

Macroinvertebrates in neotropical streams: richness patterns along a catchment and assemblage structure between 2 seasons

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Abstract. We investigated macroinvertebrate richness in 10 streams of different sizes within the Carmo River catchment in Brazil. Specifically, we tested 2 predictions of the river continuum concept (RCC): 1) within the catchment, mid-sized streams (orders 3–4) have the richest biota, and 2) macroinvertebrate assemblage structure is more stable during the dry season than during the rainy season when natural spates are frequent. We sampled the streams using individual stones as sampling units. Observed and estimated values of richness did not follow the hump-shaped pattern of richness along a gradient of stream size as predicted by the RCC; the richest streams were smaller than those predicted. No difference in assemblage structure between seasons was found on the basis of observed and estimated richness or abundance. The similarity in assemblage structure between the rainy and dry seasons was also supported by multivariate analysis. Observed richness and species composition (reflected in multivariate analysis) were strongly correlated to stream size and the presence of fine sediments over rocks. Assemblage structure in these streams seems to be deterministic, in that richness and species composition are related to physical habitat characteristics.

Key words: macroinvertebrates, assemblage structure, neotropics, streams, equilibrium states, diversity, Brazil.

Recent theories related to structure of stream assemblages have arisen mainly from studies in temperate regions, and their application to tropical streams remains mostly untested. Tropical streams differ from their temperate counterparts in many characteristics, including evolutionary history, precipitation patterns, water temperature, and diversity of riparian vegetation (Illies 1969, Covich 1988), indicating that theories developed mainly for the temperate region may not apply to tropical regions (Jackson and Sweeney 1995).

One of the most comprehensive theoretical frameworks developed for understanding patterns and processes in streams was the river continuum concept (RCC) (Vannote et al. 1980, Minshall et al. 1985a). The RCC considers a stream to be an interacting component of a major unit, the catchment. The approach used is deterministic (*sensu* Winterbourn et al. 1981), and states that the position of the stream along

the river continuum, and consequently its physical structure, determine the structure and composition of its biotic community. However, as soon as the concept was proposed, some researchers disagreed on its applicability, arguing simply that it is powerless (Winterbourn et al. 1981) or that other mechanisms, such as stream hydraulics (Statzner and Higler 1986), are more important in explaining species richness patterns.

Among several topics, the RCC addresses the question of the relative prevalence of equilibrium and nonequilibrium states of community structure (Minshall et al. 1985a). In an equilibrium community most species are controlled by biotic factors (e.g., predation and competition), whereas in a nonequilibrium community most species are controlled mainly by abiotic factors such as spates (Lake and Barmuta 1986). Minshall et al. (1985a, 1985b) have suggested that community structure varies during the year from a nonequilibrium to an equilibrium state until a new disturbance resets the system. The

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main sources of disturbance in streams are periodic spates. At 1st view, this prediction seems very attractive, especially if one has experienced a natural flood in a tropical rainforest stream. However, seasonal spates are very predictable (but see discussion in Poff 1992), and some evidence suggests the possible evolution of resistance mechanisms to spates (Dole-Olivier et al. 1997, Winterbottom et al. 1997). Nevertheless, in periods >1 y, streams are vulnerable to catastrophic spates, which undoubtedly affect the stream biota (Scrimgeour et al. 1988, Hendricks et al. 1995, Angradi 1997, A. S. Melo and C. G. Froehlich, personal observation).

Another question addressed by the RCC is the pattern of species richness along the catchment. The concept predicts that the greatest biotic richness will be found in medium-sized streams (orders 3–4), where environmental variability, mainly in temperature, might be large, consequently creating a high number of niches. Thus, in low-order streams the number of species would be low and would increase downstream until the expected maximum of richness at streams of order 3–4, after which richness decreases again. Plotting species richness as a function of stream size would produce a hump-shaped pattern. Minshall et al. (1985b) tested many models for describing this hump-shaped pattern in a catchment from the USA and proposed the lognormal model as the best fit. However, tropical streams in forest areas experience little variation in temperature during the day and the year (Dudgeon 1983, Payne 1986, Schroeder-Araujo et al. 1986, Haynes 1987). Further, differences in temperature among streams of different size are small in tropical regions, indicating that temperature might not be an important factor in determining local biotic richness. So, the hump-shaped richness pattern, which is supposed to be determined by temperature variation, may not occur in tropical catchments.

We provide a quantitative assessment of macroinvertebrate richness in several streams within a single neotropical catchment. We tested 2 predictions of the RCC: 1) the macroinvertebrate assemblage in the dry winter has greater equilibrium structure than in the rainy summer, and 2) the greatest richness of stream macroinvertebrates occurs in order 3–4 streams.

Methods

Study area

We sampled 10 streams in the Carmo River catchment, at Parque Estadual Intervales (lat $24^{\circ}18'S$, long $48^{\circ}25'W$), São Paulo state, Brazil (Fig. 1). The Park consists of 49,000 ha of protected area and has boundaries with 3 other conservation areas amounting to 132,000 ha. The vegetation is tropical ombrophilous submontane–montane forest, commonly known as tropical rain forest (Mueller-Dombois and Ellenberg 1974), and its conservation status is very good, except for exploitation of palm heart (*Euterpe edulis* Mart.) in some areas until the 1980s.

The mean annual precipitation in the area was 1696 mm (rain gauge located 1 km from stream 3; 8-y record). Rainfall is unevenly distributed across 2 seasons: one wet (130–270 mm/mo) and warm (15 – $30^{\circ}C$) from September through March and another dry (60–95 mm/mo) and cold (0 – $25^{\circ}C$) from April to August (Fig. 2).

