Correspondence between Stream Macroinvertebrate Assemblages and 4 Ecoregions of the Southeastern USA

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Abstract. Benthic invertebrates were quantified at summer baseflow from 30 streams draining largely forested watersheds within 7 river catchments (Coosa, Tallapoosa, Tennessee, Black Warrior, Conecuh, Altamaha, Chattahoochee) of 4 Level III ecoregions (Blue Ridge, Southwestern [SW] Appalachians, Piedmont, Southeastern [SE] Plains) of the southeastern USA. The study 1) compared invertebrate distributions classified by large-scale ecoregions against those of small-scale river catchments, and 2) assessed if taxonomic resolution of invertebrate identification (family vs genus/morphospecies) influenced relative classification strength of ecoregions and catchments. Principal components analysis indicated that environmental differences across catchments and ecoregions were associated more with variation in baseflow water chemistry (e.g., total alkalinity, conductivity) than with geomorphic or geographic variables. Using simple community presence/absence measures, richness of Ephemeroptera, Plecoptera, and Trichoptera (EPT richness) followed the pattern Blue Ridge > SW Appalachians = Piedmont = SE Plains. When grouped by catchment, total and EPT richness tended to be lower in lowland than in upland regions. However, Bray–Curtis presence/absence similarities coupled with flexible UPGMA (unweighted pair-group method using arithmetic averages) analyses revealed that invertebrate assemblages were distinctive among ecoregions both at the genus/ morphospecies and family levels. Differences in overall similarity among ecoregions were highly significant, with upland Blue Ridge and lowland SE Plains streams displaying the lowest interecoregional similarity, and Piedmont and SW Appalachians streams displaying the highest similarity. Faunal similarity within a given ecoregion approximated that observed within individual catchments. Family-level groupings were almost as robust at discriminating catchments and ecoregions as were classifications derived from genus/morphospecies. The ecoregion concept appears to be as useful a classification scheme as that derived from smaller river catchments in the delineation of stream invertebrate distributions in the southeastern USA.

Key words: ecoregion, classification, aquatic insects, community, benthic invertebrates, lotic, riffles, streams, southeastern USA.

The ecoregion concept hypothesizes that contiguous land forms with similar geology, soils, vegetative cover, and climate also are likely to possess similar communities (Omernik 1987, Omernik and Griffith 1991). The underlying tenets of this concept are that 1) natural variation is predictable among systems within the same geographic region where environmental features are similar, and 2) by stratifying natural variation into spatially explicit, homogenous ecoregions, one can detect responses to disturbance at 1 site by comparing it to a reference site in the same ecoregion (Hughes and Larsen 1988, Hughes 1989, Omernik and Bailey 1997). The use of ecoregions as a geographic framework on which to base catchment management is intuitively appealing because this approach can reduce the inefficiency of sampling a mul-

titude of sites to determine background physico-chemical and biological conditions, and by stratifying sites according to similar ecological conditions one can theoretically reduce extrapolation errors (Warry and Hanau 1993).

Stream ecosystems of the southeastern USA drain a diverse array of land forms encompassing several physiographic provinces (Swift et al. 1986, Isphording and Fitzpatrick 1992). This geologically heterogeneous region spans a wide range of physical and chemical conditions that provide habitat for a diverse array of species, particularly benthic invertebrates (reviewed by Hackney et al. 1992). Several topographically distinct river systems occur within this landscape that, because of their latitudinal position, have received minimal natural biological extinctions (e.g., from Pleistocene glaciation, Smith 1981). Individual river catchments have long been recognized as fundamental biogeographi-

cal units for many aquatic assemblages (Hocutt and Wiley 1986, Corkum 1989, 1990, Vinson and Hawkins 1998). Their tributaries share many species often because of similar habitat conditions, flow regimes, species dispersal, and extinction patterns (Smith 1981, Wohl et al. 1995). Thus, because of its high physical heterogeneity and biological diversity coupled with stable biogeography, the southeastern region provides an excellent landscape in which to assess the utility of ecoregions to explain diversity of stream fauna, in the context of comparing patterns within ecoregions to those of catchments. Such broad-scale assessments are especially important because so far only a handful of empirical studies from North America have explicitly examined the utility and accuracy of the ecoregion concept to account for biotic variation (e.g., Whittier et al. 1988, Lyons 1989, Hughes et al. 1990, Tate and Heiny 1995, Barbour et al. 1996, this series).

A critical factor affecting the strength of associations between ecoregions or catchments and their biota is the level of taxonomic resolution applied to the sampled organisms (i.e., "taxonomic sufficiency," sensu Ellis 1985). Two opposing schools of thought exist on this issue. The 1st argues that only the lowest taxonomic level (i.e., species) can reveal matches between biotic assemblages and environment (Resh and Unzicker 1975). Alternatively, the 2nd suggests that simple, and less expensive, identification to higher taxonomic levels such as family or order often is adequate for revealing important natural or human-influenced differences among sites (Furse et al. 1984, Warwick 1993). Despite the numerous freshwater benthological studies that pervade the literature (e.g., references in Merritt and Cummins 1996), surprisingly few of them have empirically examined the influence of taxonomic level in the context of assessing the sensitivity of ecoregions to account for patterns in aquatic biota.

The purpose of my study was to compare the degree to which distribution patterns of stream invertebrates within the southeastern USA classified by large-scale ecoregions compared with classifications by catchments at smaller spatial scales. As a secondary objective, I examined the effects of taxonomic level (i.e., family vs genus/morphospecies) on the patterns produced using ecoregion- and catchment-level classifications.

Methods

Ecoregions and study streams

I present data for streams from the following 4 southeastern ecoregions: Blue Ridge, Southwestern (SW) Appalachians, Piedmont, and Southeastern (SE) Plains [= Coastal Plains], Fig. 1). I used the ecoregion delineation scheme of Omernik (1987) except for the SE Plains in which I considered the Piedmont subregion as a separate ecoregion for 2 reasons. First, there has been a long history of separation of land forms in this physiographic province from those of adjacent SE Plains land forms (Fenneman 1938) because of the Fall Line, a sharp geomorphic boundary separating the Lower Piedmont from the Upper Coastal Plain (Harper 1943, Murray 1961). This division is generally considered a barrier to the dispersal of many vertebrate species (Mount 1975, see also Isphording and Fitzpatrick 1992, Mettee et al. 1996), which also may apply to stream invertebrate assemblages. Second, the US Environmental Protection Agency and state agencies (e.g., Alabama Department of Environmental Management, Mississippi Office of Pollution Control) are continuing to refine the boundaries of southeastern ecoregions. In particular, efforts are underway to examine efficacy of subdividing the heterogenous SE Plains ecoregion into smaller subunits (i.e., Level III ecoregions, Omernik and Griffith 1991) based on their geomorphic and ecological dissimilarities. Therefore, Piedmont streams were considered separately from others in the SE Plains to evaluate this revised classification.

