997; Richards *et al*., 1997; Wiley, Kohler & Seelbach, 1997). We may assume that the scale at which macroinvertebrates exhibit the greatest variation comprises the scale over which important physical/chemical gradients or biotic interactions control assemblage composition. For example, physical processes such as discharge and temperature strongly affect distribution patterns reflected in differences between streams or catchments (Townsend, Hildrew & Francis, 1983; Li *et al*., 1994; Wiley *et al*., 1997). Biotic interactions including predation, competition, disease (McAuliffe, 1984; Kohler & Wiley, 1997; Cooper *et al*., 1997) and life history phenomena, particularly dispersal, can create strong localized effects (Downes & Keough, 1998). Our dilemma is to identify appropriate invertebrate descriptors that respond to environmental change over a broad spatial range (*sensu* Norris, 1995).

Geophysical, chemical and anthropogenic processes constrain stream systems in a hierarchical fashion (Frissell *et al*., 1986; Hildrew & Giller, 1994). Biological responses can be examined in a similarly nested hierarchy (Downes, Lake & Schreiber, 1993; Cooper *et al*., 1998). By grouping individual taxa into phylogenetically or functionally related taxa, metrics can compare assemblages from different sites (Karr *et al*., 1985; Plafkin *et al*., 1989; Resh & McElravy, 1993) and potentially at different scales. Our study examined assemblage variability in a sequence of spatial scales using five basic metrics. We nested finer scale units within coarser ones; at the finest scale we compared samples taken within cross-sectional transects of individual streams and, at the coarsest, we compared ecoregions. As part of our design we included a wide range of sites across the Cascade and Willamette Valley ecoregions of western Oregon (Omernik & Gallant, 1986). To satisfy the requirement for replication and to measure cumulative taxon richness, our sampling effort was large. Other studies have focused on the adequacy of metrics to distinguish between streams and to measure any response to human disturbance (Whittier, Hughes & Larsen, 1988; Barbour *et al*., 1992; Kerans & Karr, 1992; Fore, Karr & Conquest, 1994); our study considered the spatial variability of assemblage metrics at several spatial scales.

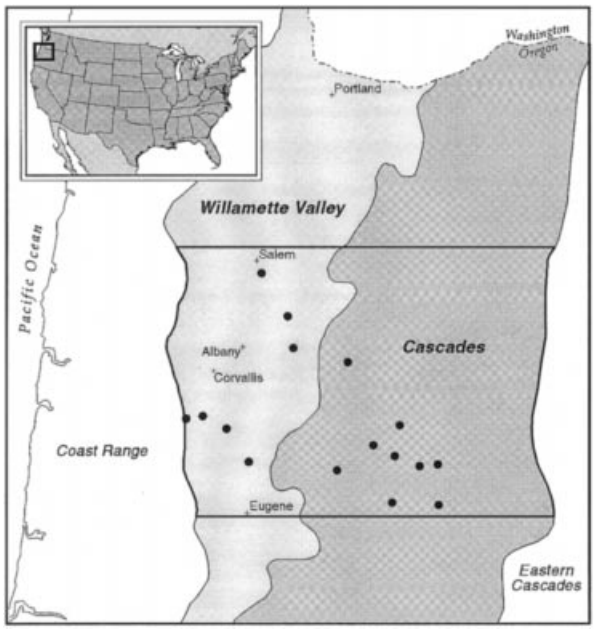

Fig. 1 Map of western Oregon showing location of the 16 study streams.

Methods

Site selection

The study was conducted over two western Oregon ecoregions (Omernik & Gallant, 1986): the Willamette Valley and the Cascade Mountains (Fig. 1). In the Willamette Valley, agriculture and urbanization have influenced low gradient, fine substratum streams for over a century, while logging and human settlement have altered the higher gradient, coarse-bedded Cascade streams over a similar period.