Streams were selected on the basis of ease of access, size, and geological characteristics. Stream 3 crosses a calcareous cave and a small swamp, and stream 10 receives water from some tributaries that originate in or pass through calcareous caves. The remaining stream sites, from the headwaters down, pass through forested areas. The streambeds are composed of several types of rock, predominantly of sedimentary origin. The size of most of the rocks ranges from 10 to 100 cm in length. A more detailed characterization of the sites is shown in Table 1.

Sample collection

We used individual stones of ~ 18 cm maximum diameter as sample units. The stones were taken from the streambed of riffles using a U-net sampler with a $250\text{-}\mu\text{m}$ mesh, designed to avoid the loss of active swimmers (Scrimgeour et al. 1993). The material collected in this device was transferred to a white tray and all visible invertebrates were removed and fixed in 80% ethanol. Stones also were examined for attached individuals. To standardize samples, we selected stones that were totally submerged, superficially embedded in the substrate, and free of excessive moss growth.

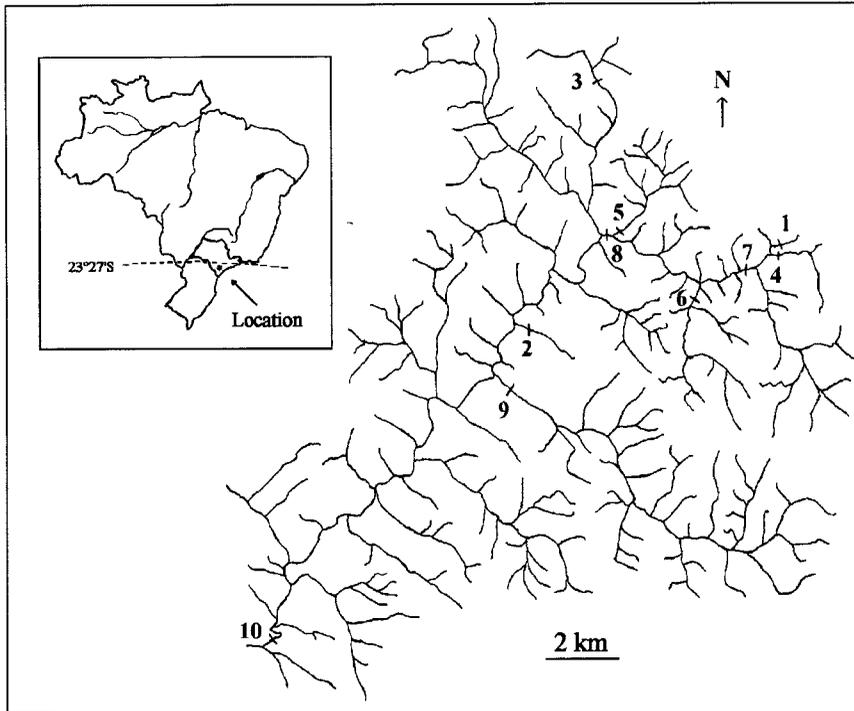


FIG. 1. Location of the Carmo River catchment in Brazil, showing the 10 sampling sites.

In each stream, 25 sample units (individual stones) were collected from a reach of at least 100 m in length. Field collections were made from February to March during the wet season and from July to August during the dry season

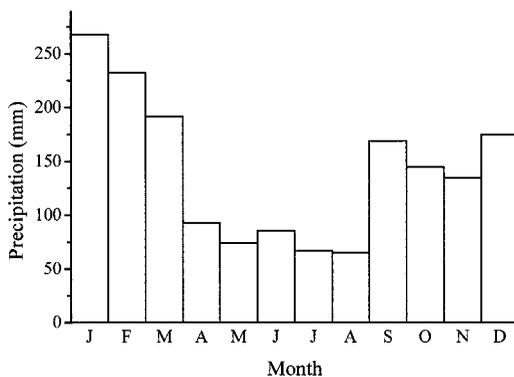


FIG. 2. Monthly precipitation in the Parque Estadual Intervales. The mean annual precipitation is 1696 mm (8-y record; source: Departamento de Águas e Energia Elétrica do Estado de São Paulo-DAEE, Centro Tecnológico de Hidráulica e Recursos Hídricos-CTH).

of 1997 (Fig. 2). Stream 10 was not sampled in the wet season because the high water level made collecting impossible.

The use of individual stones as sample units was based on the ease and efficiency of the method (Scrimgeour et al. 1993) and the fact that this method has been used in other studies, providing a comparative base (Stout and Vandermeer 1975, Minshall et al. 1985b). Individual stones can be viewed as the natural physical units of the community, where many interactions among organisms occur (Minshall and Petersen 1985). Last, each stone can be approached as an island, permitting application of some analytical techniques derived from island biogeography theory (Stout and Vandermeer 1975).

Macroinvertebrate identifications

Because of the low resolution of taxonomic knowledge for aquatic macroinvertebrates in Brazil (Vanzolini 1964, Hurlbert et al. 1981), particularly for immature insects, it was difficult to identify specimens to the species level. Hence, individuals were identified to the family level

TABLE 1. Physical characteristics of the 10 sampling sites in Parque Estadual Intervalas. — = no data available.

Parameters	Streams					
	1	2	3	4	5	6
Stream order	1	1	2	2	3	3
Link magnitude ^a	1	1	3	2	11	6
Width (m)	1	2.5	2.5	3.5	2.5	4
Summer discharge (m ³ /s)	0.010	0.089	0.083	0.091	0.156	0.339
Winter discharge (m ³ /s)	0.005	0.010	0.030	0.059	0.137	0.092
Canopy cover (%)	100	100	94	100	98	98
Stream gradient (%)	0.07	0.05	0.05	0.02	0.05	0.03
Altitude (m)	680	540	800	680	530	700
Conductivity (winter, μ S/cm)	51	33	180	48	63	45
Sediments over rocks ^b	2	—	5	1.6	2.6	1.6
Diel maximum–minimum temperature (winter, °C)	15–15	15–14	14–12	15–13	13–12	16–13

^a Number of 1st-order streams included in the subcatchment.