I included 30 small- to moderate-order streams occurring in 7 different catchments in the study (Fig. 1, Table 1). This modest number of sites, compared with other similar studies (e.g., the '100 rivers study' of Biggs et al. 1990; see also Hughes et al. 1990, Harding et al. 1997, this series), and the large range of stream sizes (e.g., order, catchment area, discharge) facilitated a highly conservative comparison of benthic assemblages classified by catchment vs ecoregion, and thus a conservative assessment of the usefulness of southeastern ecoregions to predict benthic distributions. Streams were chosen to represent environmental conditions most likely to result from natural, rather than human, influences (i.e., reference conditions). In the SE Plains
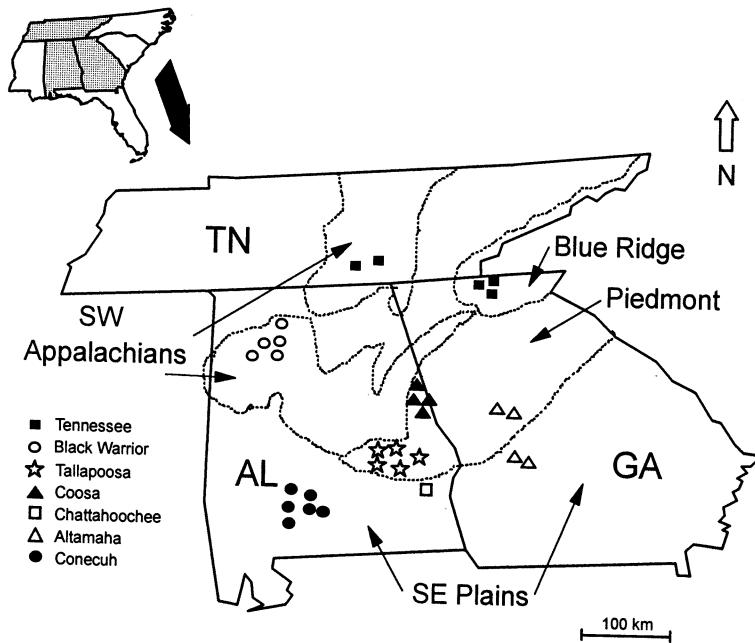
FIG. 1. Approximate locations of the 30 study streams (symbols), within the 7 catchments and 4 southeastern ecoregions (dashed areas shown by arrows) within Alabama (AL), Georgia (GA), and Tennessee (TN), USA. Geographic coordinates of streams are given in Table 1. SW = Southwestern, SE = Southeastern.

ecoregion in particular, undisturbed catchments are rare and many are likely to reflect some perturbations, so characteristics of streams in this ecoregion overall are more likely to have been affected by land use than those in the other 3 ecoregions. However, the sampling area of each stream had intact riparian zones, as indicated by high % summer shade (72–98%, see Appendix) and relatively stable channels, with no obvious local sources of impairment. Blue Ridge, SW Appalachians, and Piedmont streams drained largely forested catchments; many streams within these 3 ecoregions were located within US National Forest (NF) boundaries (i.e., Blue Ridge: Chattahootchee NF; SW Appalachians: Bankhead NF; Piedmont: Oconee, Talladega, and Tuskegee NFs). In contrast, SE Plains sites also were forested but some had considerable agricultural development, with up to 38% of the total catchment upstream in agriculture (Hamilton 1998).

Stream sampling

Physico-chemical variables.—I measured the following physical and chemical variables at each site: order, catchment area, channel gradient, and elevation at sampling point (derived from 7.5′ topographic maps of the US Geological Survey); average instream shade (spherical densiometer, see Lemmon 1957, Feminella et al. 1989); average channel width, stream depth, and substrate composition; current velocity and discharge (Marsh–McBirney Model 2000); total alkalinity, total hardness, and Mg^+, Ca^+, and Si^+ concentrations (LaMotte water chemistry kits); specific conductance (YSI Model 33); pH (standardized with buffers at pH 4.00 and 7.00, Beckman Model ϕ-10); and dissolved oxygen (YSI Model 55) at the point of sampling.

I used principal components analysis (PCA, PROC PRINCOMP, SAS STAT User's Guide, release 6.03 edition, SAS Institute, Cary, North Carolina) on standardized variables (i.e., having means of 0), to examine variation in environmental conditions across individual streams, catchments, and ecoregions. This procedure reduces the full suite of environmental variables to a smaller set of derived, orthogonal factors (principal components, see Ludwig and Reynolds 1988).

Biotic variables.—Benthic invertebrates were sampled from fast-water habitat units in each

TABLE 1. Locations of study sites. Streams with designations Q, C, or S are unnamed.

Ecoregion	Catchment	Stream (geographic coordinates)	Abbreviation
Blue Ridge	Tennessee	Turkey Creek (lat 34°44′N, long 84°02′W)	TUR
		Little Rock Creek (34°43′N, 84°06′W)	LRC
		Etowah River (34°37′N, 84°06′W)	ETO
Southwestern Appalachians	Tennessee	Chisolm Creek (35°14′N, 87°34′W)	CHS
		Factory Creek (35°22′N, 87°37′W)	FAC
	Black Warrior	Borden Creek (34°20′N, 84°22′W)	BOR
		Brushy Creek (34°20′N, 87°17′W)	BRU
		Capsey Creek (34°16′N, 87°22′W)	CAP
		Thompson Creek (34°21′N, 87°28′W)	THO
		Hubbard Creek (34°18′N, 87°30′W)	HUB
Piedmont	Coosa	C-1 (33°46′N, 85°36′W)	C-1
		C-3 (33°46′N, 85°33′W)	C-3
		Q-1 (33°47′N, 85°34′W)	Q-1
		Q-2 (33°47′N, 85°35′W)	Q-2
	Tallapoosa	Buck Creek (32°42′N, 85°52′W)	BUC
		Choctafaula Creek (32°31′N, 85°35′W)	CHO
		Ledbetter Creek (32°38′N, 85°48′W)	LED
		Mitchell Creek (32°38′N, 85°46′W)	MIT
		Sycamore Creek (32°38′N, 85°44′W)	SYC
	Chattahoochee	Uchee Creek (32°24′N, 85°22′W)	UCH
	Altamaha	Kinnard Creek (33°16′N, 83°48′W)	KIN
		Rock Creek (33°12′N, 83°30′W)	ROC
Southeastern Plains	Altamaha	Tobler Creek (32°58′N, 83°47′W)	TOB
		Hurricane Creek (33°20′N, 83°42′W)	HUR
	Conecuh	Panther Creek (31°43′N, 86°48′W)	PAN
		Long Creek (31°40′N, 86°50′W)	LON
		S-40 (31°32′N, 86°45′W)	S40
		S-41 (31°30′N, 86°46′W)	S41
		Mill Creek (31°30′N, 86°41′W)	MIL
		Redick's Creek (31°48′N, 86°42′W)	RED

stream (riffles or runs, sensu Hawkins et al. 1993), distributed over a 0.2 to 1 km reach. When both types of units were available riffles always were preferred, but in some streams (i.e., most tributaries of the Conecuh River, SE Plains), riffles were absent and runs were sampled instead. Fast-water habitats typically possess the highest species richness, abundance, and biomass of stream invertebrates (Hynes 1970, Allan 1995). Thus, concentration of sampling within these areas was likely to detect most of the species present in the streams, or at least provide a relative comparison of assemblages among ecoregions and catchments within this important microhabitat.