A set of 100 candidate stream segments in each ecoregion was randomly selected from 1:100000 scale USGS topographic maps following the protocol of the National Stream Survey (Kaufmann *et al*., 1991). Sampling was restricted to wadeable streams between 44 and 45°N, approximately between the cities of Salem and Eugene, OR (Table 1). Fourteen stream segments were selected from the candidate list in a 2×2 factorial design with ecoregion and stream size being the two factors. Stream size classes were defined as small (first order) and large (second/third order), as depicted on the topographic maps. A random number generator was used to choose exact sampling loca-

Table 1 Composite macroinvertebrate assemblage characteristics in the 16 Willamette Basin sample streams

Stream	Surber samples counted	Total density (no. m^{-2})	Taxon richness	% EPT individuals	% Dominant taxa	Shannon diversity	Alpha diversity	Stream width (m)
Cascade-large								
CAS01-Lookout	48	595	67	46.7	21.6	3.06	15.8	11.0
CAS02-Ennis	14	4232	59	23.3	30.7	2.79	11.3	3.5
CAS04-S. Fk Crabtree	14	1197	61	43.5	14.9	3.25	15.5	6.7
CAS05-N. Fk Gate	59	2631	78	27.8	20.0	2.91	15.2	7.1
Cascade-small								
CAS06-Mack	18	949	63	65.5	17.8	2.94	16.5	2.9
CAS07-Potts	16	1395	66	57.4	12.9	3.18	16.9	1.7
CAS08-Black	16	2560	62	64.6	28.7	2.86	13.6	3.1
CAS09-Calapooia Trib	45	720	66	62.4	13.0	3.31	17.1	2.2
CAS10-Walker	14	1989	48	50.9	17.4	2.94	10.0	1.7
Valley large								
VAL01-Camous	45	3563	38	10.3	61.3	1.41	6.7	3.7
VAL02-Beaver	45	747	31	9.3	57.1	1.66	6.2	5.7
VAL03-Muddy-Finley	16	999	26	4.7	40.8	2.05	4.7	6.6
VAL04-Muddy-Coburg	54	921	52	21.2	22.1	2.58	11.4	6.8
Valley small								
VAL05-Pringle	18	351	23	1.9	47.9	1.40	7.5	2.0
VAL06-Smallman	13	4894	36	2.0	18.7	2.66	6.2	5.1
VAL08-Reese	14	571	29	1.2	19.4	2.32	6.8	3.8

Table 2 Physicochemical characteristics of the streams in each of the four study strata (mean ± SD)

Characteristic	Large cascade streams	Small cascade streams	Large valley streams	Small valley streams
Basin area (km^2)	33 ± 29	4 ± 2	88 ± 63	8 ± 8
Channel gradient (%)	2.9 ± 1.1	9.7 ± 3.8	0.1 ± 0.1	0.6 ± 0.4
Wetted width (m)	7.1 ± 3.1	2.3 ± 0.6	5.7 ± 1.4	3.6 ± 1.5
% Substratum sand and finer	1 ± 2	3 ± 2	52 ± 36	61 ± 24
% Riparian canopy presence	60 ± 12	47 ± 23	27 ± 17	22 ± 19
Conductivity ($\mu S\,cm^{-1}$)	43 ± 14	36 ± 19	68 ± 15	58 ± 8
PH	7.4 ± 0.1	7.2 ± 0.3	7.3 ± 0.3	7.0 ± 0.2

tions on each stream segment. Two additional sites (Lookout and Mack Creeks) in the H. J. Andrews Experimental Forest, that is part of the Cascade Mountains Long-term Ecological Research (LTER) site, were also included for comparison with long-term data. Including these two extra LTER streams in the Cascade ecoregion, we included nine Cascade and seven Valley streams, representing a wide variety of stream conditions (Table 2). Study sites ranged from meandering floodplain streams and agricultural ditches to montane cascades and glacial-fed headwaters. Riparian vegetation included old-growth conifers, deciduous hardwoods, herbaceous grasslands and agricultural stubble (see Herlihy *et al.*, 1997, for details).

Streams in the 'small' stream size class averaged 4 (Cascade) and 8 (Valley) km^2 in basin area and measured 2 and 4 m in mean wetted widths, in contrast to areas of 33 and 88 km^2 and wetted widths of 7 and 6 m for the 'large' streams in the same ecoregions (Table 2). Streams in the Cascades were steeper (gradients from 1 to 16%) and had coarser substrata ($< 5\%$ sand or finer) than streams in the Willamette Valley (gradients $< 1\%$, $> 50\%$ substratum sand or finer). Valley streams tended to have higher conductivity, but stream pH was similar (almost all just over 7).