^b Scored qualitatively as the amount of sediment collected by washing a defined area of stones and filtering through laboratory filter paper. The presented values are mean of 3 stones and the range used was 1 to 5, where 1 is no visible residue and 5 is the largest quantity sampled over the 24 filter papers.

using available literature and then separated as morphospecies. When separation of organisms into 1 or 2 morphospecies was doubtful, we used a conservative approach and left them in a single class, a procedure also used by Townsend et al. (1987). For Elmidae, a very diverse family of beetles in the neotropics, we used only the larval stage because larval–adult associations are unavailable, and the larval stage presents a more varied external morphology. Hydracarina and Chironomidae were not included in the analysis because of difficulties in identification even to morphospecies. The procedure described above was not ideal, but it was the only practical one possible (Hawkins et al. 1982, Burton and Sivaramakrishnan 1993, Marchant et al. 1995, Oliver and Beattie 1996, Williams et al. 1997).

Data analysis

Multivariate analysis.—Differences in assemblage structure between the 2 seasons and along the stream-size continuum were explored using multivariate statistics. Total abundance for each species occurring on the 25 stones collected for each stream and season were transformed using $\log_{10}(x + 1)$. We used PCORD (version 2.01, MjM Software, Gleneden Beach, Oregon, USA) and FITOPAC (G. Shepherd, release 1996, Departamento de Botânica, Universidade Estadual de Campinas, Campinas, São Paulo, Brazil) soft-

ware to do a principal component analysis (PCA) ordination with correlation matrix and a cluster analysis using the unweighted pair-group method using arithmetic averages (UPGMA) with Sørensen distance.

Richness metrics.—Richness can be assessed by simply counting the number of species observed in an area. However, this method is strongly affected by sample size (Walther et al. 1995). Another problem is that, given limited sampling, a species-poor assemblage with equally abundant species may yield a greater richness than another truly rich assemblage with a large proportion of rare species (Stout and Vandermeer 1975). One way to solve these problems is to use an estimator of the local richness (Stout and Vandermeer 1975) that produces a richness value nearer to the true richness at the site.

We used 2 richness estimator methods: 1) the 2nd-order jackknife (J2), and 2) the Stout and Vandermeer (1975) method (SV). The J2 method was chosen because it has been well evaluated in several studies using very different data sets, including the data from this study (Melo and Froehlich, in press). The J2 computation is simple, and is done by solving the following equation:

$$J2 = SO + \{[r_1(2n - 3)/n] - [r_2(n - 2)^2] / [n(n - 1)]\}$$

TABLE 1. Extended.

Streams			
7	8	9	10
4	4	4	5
15	43	36	175
6	10	10	21
0.393	1.158	1.281	—
0.238	0.657	0.750	2,729
90	94	84	72
—	0.03	0.02	—
650	520	400	200
40	30	36	75
—	1.6	2.3	1
14–12	17–14	16–15	—

where SO is the observed richness in n unit samples, r_1 is the number of species found in only 1 unit sampling, and r_2 is the number of species that occur in 2 unit samplings.

The SV method was chosen because of its frequent use in stream ecology, particularly in the study of Minshall et al. (1985b) who addressed richness patterns within a stream size gradient, allowing a direct comparison with our results. The SV method is laborious and uses iterations to find simultaneously the values of 3 parameters (a , z , and T_∞) in a nonlinear regression fitted to the data using the following equation:

$$S = a/[A^{-z} + (a/T_\infty)]$$

where S is the observed richness found in an island of size A (i.e., 1, 2, 3, etc. stones). The fitted parameters a , z , and T_∞ are, respectively, the maximum rate of immigration, the proportionality constant related to the rate of extinction, and the total number of species in the pool from which the immigrants are derived. T_∞ is the richness value expected when the sample size is infinite and is termed here *estimated richness*. For islands of size 1 (individual stones), we used the mean observed richness on 1 stone. For islands of size 2, we recorded the species number found on 2 stones randomly drawn from the sample pool of 25 stones, and calculated the mean richness in 500 random draws. Stones were returned to the pool between draws. For islands of size 3, the same procedure was used but 3 stones were drawn from the pool. If <500 combinations were possible, all combinations were used. PCORD software was used to do the

resamplings, and the result was equivalent to an averaged collector curve. The SV formula was then fitted to the constructed curve by nonlinear regression using ORIGIN software (version 4.1, Microcal Software, Northampton, Massachusetts, USA).

Richness estimators are relatively new tools and consequently their usefulness is not fully known. Therefore, we also used *observed richness*, which was the pooled number of species from all 25 stones sampled in each stream site and season.

Species richness along the stream-size gradient.—To determine the presence of a predicted hump-shaped pattern of richness along the stream-size gradient, we fitted the observed and estimated richness data to 3 models as a function of stream size. We used discharge measured on the day of sample collection as a measure of stream size because previous use of this descriptor by Minshall et al. (1985b) allowed direct comparison between their results and the results of our study. The 1st model was linear, which implies no change or a monotonic change in richness values along the catchment. We also fitted the quadratic and the lognormal model proposed by Minshall et al. (1985b). The quadratic model is simpler than the lognormal model and the fitted curves are similar to each other. The quadratic model can be subjected to a direct t -test on the significance of the improvement achieved by the quadratic term in relation to the linear model to determine whether the quadratic term is significantly different from 0. We used the generalized form of the lognormal model, $Y = a * e^{[(X - b) 2]/c}$, where a , b , and c are parameters obtained by iteration in a nonlinear regression. We used a consensus combined p -value test (Rice 1990) to evaluate the overall significance of the 6 p -values obtained from the quadratic regressions (2 seasons, 3 richness metrics). The test evaluates the significance of the general hypotheses using the p -values obtained from different tests. It allowed us to test the significance of the quadratic term using the 6 p -values obtained.