I sampled each stream once during the summer baseflow period (August–October, from 1992 through 1997). Invertebrates were collected from 24 of the 30 streams with a Surber sampler (mesh size 250 μm, 0.093 m²), pooling 4 to 6

samples from each of 5 riffles or runs per stream (total area sampled: 1.9–2.8 m²/stream). I used only 4 quadrats/riffle in C and Q streams (Piedmont) because of the small size of their habitat units (see Appendix). However, because of the small channel size this reduced area sampled an equal or proportionally greater area per habitat unit (>50% of riffle) in these streams than was sampled in larger streams with 6 quadrats/riffle. Six of the 30 streams (i.e., S-40, S-41, Redick's, Long, Mill, and Panther Creeks; SE Plains ecoregion) contained extensive coarse woody debris that prohibited conventional Surber sampling, so I used a combination of semi-quantitative (i.e., 3-min dipnet sampling or sweeps of submerged wood and inorganic substrates, Lenat 1998) and quantitative methods (i.e., Hester–Dendy multiplates, Merritt et al. 1996; area of each multiplate = 1 Surber quadrat), and I combined these to measure benthic

composition. I attempted to sample an area approximately similar to that of streams sampled only with Surbers (i.e., total area sampled ~2.4 m²/stream) to reduce the likelihood of species–area bias (Douglas and Lake 1994, Vinson and Hawkins 1996) with the combined methods. All sweep and Surber samples were taken >3 d after major storm events (i.e., >2.5 cm rain in 24 h) to minimize hydrologic disturbance and to allow streams to return to baseflow conditions. Samples were preserved in 95% ethanol.

I used a 2-step sorting method in the laboratory. First, samples were examined macroscopically for 30 min to remove large or rare invertebrates. Second, smaller organisms were subsampled microscopically from the entire sample fraction using volumetric aliquots (see Feminella 1996 for method), from which at least 200 specimens were removed. Invertebrates were then identified and counted, and their numbers were extrapolated to estimate the total number of individuals contained in the sample fraction. The total number of invertebrates contained in the combined macroscopic and microscopic fractions was typically >300, which should have composed a subsample large enough to reduce the likelihood of artificially underestimating richness or presence/absence (see Vinson and Hawkins 1996, Larsen and Herlihy 1998). Invertebrates were identified to genus, species, or morphospecies (hereafter collectively called *morphospecies,* sensu Mayr 1969, see also Oliver and Beattie 1996). Species-level identification was not possible for most invertebrates because specimens usually were immatures (nymphs or larvae), which were unidentifiable to species given current taxonomy (Thorp and Covich 1991, Merritt and Cummins 1996).

Assessment of pattern in invertebrate assemblages

I used presence/absence data from each stream to describe invertebrate assemblage structure. Although presence/absence alone is a highly conservative measure of difference among communities (versus abundance-based indices, e.g., Shannon's *H'*), it is without question the simplest and most widely used metric for communities. It also discriminates well among sites (Magurran 1988) as long as the sampling effort is adequate to include most species and the effects of rare taxa are minimized (van Tongeren 1987). I measured the degree of faunal similarity among streams with the Bray–Curtis (1957) dissimilarity metric (Jongman et al. 1987, Ludwig and Reynolds 1988) as applied to binary data (i.e., Czekanowski measure; Southwood 1978, Romesburg 1984).

The flexible unweighted pair-group method using arithmetic averages (UPGMA, Sokal and Michener 1958) was used on Bray–Curtis (BC) distance matrices to produce dendrograms describing clusters of sites. I then used MEANSIM (Version 6, Van Sickle 1997) to calculate a measure of classification strength (M), defined as the ratio of the mean between-class similarity ($\bar{B}$) to the overall mean within-class similarity ($\bar{W}$). Values of $M \ll 1$ indicate strong classifications (i.e., large differences between groups) and values close to 1 indicate relatively weak classifications. MEANSIM also determines if classifications are statistically different than expected from a random placement of sites into classes, by calculating M based on 10,000 randomly sampled permutations, and then comparing what proportion of permuted classifications had values of $M <$ the observed M (Van Sickle 1997). I excluded all taxa present in <5% of the streams from the analysis to reduce the influence of rare taxa on UPGMA groupings. Arbitrary exclusion of rare species in classification analyses has been criticized because it can artificially downplay important natural differences in assemblage structure among sites. This artifact is particularly likely when disturbed sites with lower proportions of rare species are compared with undisturbed sites where higher proportions of rare species often occur (Cao et al. 1998). In my study, however, because most sites were considered relatively undisturbed (and hence with low likelihood of being affected by rare species bias), they were each deemed to possess some level of rare taxa that could contribute statistical noise to the classification. Therefore, I elected to remove the lowest level of rarity (i.e., excluded those cases where single streams had unique taxa) to reduce this potential bias.

I used faunal similarity patterns in streams within the same catchment (e.g., several streams within the Tennessee River catchment, streams within the Conecuh River catchment, etc.) as a basis for assessing the utility of ecoregions to classify assemblage structure. Comparison of ecoregion- and catchment-based classifications of benthic invertebrates allowed me to test the
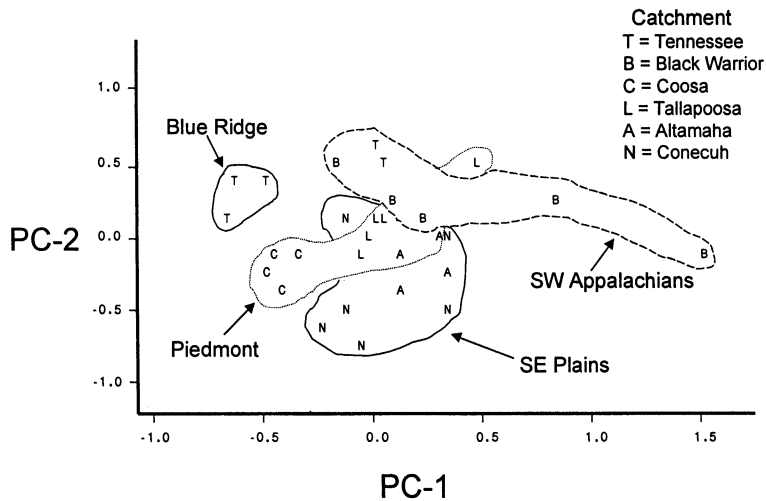
FIG. 2.   Principal components analysis (PCA) ordination of physico-chemical variables measured from the 30 southeastern streams used in this study. PC-1 was largely associated with water chemical variables (conductivity, hardness, alkalinity, pH), whereas PC-2 was largely associated with % dissolved oxygen saturation at baseflow and several physical variables (median substrate size, current velocity, discharge, stream order, % of sand in substrate). PC-1 and PC-2 together accounted for 51% of the total variation. SW = Southwestern, SE = Southeastern.

hypothesis that invertebrate assemblages in streams within 1 ecoregion are more similar than those of streams among ecoregions, irrespective of the sizes of the streams or river catchment being considered.

Assessment of taxonomic level of resolution

It is possible that different levels of taxonomic resolution applied within the ecoregion classification will produce strongly contrasting results, and thus limit the use of the classification. To examine this possibility, I 1st ran UPGMA and MEANSIM analyses on the lowest taxonomic level (morphospecies). I then reduced the benthic data to the family level or higher for many noninsect groups (i.e., decreasing number of objects and hence potentially reducing classification accuracy), and then re-ran the cluster and mean similarity analyses. I tested the hypothesis that the lower the taxonomic level of identification the greater the ability to discriminate among streams from different ecoregions or catchments.