Field and laboratory sampling

Collections were made in late September 1992. The goal was to include at least seven transects of fast water (riffle, rapid or cascade) and seven slow water (pool or glide) habitats. From the random start point on each stream, 14 study transects (cross-sections) were marked off upstream at 10-m intervals in small streams, 25-m intervals in large streams. Each transect represented one habitat type (fast or slow water), and that transect was divided into three equal sections (left, centre and right). One Surber sample (0.093 m^2) was collected from each section. In the Cascades, when there were not equal numbers of fast and slow water habitats encountered after 14 transects, the crew continued upstream, sampling in only the under-represented habitat until seven transects were sampled. In some Valley streams, fast water was absent or rare so no attempt was made to get additional fast water samples there. No samples were collected beyond twice the original 14 transect sample length, that is no more than 260 m in small streams and 650 m in large streams. In the final analysis, the number of transects per stream varied from 14 to 20. In the field, each Surber sample was filtered through a 500-μm soil sieve, placed in plastic bags (whirlpaks) and preserved in 70% ethanol.

Initially all three samples from each transect were counted in the laboratory; this protocol was followed for three Valley and three Cascade streams (Table 1). After we determined that there were relatively small differences between samples in the same transects (i.e. left, centre or right), we counted only one sample per transect for the remaining four Valley and six Cascade streams. The left, centre or right sample was picked at random for the first transect, then samples alternated in a left, centre, right order and potentially at different scales over the remaining transects. In 378 of the 449 Surber sample-units, the entire sample was counted. In the remainder, organisms were extremely abundant or organic debris made counting very difficult, so the original sample was subsampled using a 0.5-m^2 gridded sieve (Caton, 1991). In these cases at least 100 individuals per sample were counted.

Insects were identified to genus, with the exception of Chironomidae, which were identified to tribe. Molluscs, Branchiopoda and Copepoda were identified to family. Other invertebrate groups (e.g. Annelida and Arachnida) were identified to order. Unusual taxa were verified by experts, and representatives of all taxa have been archived at our laboratory at Oregon State University. Non-insect groups were identified to a lower resolution than insects, largely because of time constraints. However, they were important components in many streams and were useful in distinguishing between streams in subsequent analyses.

Because some macroinvertebrate metrics are at least partially redundant (see Hannaford & Resh, 1995), we employed a limited number of metrics that represent different aspects of assemblage structure and composition. Five metrics frequently used in biomonitoring surveys were chosen: total taxon richness, Shannon diversity (as measures of diversity), percent abundance of Ephemeroptera, Plecoptera, and Trichoptera (EPT), percent abundance represented by the most dominant taxon (as measures of proportional abundance) and total density.

Data analysis

Four metrics were calculated from each Surber sample (Table 1). Total taxon richness was the number of benthic taxa found in a sample. Taxon accumulation curves were developed for each stream by calculating cumulative taxon richness with accumulating sample size. The percent dominance was determined as the number of individuals in the most abundant taxon compared to the total number of organisms in the sample. Similarly, EPT percentage was calculated as the percentage of all individuals that were Ephemeroptera, Plecoptera and Trichoptera. Shannon diversity was calculated using proportion of individuals per taxon (Magurran, 1988). Alpha diversity was computed iteratively (Magurran, 1988).