Equilibrium vs nonequilibrium states.—We used the Minshall et al. (1985b) index to test for differences in assemblage structure in the 2 seasons. This index is calculated by:

$$\text{Index} = (a/T_\infty) * z * (Y/T_\infty) * (1 - R^2)$$

where (a/T_∞) is the relative immigration rate, z

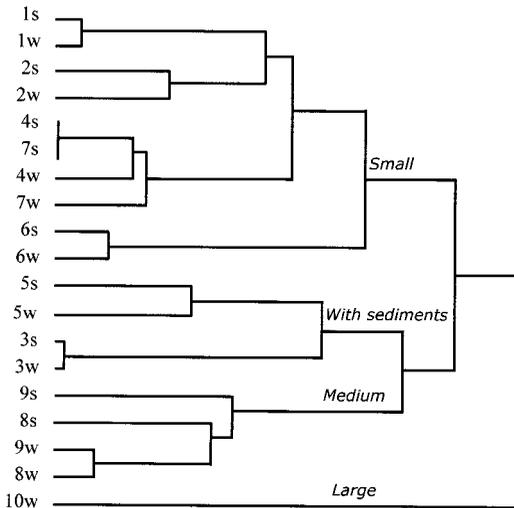


FIG. 3. Classification of sites by unweighted pair-group method using arithmetic averages (UPGMA) with Sørensen distance. s = summer samples, w = winter samples. Terms indicate stream groups.

is the proportionality constant related to the rate of extinction, (Y/T_{∞}) is the community spatial heterogeneity, and $(1 - R^2)$ is the coefficient of nondetermination for conformance of species abundance data to a lognormal curve with abundance in geometric classes using base 2 (Krebs 1989). The parameter Y is the mean number of species per stone, and a , T_{∞} , and z are the 3 parameters obtained from the SV method of richness estimation (see above). Each parameter is expected to be low in an equilibrium state and high in a nonequilibrium one. The biologi-

cal meaning of (a/T_{∞}) and z is that, in a non-equilibrium or opportunistic community, many individuals living on stones (each island) move away searching for the best living places in relation to food availability or predation risk, or are passively dislocated by spates. (Y/T_{∞}) measures the proportion of the community present on 1 stone. Nonequilibrium communities will have a greater proportion of species on a single stone relative to the species pool (T_{∞}) than equilibrium communities. $(1 - R^2)$ is related to the controversial assumption that, in equilibrium communities, species-abundance data conform to a lognormal distribution. Therefore, departures from the expected lognormal model should be a measure of how far the community is from the equilibrium state. A Wilcoxon signed rank test was used to ascertain the significance of differences between the 9 pairs of index values obtained from the 9 streams sampled in both seasons.

Results

Multivariate analysis

A total of 17,598 individuals belonging to 162 morphospecies was collected. UPGMA classification separated streams into 4 groups on the basis of morphospecies composition and abundance (Fig. 3). The 1st group included only stream 10, the largest stream in the study. It was very different in species composition (Appendix) and total abundance (Table 2) in relation to the remaining streams (Fig. 3). Of the 52 species

TABLE 2. Observed and estimated richness of macroinvertebrates at the 10 sampling sites in summer and winter. - = no data available. SO = observed richness on 25 stones, J2 = estimated richness by 2nd-order jackknife, SV = estimated richness by Stout and Vandermeer (1975) method, and N = total individuals sampled.

Streams	SO		J2		SV		N	
	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter
1	59	52	74.9	64.0	96.0	84.1	729	682
2	58	67	85.0	105.2	109.9	126.9	876	1175
3	30	34	48.0	47.4	61.1	59.4	1468	971
4	64	56	102.8	77.3	120.0	92.7	949	651
5	42	38	64.0	58.1	78.0	99.2	431	1004
6	56	61	79.3	84.3	85.6	112.1	385	1148
7	60	60	86.9	100.8	88.6	148.4	840	1149
8	45	52	71.8	72.4	100.7	92.9	636	559
9	47	56	66.3	92.0	85.2	105.0	517	856
10	-	52	-	69.2	-	63.2	-	2572

sampled in stream 10 in winter, 13 were found only at this site. Also, many species occurring at other sites were rare or absent in stream 10 (e.g., Hyalellidae sp. 1, Hydropsychidae sp. 1, Hydropsychidae sp. 2, Turbellaria sp. 1, and Calopterygidae sp. 1). The 2nd group included small streams 1, 2, 4, 6, and 7, the most species-rich streams in our study. Stream 6 had a distinctive species composition and was separated early within this group of streams. Of the 74 species found in summer and winter samples, 11 occurred only in stream 6 (Appendix). The 3rd and 4th groups were less distinctive and included, respectively, medium-sized streams 8 and 9 and low-order streams 3 and 5 (Fig. 3). Streams 3 and 5 had fewer species than other low-order streams (streams 1, 2, 4, 6, and 7) (Table 2), and stream 3 had a high quantity of fine sediments over rocks (Table 1).