Assessment of year-to-year variation

Benthic data were compiled for streams sampled on only 1 date, and streams and catch-

ments/ecoregions often were sampled in different years (Appendix). Therefore, patterns in baseflow assemblage structure among streams may have been subject to high year-to-year variation (Feminella 1996, Bailey et al. 1998) that could potentially compromise classifications between catchments and ecoregions (but see Barbour et al. 1996). It was beyond the scope of this study to evaluate temporal variation for all streams and ecoregions over the study period (1992–1997). However, in a subset of streams (Brushy, Borden, Capsey, Thompson Creeks) from 1 catchment and ecoregion (Black Warrior, SW Appalachians, respectively) I quantified year-to-year variation in several biotic features (i.e., total Ephemeroptera, Plecoptera, and Trichoptera [EPT] taxa per riffle, total taxa per riffle, Shannon's H', density) by sampling these streams annually over a 4- to 5-y period (i.e., Brushy, Borden, Capsey Creeks from 1992–1996; Thompson Creek from 1993–1996). I then directly assessed temporal variation in biotic measures by computing the coefficients of variation (CV, %), and comparing average CV between 1) single streams sampled over several years and 2) multiple streams sampled during the same year (1993). If year-to-year variation within a single stream was high, I predicted that be-

tween-year CV of a given stream would approach or exceed between-stream CV of a given year.

Results

Environmental conditions

PCA of the environmental variables measured from the 30 streams revealed that 3 main factors (PC-1, PC-2, PC-3) accounted for most (66%) of the variation in the data set. PC-1 (32% of total variation) consisted mostly of water chemical variables (i.e., high positive loadings by total hardness, total alkalinity, Mg^+, and conductivity). PC-2 (19% of total) consisted mostly of physical variables (i.e., high positive loadings by median substrate size, current velocity, discharge, and stream order; negative loading by % sand in substrate). PC-3 (15% of total) contained a combination of physical and chemical variables (i.e., high negative loadings by average stream depth and % sand; positive loadings by Si^+ concentration and dissolved oxygen saturation). Physical variables associated with catchment size (e.g., order, area, stream width) were much less important contributors to the ordination (i.e., loaded on PC-2 or lower) than chemical variables, despite the large range of sizes of streams (Appendix). Neither of the variables associated with geographic position (i.e., gradient, elevation) contributed much to the first 3 principal components.

Ordinations showing the relationships of the 30 streams and catchments plotted on the first 2 principal components (51% of the total variation) revealed that streams in only 1 ecoregion (Blue Ridge, Tennessee River catchment) were closely associated in PC space and were well segregated from the other 3 ecoregions (Fig. 2). In contrast, Piedmont, SW Appalachians, and SE Plains streams showed considerable overlap, particularly in terms of Piedmont streams overlapping both SW Appalachians and SE Plains; the latter 2 ecoregions were more segregated from each other. Streams within the Blue Ridge, Piedmont, and SW Appalachian ecoregions largely differed only in variables described by PC-1 (i.e., water chemistry), whereas streams within the SE Plains differed almost equally between PC-1 and PC-2 (physical and chemical variables, Fig. 2). When examined by catchment, the Coosa River streams were reasonably seg-

TABLE 2. Average number of invertebrate taxa collected per stream. Other = rare taxa within the Tricladida, Nematoda, Decapoda, Isopoda, Oligochaeta, Hirudinea, and Hydracarina. Uncorrected total = the total number of taxa collected in each ecoregion, not accounting for differences in sampling effort (i.e., number of streams sampled/ecoregion). The numbers of streams are in parentheses. SW = Southwestern, SE = Southeastern.

	Ecoregion			
Taxon	Blue Ridge (3)	SW Appalachians (7)	Piedmont (12)	SE Plains (8)
Ephemeroptera	5.3	3.0	1.6	1.8
Odonata	0.7	0.7	0.3	0.9
Plecoptera	2.3	0.7	0.7	0.5
Trichoptera	4.0	1.4	1.3	1.0
Diptera	7.3	4.4	3.1	4.9
Megaloptera	0	0.3	0.3	0.4
Coleoptera	2.0	1.4	1.0	1.3
Mollusca	0	0.6	0.4	1.1
Other	4.3	1.9	1.1	0.6
Uncorrected total	78	101	117	99

regated from all other catchments, and Tennessee River streams were segregated from Coosa, Tallapoosa, Altamaha, and Conecuh River catchments; streams in the Black Warrior, Tallapoosa, Altamaha, and Conecuh River catchments showed reasonably high overlap in PC-1 and PC-2 (Fig. 2).

Benthic invertebrate assemblages

Faunal composition.—A total of 158 invertebrate taxa in 71 families was quantified, excluding rare species that were found in only 1 of the 30 streams (28 taxa). Most taxa were aquatic insects (~85% of total richness); the remaining taxa were crustaceans, aquatic mites, oligochaetes, bivalves, gastropods, nematodes, and flatworms.

On average, Blue Ridge streams had higher numbers of EPT taxa than streams in other ecoregions (Table 2). This pattern also held when data were expressed as total EPT richness per stream ($F = 4.64$, $p = 0.01$, Fig. 3A); in contrast, average total richness per stream did not differ among ecoregions ($F = 1.03$, $p = 0.397$). There was a trend toward decreased mollusc
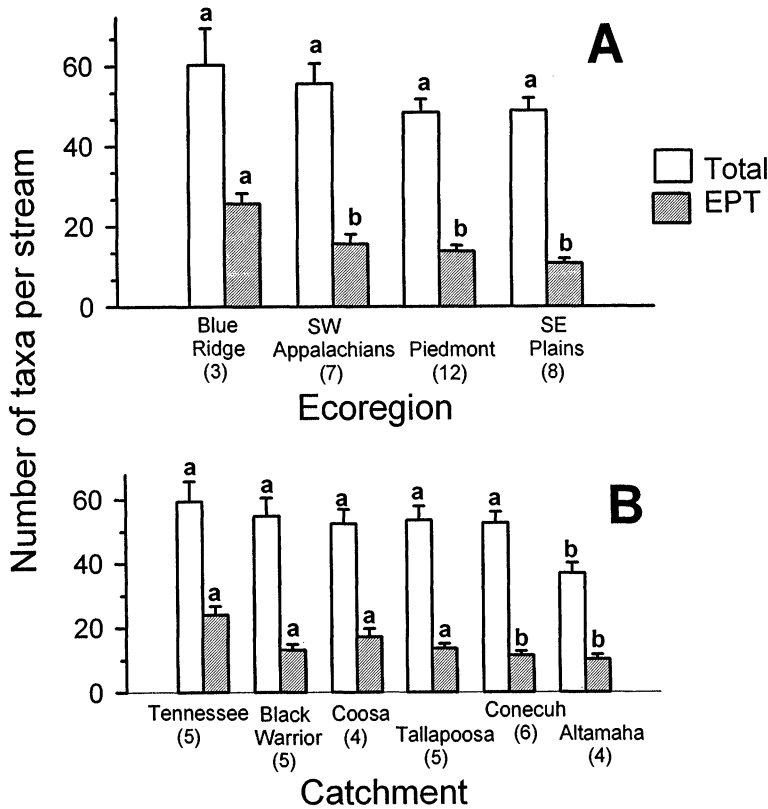
FIG. 3. Average invertebrate richness per stream ($\bar{x}$ + 1 SE) across (A) 4 southeastern ecoregions and (B) 6 southeastern catchments, as the total number of invertebrate taxa and total number of Ephemeroptera, Plecoptera, and Trichoptera (EPT) taxa. Values in parentheses under catchment and ecoregion names are the number of streams included. Uchee Creek (single stream studied from the Chattahoochee catchment) was omitted from B. Values sharing the same lower case letter (above bars) were not significantly different at α = 0.05.
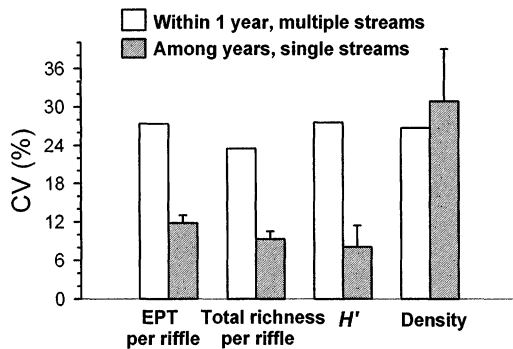