An analysis of variance (ANOVA) model was used to decompose the different sources of spatial variation, ranging from fine scale (within transects) to coarse (between ecoregions; Table 3). The data were fitted to a mixed linear model using the General Linear Model procedures of SAS (SAS Institute, 1988). The model incorporated three fixed effects, and three random effects. The fixed factors and their levels were: ecoregion (Cascade, Valley), stream size class (small, large), and sample location on the transect (left, centre, right). Individual streams, habitat type within stream (fast water, slow water) and transect location within the stream were random components of the model that were nested: stream within ecoregion and stream size, habitat type within stream, transect within habitat, and location on transect. Thus, total variance for each metric was decomposed into the following factors: Landscape Scale: 1) Ecoregion, 2) Stream size class, 3) Ecoregion * size interaction, 4) Among stream within Ecoregion * size class;

Table 3 Partially nested analysis of variance of spatial variations in macroinvertebrate metric scores. Sixteen streams were sampled in two ecoregions and two size classes. In each stream, there were two habitat types, and samples were collected from between 14 and 20 transects, and one or three positions on each transect

Source of variation		d.f.[a]	Type[a]	Expected mean squares
Among ecoregions	= E	1	F	$\sigma^2_R + 1.24\sigma^2_{T(H(S(E*Z)))} + 9.05\sigma^2_{H(S(E*Z))} + 15.52\sigma^2_{S(E*Z)} + 119.42\phi_E$
Among size classes	= Z	1	F	$\sigma^2_R + 1.25\sigma^2_{T(H(S(E*Z)))} + 9.11\sigma^2_{H(S(E*Z))} + 15.88\sigma^2_{S(E*Z)} + 123.79\phi_Z$
Ecoregion * size interaction	= E*Z	1	F	$\sigma^2_R + 1.24\sigma^2_{T(H(S(E*Z)))} + 9.08\sigma^2_{H(S(E*Z))} + 15.57\sigma^2_{S(E*Z)} + 59.91\phi_{E*Z}$
Among streams (EcoxSize)	= S(E*Z)	12	R	$\sigma^2_R + 1.64\sigma^2_{T(H(S(E*Z)))} + 15.11\sigma^2_{H(S(E*Z))} + 23.76\sigma^2_{S(E*Z)}$
Among habitat within stream	= H(S(E*Z))	13	R	$\sigma^2_R + 1.61\sigma^2_{T(H(S(E*Z)))} + 11.35\sigma^2_{H(S(E*Z))}$
Among transect w/in habitat	= T(H(S(E*Z)))	222	R	$\sigma^2_R + 1.94\sigma^2_{T(H(S(E*Z)))}$
Among transect location within habitat	= L(H(S(E*Z)))	20	F	$\sigma^2_R + 9.85\phi_{L(H(S(E*Z)))}$
Residual	= R	177	R	σ^2_R
Total		447		

[a] d.f. = degrees of freedom, F = fixed effect, R = random effect.

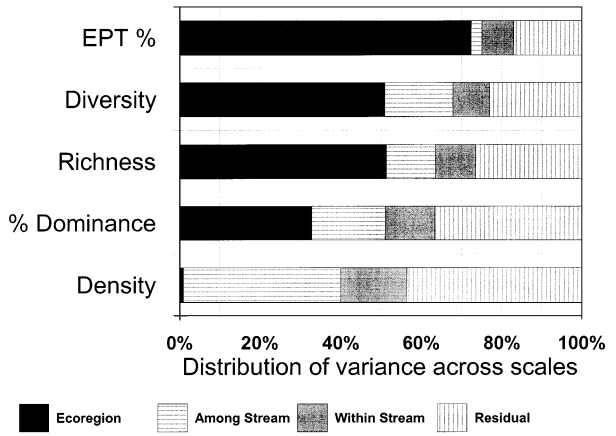

Fig. 2 Total variance components for study metrics.

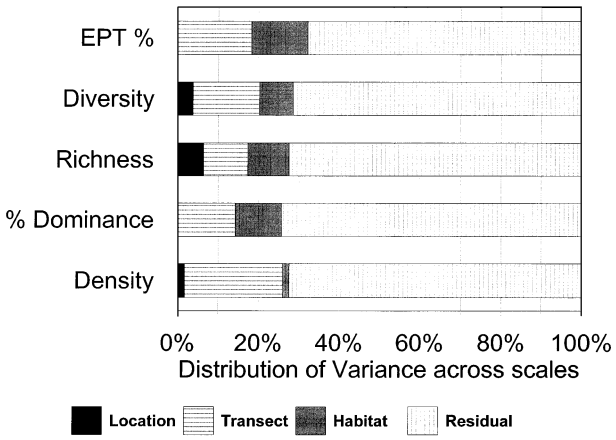

Fig. 3 Within-stream variance components for study metrics.