The PCA ordination represented the position of each stream in species space similar to the UPGMA classification (Fig. 4). Axis 1 of the PCA ordination separated the streams along a size gradient, except for low-order streams 3 and 5 that were scored near medium-sized streams 8 and 9. As in the UPGMA classification, stream 6 was similar to streams 1, 2, 4, and 7 on axis 1, but differed between axes 2 and 3 (Fig. 4). The percentages of explained variance for the first 3 axes were, respectively, 15.65, 11.12, and 10.52%, totaling 37.29%. Although the explained variance might seem low, the eigenvalue obtained for each axis is divided by the total variance in the data set. The total variance is the number of variables (species) in the data set when using PCA analysis with correlation matrices. Because we used a large number of variables (162 morphospecies), the apparently low variances explained by each axis are expected. In fact, the expected variances obtained by chance (broken-stick method, see Jackson 1993) for the first 3 axes (3.49, 2.88, and 2.57%, respectively) are ~4-fold lower than those obtained in the analysis, indicating the effectiveness of the analysis.

Summer and winter samples from the same stream tended to be positioned near each other in the UPGMA classification and PCA ordination, indicating an absence of a strong change in assemblage structure between the 2 seasons. For the 9 streams sampled during both seasons, the UPGMA analysis classified 5 streams as pairs (summer and winter) in the 1st level of the

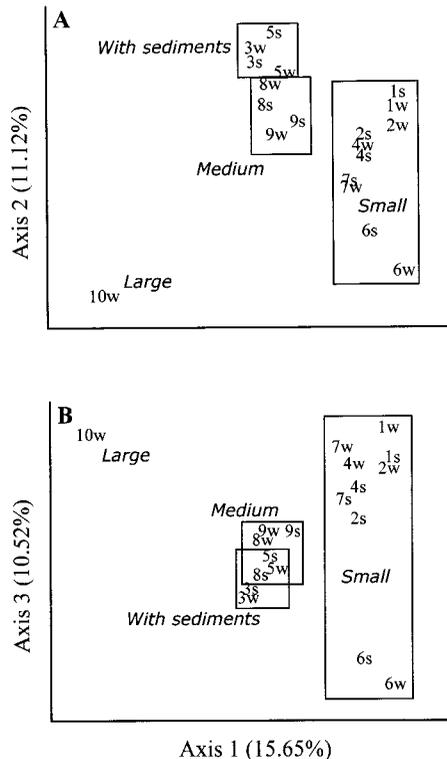


FIG. 4. Principal component analysis (PCA) ordination of sites. A.—Axes 1 and 2. B.—Axes 1 and 3. The cumulative % explained by the first 2 axes was 26.77 and by the first 3 axes was 37.29. s = summer, w = winter. Boxes indicate stream groups produced by unweighted pair-group method using arithmetic averages (UPGMA) analysis.

clustering and 4 as pairs in the 2nd level (Fig. 3). The PCA ordination produced similar scores for summer and winter samples in each stream in the first 3 axes (Fig. 4).

Species richness along the stream-size gradient

Species richness in streams 3 and 5 was markedly lower than in other low-order streams, perhaps because of the large amount of fine sediments over rocks in these 2 streams, so we excluded these 2 streams from the analysis of richness along the stream-size gradient. For the remaining streams (7 in summer and 8 in winter), the richness values plotted as a function of discharge produced only a weak hump-shaped pattern (Fig. 5). Moreover, the richest streams (2nd-order stream 4 in summer and 1st-order stream 2 in winter) were smaller than expected

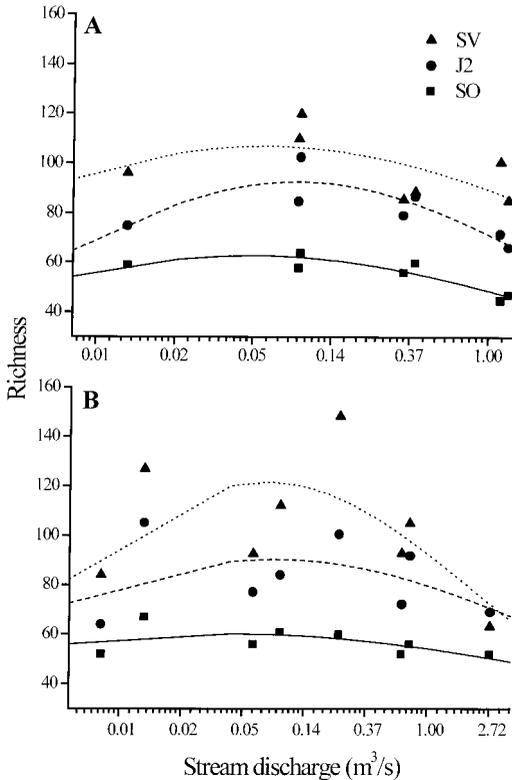


FIG. 5. Relationship of observed and extrapolated richness to the stream discharge gradient in summer (A) and winter (B). Curves were fitted using the lognormal model. SV = estimated richness by Stout and Vandermeer (1975) method, J2 = 2nd-order jackknife method, and SO = observed richness.

by theory (orders 3–4), as if the peaks of the richness curves were dislocated to the left in Fig. 5. All regression coefficients in the linear models were negative, indicating decreasing richness from headwater streams to large streams.

The values of the coefficients of determination produced by linear (r^2), quadratic (R^2), and lognormal (R^2) models were low, except for quadratic and lognormal models using SO and J2 in summer (Table 3). The lognormal model produced higher coefficients of determination than the quadratic model in 3 cases, whereas the quadratic model was better in the remaining 3 cases. The differences between the fits of the models were very small, and we concluded that the quadratic model fit the data as well as the lognormal model proposed by Minshall et al. (1985b).

We used a t -test to ascertain the significance of the improvement achieved by including the quadratic term in the quadratic model. For the 6 data sets (summer and winter for SO, J2 and SV), the quadratic term was significant ($p < 0.05$) in 2 cases, summer SO and summer J2 (Table 3). Using the 6 p -values together, the consensus combined p -value test produced a significant value of $p = 0.006$, so we rejected the null hypothesis of no difference of the quadratic term from 0.