FIG. 4. Within- versus among-year variation (coefficient of variation [CV, %], $\bar{x}$ + 1 SE) in several benthic invertebrate measures, observed for 4 streams (Brushy, Borden, Capsey, and Thompson Creeks) from the Black Warrior River catchment, Southwestern Appalachians ecoregion. H' = Shannon's diversity.

and megalopteran richness from the SE Plains streams to the Blue Ridge (Table 2), although it involved fewer taxa. The Altamaha catchment streams had lower total richness than streams in all other catchments (F = 3.24, p = 0.019, Fig. 3B); Altamaha and Conecuh streams had lower average numbers of EPT taxa than streams in the other catchments (F = 6.37, p = 0.0005).

Year-to-year variation.—The magnitude of annual variation within a single stream depended upon the biotic measure used. Average annual variation in invertebrate density was as high between years for single streams as it was among streams sampled in the same year (CV $\approx$30%, Fig. 4). However, average year-to-year variation in total and EPT richness per riffle and diversity (Shannon's H') for single streams (between 8 and 11%, depending on measure) was considerably lower than variation among streams in
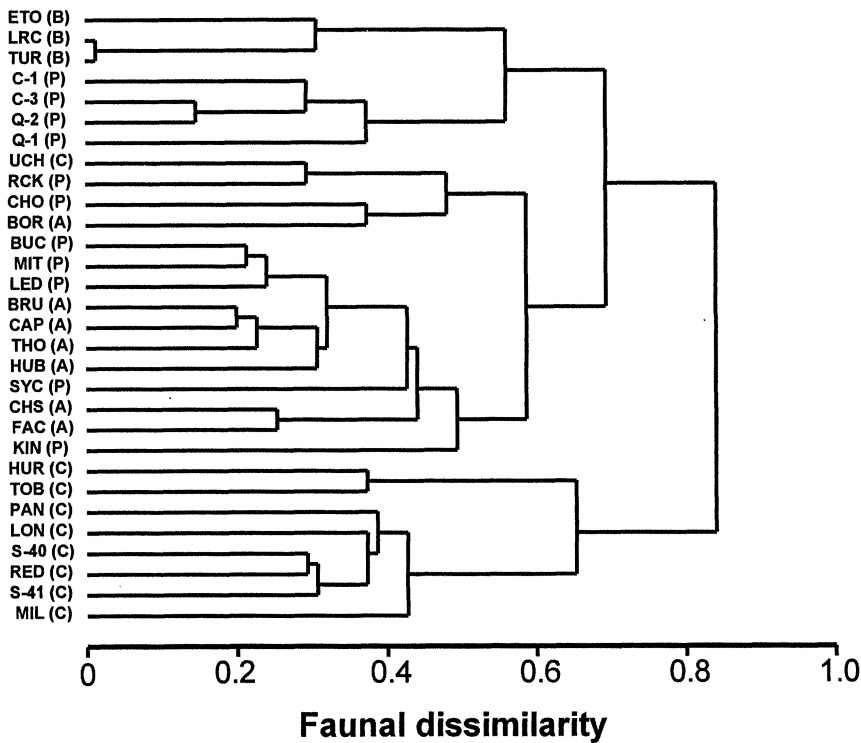
FIG. 5. Flexible unweighted pair-group method using arithmetic averages (UPGMA) dendrogram using Bray–Curtis dissimilarities, for invertebrate morphospecies (i.e., 1.0 = maximum dissimilarity between clusters). See Table 1 for stream abbreviations. Letters in parentheses designate ecoregion (i.e., B = Blue Ridge, A = Southwestern Appalachians, P = Piedmont, C = Southeastern [Coastal] Plains).

the same year (>23%, Fig. 4). Relatively low among-year variation for single streams suggests that year-to-year differences in invertebrate assemblages were minimal for richness. Therefore, my characterization of richness-based assemblage structure from a single sampling of invertebrates during summer baseflow, and the use of invertebrate presence/absence data appeared to be robust enough to describe real differences in faunal composition among streams (see also Hawkins et al. 2000).

Assemblage structure based on morphospecies

Ecoregion.—Bray–Curtis distances for invertebrate morphospecies revealed that some ecoregions were clearly distinct from others (Fig. 5). For example, all streams in the SE Plains except Uchee Creek clustered together and were most dissimilar from streams in the other 3 ecoregions (0.85 dissimilarity level). Piedmont and SW Appalachian streams clustered together with no clear ecore-

gional separation. However, all streams in the SW Appalachians except Borden Creek grouped together close to the 0.60 dissimilarity level. The 11 most similar clusters in the dendrogram (2 or 3 streams/cluster) always contained streams in the same ecoregion (Fig. 5).

The matrix of mean similarities also revealed that streams in the same ecoregion usually (except the SW Appalachians–Piedmont contrast) were more similar to each other than were streams in different ecoregions (Table 3A). Within-class similarity decreased across ecoregions in the order Blue Ridge > SW Appalachians > SE Plains > Piedmont. Of the 4 ecoregions, Blue Ridge and SE Plains streams were the least similar to each other (average BC value = 0.304), and Piedmont and SW Appalachians were the most similar (BC = 0.558, Table 3A). Differences in overall mean similarity among ecoregions were highly significant ($M = 0.782$, $p < 0.0001$).

Catchment.—Morphospecies associations by river catchment paralleled those of ecoregions:

TABLE 3. Matrix of average Bray–Curtis similarities for invertebrate morphospecies (158 taxa), listed by ecoregions (A) and catchments (B) in which 29 of the 30 southeastern streams were located. Uchee Creek (single stream studied from the Chattahoochee catchment) was excluded from B. The numbers of streams are in parentheses. SW = Southwestern, SE = Southeastern.

	Blue Ridge (3)	SE Plains (8)	Piedmont (12)	SW Appalachians (7)
A. Ecoregion				
Blue Ridge	0.742	0.304	0.439	0.469
SE Plains		0.549	0.410	0.430
Piedmont			0.529	0.558
SW Appalachians				0.623

	Tennessee (5)	Altamaha (4)	Conecuh (6)	Coosa (4)	Tallapoosa (5)	Black Warrior (5)
B. Catchment						
Tennessee	0.589	0.410	0.338	0.491	0.500	0.504
Altamaha		0.514	0.413	0.416	0.507	0.532
Conecuh			0.624	0.361	0.428	0.433
Coosa				0.549	0.493	0.499
Tallapoosa					0.580	0.607
Black Warrior						0.588

streams within the same catchment usually showed higher average similarities than did streams in different catchments (i.e., compare the 6 intracatchment BC values to intercatchment values in Table 3B). Differences in mean similarity among catchments were highly significant ($M = 0.793$, $p < 0.0001$). The upland Tennessee River and the lowland Conecuh River catchments were the most dissimilar (average BC similarity = 0.338, Table 3B), whereas the upland Black Warrior River and upland Tallapoosa River catchments were the most similar (average BC = 0.607). Faunal similarity between catchments was higher than that observed within catchments in only 2 of 15 cases (i.e., Black Warrior–Altamaha and Black Warrior–Tallapoosa contrasts > all intracatchment BC values, Table 3B).

