

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

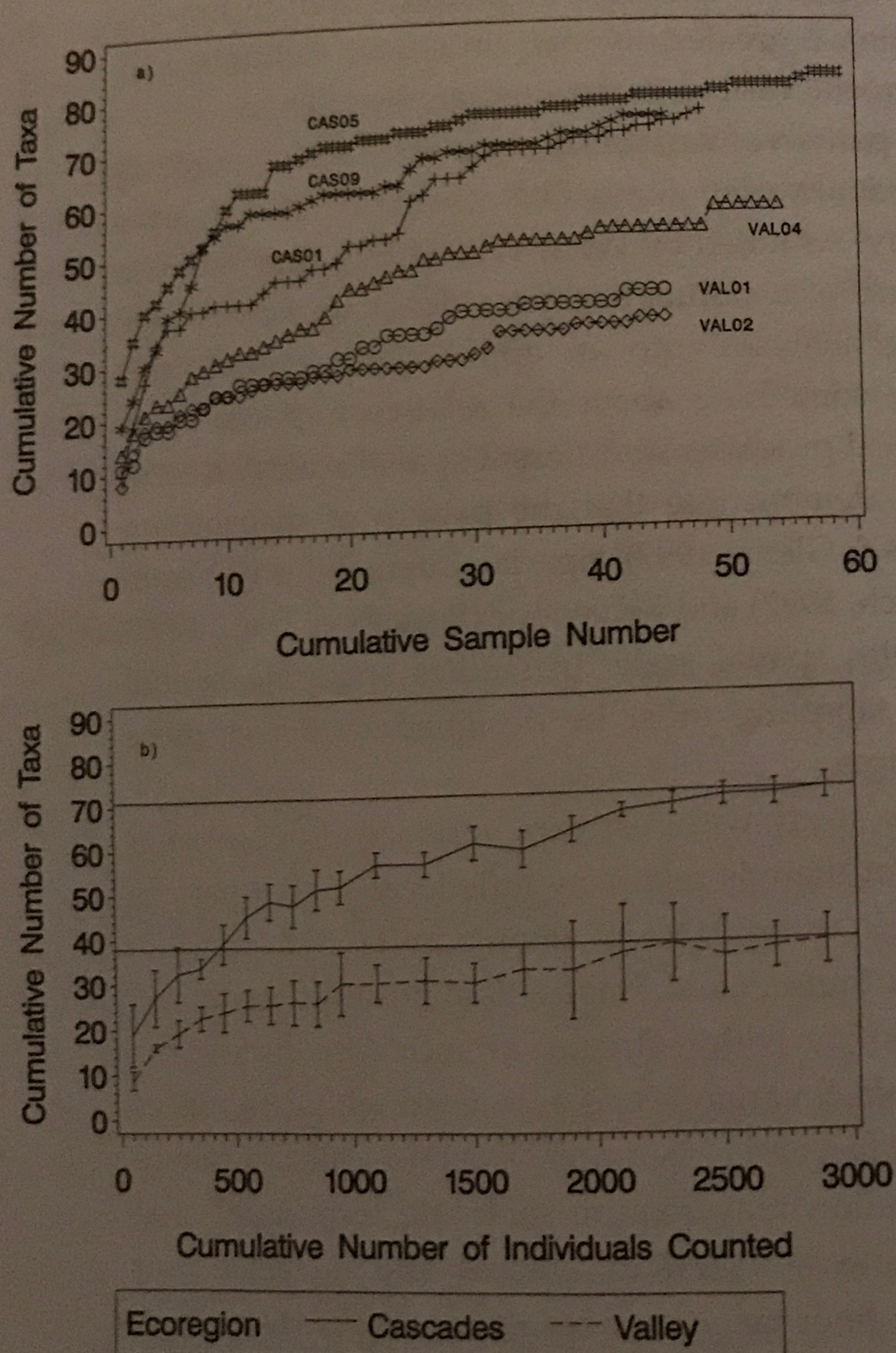


Fig. 4 a) Cumulative taxon curves developed by number of Surber samples for the six streams in which all samples were counted; CAS denotes mountain streams, VAL denote valley streams. b) Cumulative taxon curves for all nine Cascade streams (solid line) and all seven Valley streams (broken line). (Error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