Equilibrium vs nonequilibrium states

Table 4 shows the values of the 4 parameters proposed by Minshall et al. (1985b) to measure equilibrium state, and the composite index obtained for summer and winter for each of the 9 streams. Low values indicate closeness to equilibrium. We predict low values in winter when

TABLE 3. Statistics of linear, quadratic, and lognormal models fitted to observed (SO) and extrapolated species richness by 2nd-order jackknife method (J2) and Stout and Vandermeer (1975) method (SV) along the catchment in summer and winter. n = number of streams sampled, r^2 and R^2 = coefficients of determination, and b_1 and b_2 = regression coefficients.

Data set	n	Linear			Quadratic			Lognormal
		r^2	b_1	p	R^2	b_2	p	R^2
Summer SO	7	0.489	-2.863	0.080	0.853	-1.555	0.035	0.841
Summer J2	7	0.119	-2.427	0.449	0.743	-3.498	0.035	0.749
Summer SV	7	0.154	-3.028	0.384	0.325	-2.010	0.371	0.346
Winter SO	8	0.164	-0.998	0.319	0.336	-0.551	0.306	0.342
Winter J2	8	0.011	-0.711	0.808	0.221	-1.712	0.297	0.211
Winter SV	8	0.063	-3.039	0.548	0.460	-4.111	0.113	0.428

TABLE 4. Assemblage parameters related to equilibrium state in 9 streams in summer and winter samples.

Streams	a/T _z ^a		z ^b		1 - R ^{2c}		Y/T _z ^d		Index × 100 ^e	
	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter
1	0.136	0.146	0.77	0.76	0.205	0.220	0.122	0.131	0.260	0.320
2	0.116	0.122	0.70	0.68	0.206	0.054	0.100	0.103	0.168	0.046
3	0.136	0.206	0.60	0.59	0.146	0.351	0.120	0.164	0.143	0.698
4	0.139	0.131	0.65	0.77	0.050	0.329	0.118	0.116	0.054	0.387
5	0.102	0.085	0.76	0.61	0.094	0.114	0.091	0.075	0.066	0.044
6	0.103	0.141	0.09	0.67	0.125	0.015	0.091	0.122	0.106	0.017
7	0.153	0.091	0.80	0.62	0.188	0.080	0.130	0.078	0.301	0.035
8	0.085	0.134	0.70	0.70	0.118	0.309	0.077	0.111	0.054	0.322
9	0.094	0.106	0.81	0.75	0.146	0.201	0.094	0.101	0.105	0.161

^a Relative immigration rate.

^b Proportionality constant related to the rate of extinction.

^c Coefficient of nondetermination for conformance to lognormal model.

^d Spatial heterogeneity of community.

^e Index = multiplication of 4 previous parameters.

spates are rare, compared to summer values. However, of the 9 streams sampled in both seasons, only 3 showed a lower value in winter. No significant difference in assemblage structure as measured by the composite index was detected between the 2 seasons (Wilcoxon signed rank test, $p = 0.441$).

Species richness and abundance between seasons

Observed species richness in streams sites was similar in summer and winter samples (Table 2), corroborating the lack of seasonal change in assemblage structure found in the multivariate analyses and with the Minshall et al. (1985b) index. Observed species richness decreased in 3 streams, increased in 5, and did not change in stream 7 from summer to winter. The changes were not statistically significant (Wilcoxon signed rank test, $p = 0.399$). The greatest variation in observed richness occurred in stream 9, with an increase of 9 species from summer to winter.

Estimated species richness by J2 and SV methods was more variable between seasons than SO. Estimated richness by both methods decreased in 4 and increased in 5 streams from summer to winter, but the changes were not statistically significant (Wilcoxon signed rank test, $p = 0.635$ for J2 and $p = 0.314$ for SV methods). For stream 7, SV estimates increased by 59.8 species from summer to winter but SO did not change, suggesting that this increase might be

an artifact of the method (Melo and Froehlich, in press).

In contrast to the similarity of SO between the 2 seasons, the numbers of individuals collected were very different. For example, total abundance in stream 6 was 3 times higher in winter than in summer. Nonetheless, as noted for observed and estimated richness, no overall tendency for abundances to increase or decrease from summer to winter was observed (Wilcoxon signed rank test, $p = 0.260$) (Table 2).

Discussion

Species richness along the stream-size gradient

Both PCA ordination and UPGMA classification of morphospecies abundance data separated the streams mostly along a gradient of size. This gradual modification in faunal composition with increasing stream size agrees with previous work (Hynes 1971, Allan 1975), including 1 study from the neotropical region dealing with mayflies and stoneflies (Froehlich and Oliveira 1997). The richness pattern found along the catchment was similar to some extent to that postulated by the RCC. In our study, the richest streams were of lower order than the richest streams in the catchments studied by Stanford and Ward (1983) and Minshall et al. (1985b). In addition, the lognormal model proposed by Minshall et al. (1985b) fitted the data poorly, producing a low R^2 , even with richness data estimated using the same SV method used by

Minshall et al. (1985b). Moreover, if the richness data for stream 1 are removed from the models illustrated in Fig. 5, the relationship becomes a linear gradient with small streams supporting a richer macroinvertebrate fauna than large streams. In fact, in all 6 cases the regression coefficients (b_i) of the linear model were negative (Table 3). Thus, our study agrees with work done in other regions that provides little or no evidence of a hump-shaped pattern of richness along a gradient of stream size (Burton and Sivaramakrishnan 1993, Lake et al. 1994).