Assemblage structure based on families

Ecoregion.—Patterns for invertebrates identified to the family level or higher (i.e., 71 taxa, reduced from 158) generally were consistent with those observed for morphospecies. Sites in the SE Plains still clustered together and were most dissimilar from other ecoregions, but at this taxonomic level Uchee and Hurricane Creeks were excluded from the group (Fig. 6). Streams in Piedmont and SW Appalachians

ecoregions remained intermixed in the dendrogram, yet all but 1 of the SW Appalachian sites (again Borden Creek) remained closely clustered. Also like morphospecies, the 11 most similar clusters (2 to 4 streams/cluster) always contained streams in the same ecoregion (Fig. 6). Overall faunal similarity among sites increased when this more conservative taxonomic classification scheme (vs morphospecies) was used, as indicated by the smaller range of dissimilarity values in Fig. 6 than Fig. 5. Differences in mean similarity among ecoregions were highly significant ($M = 0.873$, $p < 0.0001$).

Average faunal similarities within ecoregions at the family level displayed a slightly different pattern than that observed for morphospecies, with Blue Ridge streams showing the highest within-class similarity and SE Plains streams the lowest; SW Appalachians and Piedmont showed intermediate within-class similarities (Table 4A). There were 2 cases where average interecoregional similarity exceeded intraecoregional similarity (i.e., SW Appalachians–Piedmont and SW Appalachians–Blue Ridge contrasts > all intraecoregional BC values, Table 4A), whereas for morphospecies this situation occurred in only 1 case (SW Appalachians–Piedmont, Table 3A).
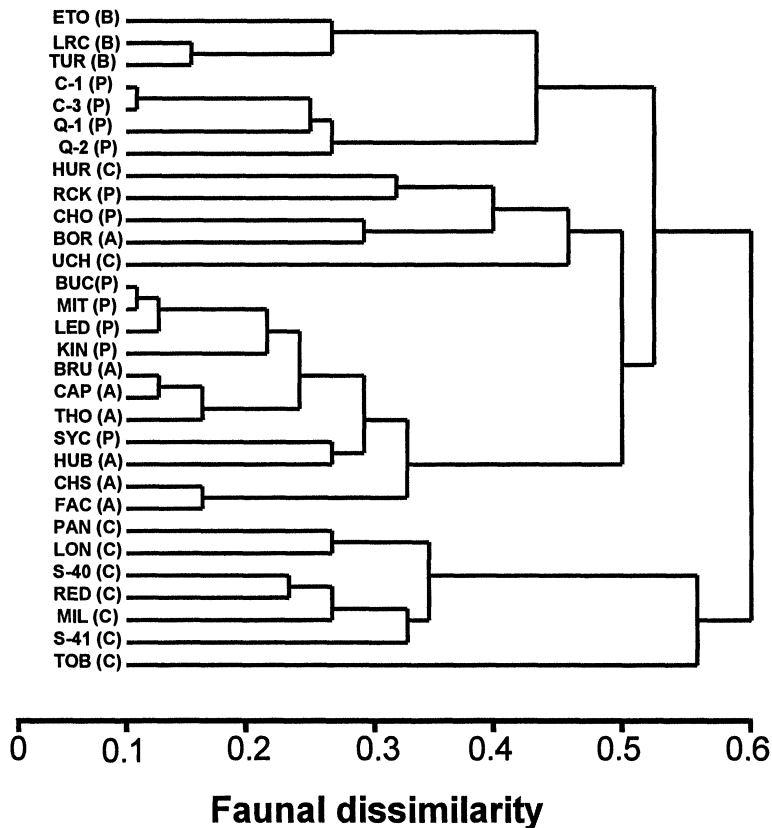
FIG. 6. Flexible unweighted pair-group method using arithmetic averages (UPGMA) dendrogram using Bray–Curtis dissimilarities, for invertebrate families or other higher taxonomic levels (i.e., 1.0 = maximum dissimilarity between clusters). See Table 1 for stream abbreviations. Letters in parentheses designate ecoregion (i.e., B = Blue Ridge, A = Southwestern Appalachians, P = Piedmont, C = Southeastern [Coastal] Plains).

Catchment.—Use of family-level identification revealed that streams within the same river catchment were among the most similar, as with morphospecies (Table 4B). However, there were more exceptions to this pattern (i.e., intercatchment BC similarity > all intracatchment BC values in 5 of 15 cases, Table 4B). The highest intercatchment similarity occurred between the Black Warrior and Tallapoosa River (average BC value = 0.697). As with all previous morphospecies or ecoregions contrasts, differences in mean similarity of families among catchments were highly significant ($M = 0.875, p < 0.0001$).

Discussion

Efficacy of southeastern ecoregions

My study showed that the 4 southeastern ecoregions examined could be delineated on the

basis of the stream invertebrate assemblages they contain. This finding supports the hypothesis that ecoregions represent a useful framework with which to characterize natural variation in aquatic biota (Hughes and Larsen 1988). The concordant patterns shown by biota from most streams within an ecoregion were particularly compelling because only a small number of streams ($n = 3$–12) were sampled from each ecoregion, streams were sampled in only 1 season, and only 1 habitat type was surveyed and included in the analysis. Biotic resolution among ecoregions might become even more pronounced if sampling included more habitats, such as within pools, or over a more extended period, such as in different seasons or years.

It is tempting to suggest that many of the study streams could legitimately serve as reference sites against which putatively impaired

TABLE 4. Matrix of average Bray–Curtis similarities for invertebrate families or other higher taxonomic levels (71 taxa), listed by ecoregions (A) and catchments (B) in which 29 of the 30 southeastern streams were located. Uchee Creek (single stream studied from the Chattahoochee catchment) was excluded from B. The numbers of streams are in parentheses. SW = Southwestern, SE = Southeastern.

	Blue Ridge (3)	SE Plains (8)	Piedmont (12)	SW Appalachians (7)
A. Ecoregion				
Blue Ridge	0.772	0.496	0.573	0.628
SE Plains		0.613	0.528	0.569
Piedmont			0.628	0.644
SW Appalachians				0.718

	Tennessee (5)	Altamaha (4)	Conecuh (6)	Coosa (4)	Tallapoosa (5)	Black Warrior (5)
B. Catchment						
Tennessee	0.689	0.530	0.531	0.612	0.611	0.641
Altamaha		0.610	0.528	0.515	0.590	0.619
Conecuh			0.676	0.500	0.576	0.576
Coosa				0.634	0.589	0.595
Tallapoosa					0.686	0.697
Black Warrior						0.670

sites in the same ecoregion could be evaluated (NRC 1992). However, this suggestion must be tempered with the knowledge that sample sizes were extremely low, particularly for the Blue Ridge ecoregion. It is certainly possible that much more intraecoregional variation in physico-chemical or biota conditions existed in the Blue Ridge ecoregion, and that sampling only 3 streams in this ecoregion captured only a minor portion of that variation. Nevertheless, the water chemistry in these streams (Appendix) was generally similar to that observed for other Blue Ridge streams (Silsbee and Larson 1982, Mulholland et al. 1992), which differed strongly from streams in other contiguous ecoregions showing higher concentrations of dissolved ions (Puckett and Bricker 1992). Therefore, my characterizations appear reasonable. Unfortunately, because of the low numbers of sites sampled, I was unable to partition sites into subregions (Level IV ecoregions, e.g., Griffith et al. 1994) to learn if invertebrate assemblages fitted this finer classification as well. The subregion classification has shown some promise in separating streams within other southeastern ecoregions by invertebrate biota (e.g., SE Plains streams in Florida, see Barbour et al. 1996).