Within Stream Scale, 5) Habitat type within stream, 6) Among transects within habitat type, 7) Among locations within habitat type, 8) Residual.

The residual term depicted sample to sample variability within a stream reach not accounted for by spatial factors defined in our model. Variance components were calculated using the Type III expected mean square error and the model coefficients from the SAS GLM procedure. To insure that residuals had homogeneous variance, several of the variables were transformed; square root for taxon richness, $\log_{10}$ for percent dominance and total density, and an empirical logit for EPT percentage (McCullough & Nelder, 1989). Technically, fixed factors have non-centrality parameters, not variance components. We estimated a function of the non-centrality parameter for fixed factors that was analogous to a variance component and used it in comparisons in the same way as we used variance components.

To quantify the magnitude of within-stream variation relative to mean metric values, precision values were calculated for each metric as coefficients of standard variation, i.e. pooled standard deviation/grand mean. Pooled standard errors (SDpool) were determined by calculating a sum square error (SSE) for metric values within each stream, summing the SSE across all streams, then dividing the total SSE by total degrees of freedom: $\text{SDpool} = [\text{Total SSE}/(n-1)]^{0.5}$, where n was the number of samples within each stream summed over all streams.

Results

For all metrics, there was a strong landscape (ecoregion and/or stream) signal. Total taxon richness ranged from 48 to 78 in the Cascade ecoregion, versus 23–52 taxa in the Willamette Valley ecoregion (Table 1). Shannon diversity was typically higher, and percent EPT much higher in the Cascade streams. Mean percent dominance was usually higher in the Willamette streams (four out of seven streams $> 40\%$) than in the Cascades (all $< 31\%$). Mean macroinvertebrate density in the study streams was highly variable, from 351 to 4894 individuals m^{-2}, and did not indicate a strong contrast between ecoregions.

Ecoregion and stream scales accounted for 42–71% of total variance in study metrics (Fig. 2). More than 50% of the variance was due to differences between ecoregions for percent EPT, Shannon diversity, and taxon richness, with 34% of percent dominance explained at the same scale. However, relatively little variance in total density was attributable to ecoregions; the stream component was relatively large (Fig. 2). Stream size class (not shown in Fig. 2) accounted for less than 1% of total variance for all metrics except total density, for which it accounted for 3% of total variance. The ecoregion by size class interaction was virtually zero for all metrics.

Within-stream variance (attributable to habitat-type, transects within habitats and locations within habitat) comprised a much smaller part of total variance than coarser scale components (Fig. 3). Metric differences within streams were less distinctive than those between streams or ecoregions. The residual term contributed the most variance, comprising 60–70% of within-stream variation, and a large portion (20–40%) of total variation.

The sum of transect and habitat variances comprised at least 25% of within-stream variance for all metrics (Fig. 3). For total density, variance associated with habitat was very small, but habitat type constituted 8–15% of within-stream variance for other metrics. Besides habitat and transect-to-transect differences, the majority of within-stream variance was residual (Fig. 3). Sample location on a transect explained negligible amounts of variance (0–3%).

Taxon accumulation curves reflected the high variability within streams and illustrated differences between ecoregions (Fig. 4). Curves developed for Cascade streams were steeper than those for the Willamette Valley, drawn for either cumulative Surber sample sizes (Fig. 4a) or by cumulative number of individuals counted (Fig. 4b). The difference between curves illustrates the consistently higher taxon richness found in Cascade streams in contrast to those in the Willamette Valley (Table 1). For data shown here (Figs. 4a,b), the samples were accumulated in the order in which they were collected in the field. We also have performed a bootstrap analysis, and the results were virtually identical if samples were accumulated in random order. When all 16 streams were averaged to examine how many taxa were added with increasing sample size, an average of four to eight new taxa were added in the first four samples; one or two taxa were added beginning with the fifth and continuing through 23 subsequent samples. The unusually high number of samples revealed that curves in both ecoregions were slow to attain an asymptote.