Variation in water temperature from upstream to downstream is the main determinant of patterns of richness along a catchment, according to the RCC, which predicts that greater species richness would occur at sites with larger variations in daily and seasonal temperatures than at sites with more stable temperatures. In our 2nd-order streams, where the greatest richness was observed, temperature variation was very small (Table 1), as it was in streams studied by Nair et al. (1989) in India, indicating that temperature should not be an important factor in determining richness in tropical streams. Death and Winterbourn (1995) pointed out that habitat stability was the main factor controlling richness and equitability. More stable habitats would support a richer community and moderately stable habitats would support a more equitable composition. It was not possible to carry out stability measurements in our study, but we feel that the Death and Winterbourn (1995) explanation is plausible and should receive more attention from stream ecologists.

Assemblage structure in summer and winter

The hypothesis that we should find communities in different states of equilibrium during the year in the same stream (Minshall and Petersen 1985, Minshall et al. 1985b) was not supported using the index proposed by Minshall et al. (1985b). The similarity in assemblage structure and composition found in the same stream between the 2 seasons, both in the classification and ordination, also indicated that the assemblages did not undergo major seasonal alterations in spite of differences in flow. The absence of a major change in assemblage structure, even in number of collected individuals (Table 2), is in sharp contrast with previous neotropical studies (Flecker and Feifarek 1994, Uieda and

Gajardo 1996, Oliveira et al. 1997, Jacobsen and Encalada 1998, Kikuchi and Uieda 1998), but it agrees with the recent work of Ramírez and Pringle (1998) in a lowland tropical stream in Costa Rica. We speculate that the fauna is adapted to the predictable summer spates, and only an unusual catastrophic spate can alter the assemblage structure. The threshold for a spate to produce a significant change must be relatively high (Angradi 1997), and depends on substrate stability (Giberson and Cobb 1995, Biggs et al. 1999).

Flecker and Feifarek (1994) studying invertebrates in Venezuela and Biggs et al. (1999) studying periphyton in New Zealand streams noted a strong relationship between the amount of time since the last spate and the number of individuals they collected. Flecker and Feifarek (1994) used >25 mm of rainfall as indicative of rainstorms capable of producing significant loss of individuals from the streambed. During our summer sampling period, a storm producing 24.5 mm apparently did not cause bed movement. Five days before our summer sampling, 22.1, 45.5, and 18.1 mm of rainfall were recorded on 3 consecutive days and, 28 d before sampling began, 54.9, 69.6, 94.4, and 29.1 mm of rainfall were recorded on 4 consecutive days. It is likely that the rainfall 28 d before collecting caused some reduction in abundance, but it also seems that 28 d should have been enough for recovery. Flecker and Feifarek (1994) saw complete recovery in 2 streams after 20 to 25 d.

Species composition and abundance among streams

The morphospecies assemblage in stream 6 was unique in that a considerable number of species occurred only at this site or in low abundance at other sites. In the multivariate analyses, stream 6 was distinctly different from other low-order streams, despite its similarity in physical characteristics, particularly to nearby stream 7. This apparently erratic distribution of some species also occurred in other streams. Species absent or rare in many streams had high abundance in another (e.g., 342 and 7 individuals of Glossosomatidae sp. 2, respectively, in streams 2 and 6; 203 and 20 individuals of Hydropsychidae sp. 5, respectively, in streams 7 and 10; in both cases, no specimens were found in the remaining 8 streams). Alternatively, some species abundant at most sites were absent or

occurred in low numbers at related sites (e.g., 4 individuals of *Leptohyphidae* sp. 2 in stream 1, and 36–195 individuals in the remaining 9 streams). Erratic patterns of distribution were also observed by Bunn and Hugues (1997), who found the abundance of many macroinvertebrates in streams was influenced by stochastic processes derived from the reproductive success of a few females. Such stochasticity could occur over a temporal scale; species currently absent or rare may be very abundant a few years later (see Froehlich and Oliveira 1997 for an example with a *Plecoptera* nymph).

Stream 10 showed a remarkably high total abundance (Table 2) and a distinctive morpho-species composition (Appendix), resulting in low similarity to other sites (Figs 3, 4). Hynes (1971) also found exceptionally high abundance for 2 large streams in his study of zonation in neotropical streams in Trinidad, West Indies. Minshall and Robinson (1998) found that large streams (>4th-order) were distinct from small streams. We are unaware of studies that have explored the possible role of the distinct habitat characteristics of large streams in supporting higher abundance of invertebrates than in smaller streams. Both Stout and Vandermeer (1975) and Fox (1977) considered the importance of abundance-reducing forces as richness-producing mechanisms in tropical and temperate streams. These authors suggested that lower food resources and/or higher competition and predation pressures in the tropics could reduce the number of individuals living on a single stone. Stream 10 had a more open canopy than the 9 smaller streams (Table 1), and presumably primary production was greater on rocks in stream 10 than in the smaller streams. Thus, the habitat may have been able to support more individuals.

In conclusion, stream macroinvertebrate assemblages in our study were not a random assemblage of species (Roughgarden 1989). Instead, the assemblage at a site was a function of the physical structure of the site, especially the size of the stream and presence of sediments over rocks. Thus, we found similar values of SO , and close proximity both in classification and ordination for sites similar in physical structure but separated by long distances (e.g., streams 1 and 2, 8 and 9, Fig. 1). The richness pattern along the catchment conformed weakly to the hump-shaped pattern predicted by RCC, but

the richest streams (1st- and 2nd-order) were smaller in size than the postulated mid-sized streams (3rd- and 4th-order). The absence of seasonal change in the composition of the macroinvertebrate assemblage contrasts with current theories about prevalence of different equilibrium states during the year, at least in years without unusual catastrophic floods. Ecological theories developed for temperate streams may not be adequate for tropical streams (Jackson and Sweeney 1995). Cautious analysis is needed before applying these temperate theories to tropical stream ecosystems.