The low-elevation SE Plains was clearly the most biologically distinctive ecoregion in my study. This ecoregion also displayed the most disparate environmental conditions relative to the 3 upland ecoregions in terms of channel geomorphology (e.g., lowest gradient and current velocity), substrate (e.g., lowest median particle size, highest % sand in substrate), and water chemistry (e.g., lowest baseflow oxygen concentrations) (Appendix). Perhaps these factors, in conjunction with the biogeographic history of the SE Plains (Berner and Pescador 1988, Felley 1992), contributed to its biotic uniqueness (see also Benke et al. 1984, Bass and Cox 1985). In addition, highly variable flow regimes in SE Plains streams also may decrease faunal similarity to upland streams. Small- to moderate-sized runoff-fed coastal plains streams displaying high discharge during winter often show negligible flow during summer because of reduced rainfall and continued high evapotranspiration (Felley 1992). Diminished flow can thus severely limit effective habitat and the use of these types of streams by flow-dependent taxa. This situation may have occurred in some of the SE Plains streams I studied, where differences between winter and summer baseflow in exceeded 500% (i.e., from ~500 to 1 L/s in Conecuh streams in 1997; Hamilton 1998, J. Feminella, unpublished data). Finally, I also cannot rule out the possibility that SE Plains streams

were more disturbed by human activities than streams in other ecoregions because catchment deforestation and agricultural development were highest in this ecoregion. However, I found no strong relationships between a number of land-use variables and stream invertebrate assemblages in separate analyses involving only SE Plains streams (J. Feminella, unpublished data), which are patterns that would be expected if land use (vs natural) attributes had a major influence on biota in these systems.

Biotic separation among ecoregions other than the SE Plains was much less pronounced and more variable, and depended on the ecoregion and the biotic measures examined. On one hand, EPT richness decreased from high- to low-elevation ecoregions (Fig. 3, Table 2), with mid-elevation SW Appalachians and Piedmont ecoregions more closely resembling lowland SE Plains streams than richer upland streams in the Blue Ridge ecoregion (Wallace et al. 1992). Marked faunal dissimilarities between upland–lowland transitional zones also have been reported elsewhere (e.g., Pacific Northwest: Whittier et al. 1988, Corkum 1989; Eastern Canada: Corkum 1991; North Carolina: Lenat 1988; Southern Rockies: Tate and Heiny 1995; but see Quinn and Hickey 1990). Alternatively, ecological differentiation between the SW Appalachians and Piedmont was much less distinct because these ecoregions displayed considerable overlap in environmental features (Fig. 2) and in invertebrate richness and species composition (Figs 3A, 5, Table 3A). That these ecoregions were the most similar was unexpected because the Piedmont was considered a subregion of the SE Plains in the original Omernik (1987) classification; thus, Piedmont streams would have been expected to display higher similarity to SE Plains streams. My results imply that Piedmont sites lie closer to other upland sites. Indeed, others have reported that Piedmont streams display high faunal similarity with other upland streams such as those in the Blue Ridge ecoregion (Mulholland and Lenat 1992), although in my study Piedmont streams appeared more like SW Appalachians streams than Blue Ridge streams. In this sense, it may be prudent to consider either combining some Piedmont sites with those of the SW Appalachians (e.g., those of upper Piedmont, Level IV classification) or perhaps considering the Piedmont as a subregion of the SW Appalachians in general. Irrespective of the degree to which we choose to reclassify the Piedmont, my data suggest that it is clearly transitional between upland and lowland ecoregions, in terms of biotic and environmental variables. This finding supports the Level III classification that separates the Piedmont ecoregion ecologically from the SE Plains (Omernik 1987).

Invertebrate assemblages may vary strongly with stream size, with small (e.g., 1st-order) streams being less taxonomically diverse than larger streams (e.g., 4th- or 5th-order, Minshall et al. 1985, Grubaugh et al. 1996). This generalization was not apparent in my study. The 4 smallest streams surveyed (i.e., 1st-order Piedmont streams C-1, C-3, Q-1, Q-2; Appendix) had total richness values ($\bar{x}$ = 72 taxa/stream) that were virtually identical to those in the highest-order streams examined (i.e., 7 SW Appalachians streams ranging from 3rd- to 5th-order, $\bar{x}$ = 71 taxa/stream; J. Feminella, unpublished data). Moreover, I could not detect any significant relationships across the 30 streams (using linear or quadratic models, $p > 0.05$) between richness and stream size (as stream order or catchment area; J. Feminella, unpublished data). Results from other benthic studies in the southeast also have suggested that invertebrate taxonomic composition may be more influenced by catchment-specific differences in habitat features (e.g., local geomorphology, flow regimes) and evolutionary history than stream size (Mulholland and Lenat 1992, Wohl et al. 1995).

Ecoregions and catchments

Omernik and Bailey (1997) argued that ecoregion and catchment concepts should be thought of as complementary rather than competing frameworks in the monitoring and assessment of aquatic ecosystems. In this context, patterns observed within more topographically distinct catchments could constitute the study units of interest, whereas ecoregions could represent the geographic constructs by which the state or behavior of natural elements could be extrapolated and thus tested for generality (Omernik and Bailey 1997). A useful starting point for such a holistic approach would be to examine the degree to which patterns in biological attributes, such as benthic invertebrate distributions, classified at the catchment scale apply to broader-scale ecoregions.

The 4 southeastern ecoregions examined here were as informative at classifying stream invertebrate assemblages as were individual catchments subsumed within the larger ecoregions. That both classification schemes accounted for similar biotic variation implies that ecoregions were indeed ecologically homogenous (sensu Omernik and Bailey 1997) or that smaller-scale catchments were as environmentally heterogenous as larger-scale ecoregions, and thus as likely to support a similar array of invertebrate taxa. The geologically diverse Black Warrior River catchment (containing 5 of the 30 study streams), where tributaries display strongly contrasting parent geology (Johnston 1930, Mettee et al. 1989), suggests that such high intra-catchment variation in environmental and biological features is likely. Streams in this catchment may be underlain by highly erodible, ion-rich limestone (e.g., Borden and Thompson Creeks) or more resistant, ion-poor sandstone (e.g., Brushy, Capsey, and Hubbard Creeks). These geological differences can produce fundamentally different streamwater chemical conditions (Puckett and Bricker 1992; Fig. 2; see also conductivity, alkalinity, and hardness values for the above streams in the Appendix), which in turn may strongly influence invertebrate assemblages (Krueger and Waters 1983, Huryn et al. 1995). If such localized geological mosaics are commonplace within southeastern catchments, and invertebrate assemblages are distributed accordingly, then corresponding ecoregions may be robust enough to adequately characterize biota at the scale of individual catchments.

If ecoregions and catchments are truly complementary, then tributaries of catchments in the same ecoregion should have more similar fauna than tributaries of catchments that traverse >1 ecoregion. The Altamaha River catchment (flowing from Piedmont to SE Plains) from which I sampled 4 similar-sized streams, 2 in each ecoregion (i.e., Rock and Kinnard Creeks—Piedmont; Tobler and Hurricane Creeks—SE Plains, Appendix), allowed me to explore this idea. Despite similar size and a common longitudinal connection to the mainstem, between-stream resemblance corresponded more closely to ecoregion than to catchment. Streams in different ecoregions consistently displayed higher dissimilarity (BC values ~0.8) than streams in the same ecoregion (BC ~0.3–0.6, depending upon contrast; Fig. 6).