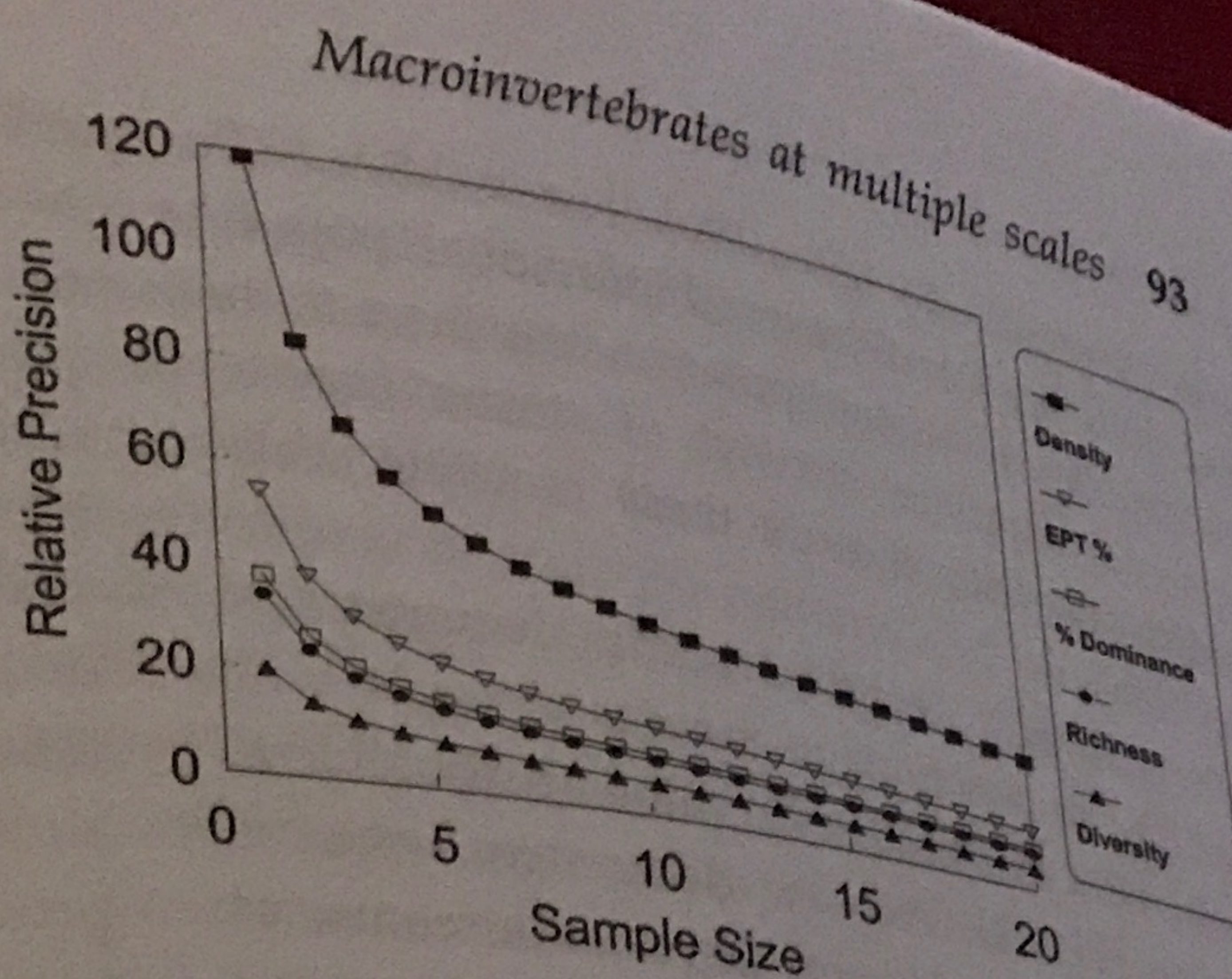


Fig. 5 Relative precision of five assemblage metrics, calculated as coefficients of variation.

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.

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 m² 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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