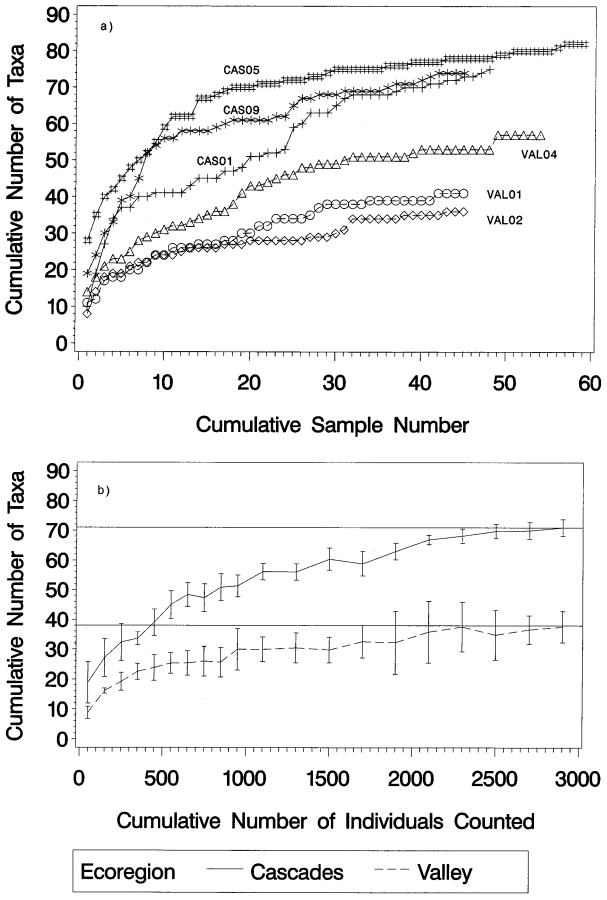

Fig. 4 a) Cumulative taxon curves developed by number of Surber samples for the six streams in which all samples were counted; CAS denotes mountain streams, VAL denote valley streams. b) Cumulative taxon curves for all nine Cascade streams (solid line) and all seven Valley streams (broken line). (Error bars are standard errors.)

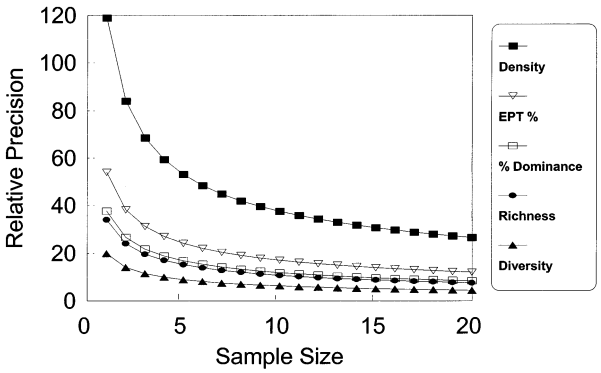

Fig. 5 Relative precision of five assemblage metrics, calculated as coefficients of variation.

Assemblage metrics varied in how they reflected within-stream variability (Fig. 5). Total density was the most variable metric; the coefficient of variation was greater than 50% with five samples, and only 40% after nine samples (Fig. 5). Other metrics demonstrated lower coefficients of variation, in part because their mathematical attributes varied less than raw abundance numbers. Taxon richness, percent EPT, percent dominance and Shannon diversity had coefficients of less than 25% within five samples (Fig. 5).

Discussion

The spatial organization of catchments, from basins to microhabitat, establishes the geomorphic and physical template for biological processes (Frissell *et al.*, 1986; Gregory *et al.*, 1991; Poff *et al.*, 1997). Biological interactions and movement patterns also con-

tribute to heterogeneity at multiple levels (May 1975; Crowl *et al*., 1997). To understand individual, population, community and metapopulation responses to the environmental template, surveys of stream invertebrates must take into account these multiple scales (Norris, 1995).