Taxonomic level of resolution: how low should we go?

The species-level approach has the greatest potential to discern biological differences among sites in water-quality biomonitoring (Resh and Unzicker 1975, Cranston 1990, Resh and McElravy 1993). However, because financial resources often are constrained and taxonomic resolution often is limited for obscure taxa or immature specimens, species-level resolution may neither be practical nor possible. The resulting differential taxonomic effort can confound comparisons across studies. Thus, it is essential to learn if higher-level, but more feasible and thus comparable, taxonomic treatments can be used to avoid these problems (Warwick 1993).

In my study, family-level resolution was practically as informative as the morphospecies level at discriminating ecoregions, despite the reduced number of taxonomic units (>50% fewer taxa). In a recent quantitative analysis of 10 freshwater benthic invertebrate data sets, Bowman and Bailey (1997) also concluded that higher-level (family and order) taxonomic resolution paralleled community characterizations at the species level (see also Warwick 1993). Results of my study imply that fundamental faunal differences exist among streams, catchments, and ecoregions, and that higher-level taxonomic aggregation was sensitive enough to reveal these differences. These data also support the assertion that such conservative taxonomic treatment may reduce the noise observed at the species level resulting from biogeographical variation (Bowman and Bailey 1997).

The use of families to discriminate ecoregions and catchments did, however, cause a loss of information. Family-level aggregation produced generally lower faunal dissimilarities among streams and higher M values than morphospecies aggregation (i.e., 0.873 vs 0.782 for ecoregion, 0.875 vs 0.793 for catchment), indicating weaker classification strength at the family level. Moreover, certain streams included in primary ecoregion clusters based on morphospecies were excluded from these clusters when specimens were identified only to family level (compare Figs 5 and 6). Decreased resolution in identifying similar sites could be risky for stream bioassessments, where such conservative taxonomic treatment may cause streams or sites to

be classified into incorrect categories of water quality or biotic integrity (Hawkins et al. 2000). My results underscore the need for additional multilevel taxonomic assessments of community variation, which are rare in benthic community ecology (but see Osborne et al. 1980, Warwick 1988a, 1988b, Hawkins et al. 2000).

In summary, despite the limited sample size, I demonstrated that 1) stream benthic invertebrates and their habitats were classifiable by ecoregions and catchments in the southeastern USA, and 2) that the commonly used genus/species/morphospecies level of taxonomic resolution was not essential to detect a match between a given ecoregion and its invertebrate fauna. These results are part of a growing body of literature that suggests that coarser levels of taxonomic treatment may display acceptable resolution between sites across large ecoregions, even for relatively unimpaired streams that may differ only in natural features within their catchments.

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APPENDIX. Characteristics of the 30 study streams. Catchment area, elevation, and mean channel gradient were determined from 7.5' topographic maps of the US Geological Survey. Channel measurements (width, current, and substrate size [= diameter]) were determined from 5 riffles or runs per stream. See Table 1 for stream abbreviations.

Stream	Order	Sampling year	Catchment area (ha)	Channel gradient (m/m)	Elevation (m)	Mean % summer shade
TUR	1	1992	598	0.034	762	96
LRC	2	1992	910	0.023	695	95
ETO	2	1992	1480	0.018	533	88
CHS	3	1992	2010	0.004	207	77
FAC	4	1992	2620	0.003	226	77
BOR	4	1993	2200	0.002	177	76
BRU	4	1993	1780	0.003	224	86
CAP	3	1993	2370	0.002	177	80
THO	5	1993	4360	0.003	183	74
HUB	5	1993	2810	0.023	207	68
C-1	1	1994	39	0.013	350	91
C-3	1	1994	32	0.031	338	89
Q-1	1	1994	31	0.021	356	95
Q-2	1	1994	21	0.026	360	98
BUC	2	1993	1405	0.009	110	89
CHO	3	1992	3920	0.003	95	72
LED	2	1993	1149	0.010	116	81
MIT	1	1993	1120	0.007	122	61
SYC	1	1992	1280	0.007	134	97
UCH	2	1992	1820	0.004	113	92
KIN	1	1992	2020	0.005	128	84
ROC	2	1993	1200	0.007	128	92
TOB	1	1993	830	0.009	119	73
HUR	2	1993	2340	0.005	107	81
PAN	2	1997	2671	0.002	88	85
LON	3	1997	3786	0.002	79	94
S40	1	1997	1482	0.004	91	97
S41	1	1997	526	0.006	85	98
MIL	2	1997	1036	0.005	61	69
RED	1	1997	1989	0.002	82	95

APPENDIX.   Extended.

Dis-charge (L/s)	Mean width (m)	Mean current (m/s)	Median sub-strate size (mm)	% sand	Total hardness (mg/L)	Total alkalin-ity (mg/L)	Specific conduc-tance (μS/cm)	pH (units)	Dis-solved O$_2$ (mg/L)	% O$_2$ satura-tion
83	3.07	0.632	102	5.0	8	24	18	6.47	7.9	77
184	3.90	0.704	115	1.0	4	14	12	6.45	7.6	73
336	3.36	0.720	102	1.5	6	18	17	6.58	7.7	76
469	5.07	0.745	56	0.3	28	26	58	7.68	7.5	79
659	6.37	0.687	51	0	20	28	42	7.20	7.2	76
20	2.03	0.270	7	13.6	160	174	309	7.50	6.4	63
25	4.18	0.362	115	1.6	16	28	37	8.03	7.5	79
19	3.14	0.216	205	2.0	40	40	74	7.00	8.6	85
16	1.64	0.327	96	0	70	84	148	8.01	8.1	86
73	6.93	0.479	947	1.0	20	12	25	6.50	9.9	100
7	1.03	0.276	54	0.8	8	24	31	6.94	7.7	90
2	0.95	0.246	96	0.7	12	28	27	6.81	8.0	90
2	0.72	0.244	16	2.0	4	20	22	6.36	8.1	92
2	0.46	0.218	15	1.4	4	24	31	6.01	8.4	89
41	1.87	0.472	24	8.3	20	40	44	7.91	8.9	85
143	3.62	0.568	118	8.0	52	42	114	7.62	9.0	93
29	1.96	0.588	30	4.0	20	38	67	8.03	8.4	85
15	3.05	0.279	61	0.5	16	36	64	8.07	8.8	89
31	1.62	0.360	54	5.2	26	32	61	7.27	9.0	95
110	2.03	0.570	13	14.0	22	24	50	6.36	5.7	74
104	1.62	0.091	15	12.0	28	40	74	7.20	9.7	94
19	2.89	0.305	96	2.2	42	64	121	8.11	7.9	89
10	1.28	0.263	3	42.0	24	48	81	7.85	6.7	76
10	1.26	0.194	7	12.0	32	60	95	7.73	7.0	82
1	0.64	0.105	3	23.0	33	48	111	7.03	3.1	41
1	2.11	0.423	12	22.0	38	60	94	7.03	7.2	92
6	1.50	0.141	<2	100.0	16	30	78	6.75	2.4	28
16	1.17	0.244	<2	100.0	12	24	47	6.35	4.4	52
38	1.78	0.528	26	40.0	12	18	41	6.59	8.1	100
53	3.52	0.246	<2	100.0	18	20	32	6.59	7.1	80