Our hierarchically designed study demonstrated that variability in assemblage metrics changes with spatial scale, with less metric variation attributable to smaller scales (Fig. 2). We saw differences between macroinvertebrate assemblages between streams, as well as between the Willamette and Cascade ecoregions, as reported by other investigators (Whittier *et al*., 1988; Barbour *et al*., 1992; Vinson & Hawkins, 1996). The proportion of EPT taxa, Shannon diversity, percent dominance and taxon accumulation curves were useful in discriminating, at landscape scales, between ecoregions. In the large spatial scope of our study, differences in richness measures varied between spatial scales; these differences were not detectable in an Australian study conducted at smaller scales (Downes, Lake and Schreiber, 1993). The contrasting metric responses in these very different ecosystems also highlight the importance of regionally specific patterns.

Whereas the River Continuum concept would suggest easily detectable differences as streams become larger (Vannote *et al*., 1980; Barbour *et al*., 1992), there was no variability in assemblage metrics that could be attributed to stream size (small and large wadeable streams) in our study. Measures sensitive to particular taxa, such as similarity indices or functional feeding groups, may be more sensitive to differences among streams of varying sizes. Wiley *et al*. (1997) observed species-specific differences in variance composition among fish and macroinvertebrates over long time and spatial intervals. In their study, disease and competition controlled site-specific variation among the caddisflies *Glossosoma nigrior* Banks and *Goera stylata* Ross, but regional climatic or hydrological variation seemed to influence *Baetis* more strongly. Variance in individual taxa rather than composite assemblage measures may be more useful in distinguishing differences within streams.

A notable observation was that every stream had a very large pool of taxa. New taxa were added to our cumulative list even after collecting over 50 Surber samples and counting thousands of individuals. These rare taxa contribute to within-stream variability, and taxon richness measures are very sensitive to sampling effort. The relationship between the number of taxa and area or individuals sampled is well known (Arrhenius, 1921; Preston, 1948; Hart & Horwitz, 1991; Douglas & Lake 1994). Taxon richness has been thought to reach a theoretical asymptote when 100–900 organisms were counted (May, 1975; Barbour & Gerritson, 1996; Vinson & Hawkins, 1996), but empirical evidence, particularly at small scales, indicates otherwise (Hart & Horwitz, 1991). Similarly, in our Cascade study streams cumulative taxon curves did not approach an asymptote until over 2000 individuals had been counted (Fig. 4b). Macroinvertebrates respond to multiple micro-habitat components such as food availability (Downes *et al*., 1993), wood (O'Connor, 1991) and stone (Downes & Lake, 1991; Hart & Horwitz, 1991; Douglas & Lake, 1994) substrates. As sampling size increased in our study, opportunity for including a greater diversity in stream habitats, and consequent variety in invertebrates, occurred.

The pattern of variability at multiple scales suggests that spatial variation must be considered at each level of study. As noted by Wiley *et al*. (1997), 'the variance structure of a population provides a framework for placing analyses into an appropriate context, and implies something about the relative importance of ecological processes at different spatial scales'. Recent studies demonstrate that the pattern of distribution (Collins & Glenn, 1997), riparian interactions (Johnson & Covich, 1997) and behaviour (Peckarsky *et al*., 1997) vary with spatial scale. In studies spanning spatial scales, sampling must be designed to detect these differences.

In our study within-stream variance structure suggests that there is relatively little local spatial pattern detectable using 0.093 m^2 sample units. Both location within a transect and longitudinal position accounted for little of the within-stream variance. Also, little of the within-reach variance was associated with differences between fast and slow water. The fine scale microhabitat variation may require sampling techniques that incorporate localized differences and analyses that focus on finer taxonomic resolution as discussed earlier. For discriminating patterns at larger scales, a random arrangement of samples within habitats of interest may be sufficient. Most gains in metric precision will come from increasing the number of samples taken, rather than from specific sample locations. For comparisons between streams, standardizing sample

effort (in areas or numbers of organisms counted) is also important (see Vinson & Hawkins, 1996).

The survey design used here illustrates a method for quantifying spatial variation, and the variance structure suggests ways of optimizing sampling effort. Assemblage metrics derived from samples collected across a wide scale can be useful in characterizing differences between ecoregions and streams. Both the number and appropriate distribution of samples will influence the precision by which invertebrate metrics in streams are estimated.

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