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APPENDIX. Morphospecies composition in 10 streams in the Parque Estadual Intervalas. Horizontal lines indicate classes based on the number of streams in which morphospecies occurred.

	Streams									
	1	2	4	6	7	3	5	8	9	10
Hydrobiosidae sp. 1	X	X	X	X	X	X	X	X	X	X
Leptophlebiidae sp. 2	X	X	X	X	X	X	X	X	X	X
Oligochaeta sp. 1	X	X	X	X	X	X	X	X	X	X
Empididae sp. 1	X	X	X	X	X	X	X	X	X	X
Simuliidae sp. 1	X	X	X	X	X	X	X	X	X	X
Hydropsychidae sp. 3	X	X	X	X	X	X	X	X	X	X
Leptohyphidae sp. 2	X	X	X	X	X	X	X	X	X	X
Simuliidae sp. 2	X	X	X	X	X	X	X	X	X	X
Baetidae sp. 5	X	X	X	X	X	X	X	X	X	X
Hyalellidae sp. 1	X	X	X	X	X	X	X	X	X	
Hydropsychidae sp. 2	X	X	X	X	X	X	X	X	X	
Turbellaria sp. 1	X	X	X	X	X	X	X	X	X	
Hydropsychidae sp. 1	X	X	X	X	X	X	X	X	X	
Calopterygidae sp. 1	X	X	X	X	X	X	X	X	X	
Hydroptilidae sp. 1	X	X	X	X	X	X		X	X	X
Leptophlebiidae sp. 1	X	X	X	X	X		X	X	X	X
Glossosomatidae sp. 1	X	X	X	X	X		X	X	X	X
Coenagrionidae sp. 1	X	X	X		X	X	X	X	X	X
Leptohyphidae sp. 1	X	X	X		X	X	X	X	X	X
Hydroptilidae sp. 7		X	X	X	X	X	X	X	X	X
Baetidae sp. 1	X	X	X	X	X	X		X	X	
Calamoceratidae sp. 1	X	X	X	X	X		X	X	X	
Leptoceridae sp. 1	X	X	X	X	X		X	X	X	
Tipulidae sp. 2	X	X	X	X	X		X	X	X	
Leptophlebiidae sp. 4	X	X	X		X		X	X	X	X
Naucoridae sp. 1	X	X		X	X	X		X	X	X
Elmidae sp. 5	X	X	X		X	X	X	X	X	X
Corydalidae sp. 1	X	X	X		X	X	X	X	X	X
Elmidae sp. 12		X	X		X	X	X	X	X	X
Hydroptilidae sp. 10			X	X	X	X	X	X	X	X
Elmidae sp. 2	X	X	X	X	X		X		X	
Leptophlebiidae sp. 3	X	X	X	X	X			X	X	
Tipulidae sp. 1	X	X	X	X	X			X	X	
Perlidae sp. 2	X	X	X	X	X			X	X	
Ceratopogonidae sp. 3	X	X	X	X	X			X	X	
Leptoceridae sp. 2	X	X	X	X	X			X	X	
Leptoceridae sp. 3	X	X	X		X	X	X		X	
Perlidae sp. 1	X	X	X	X	X				X	X
Elmidae sp. 1	X	X	X	X	X				X	X
Leptohyphidae sp. 4	X	X	X	X	X				X	X
Calamoceratidae sp. 2	X	X	X	X	X				X	
Libellulidae (?) sp. 1	X	X	X	X			X	X		X
Philopotamidae sp. 3	X	X	X			X	X	X	X	
Gripopterygidae sp. 1		X	X	X	X		X	X	X	
Aeglididae sp. 1	X		X		X	X	X	X	X	
Baetidae sp. 3	X		X	X	X			X	X	X
Helicopsychidae sp. 5	X	X	X	X	X				X	
Gomphidae sp. 1	X	X	X	X			X	X		
Baetidae sp. 2	X	X	X	X				X	X	
Ceratopogonidae sp. 2	X	X	X		X		X		X	
Hydroptilidae sp. 2	X	X	X		X			X	X	
Psephenidae sp. 2		X		X	X	X		X	X	
Gripopterygidae sp. 5		X		X	X		X	X	X	

APPENDIX. Continued.

	Streams									
	1	2	4	6	7	3	5	8	9	10
Psychodidae sp. 1	X		X		X			X	X	X
Psephenidae sp. 1			X		X		X	X	X	X
Leptohyphidae sp. 3				X	X		X	X	X	X
Scirtidae sp. 1	X	X	X	X	X					
Perlidae sp. 5	X	X	X	X	X					
Hydroptilidae sp. 9	X	X	X	X	X					
Euthyplociidae sp. 1	X	X	X		X		X			
Leptoceridae sp. 4	X	X		X	X			X		
Polycentropodidae sp. 3	X	X	X		X					X
Megapodagrionidae sp. 1	X	X	X				X			X
Sericostomatidae sp. 1		X	X	X			X		X	
Elmidae sp. 6			X	X	X			X	X	
Hydroptilidae sp. 6		X			X	X	X			X
Elmidae sp. 13					X	X		X	X	X
Helicopsychidae sp. 2	X	X	X		X					
Leptophlebiidae sp. 6	X	X	X					X		
Leptohyphidae sp. 5		X	X	X			X			
Perlidae sp. 6		X	X	X			X			
Gripopterygidae sp. 4			X	X	X				X	
Hydropsychidae sp. 4			X	X	X				X	
Hydroptilidae sp. 5	X				X		X	X		
Elmidae sp. 7				X	X	X		X		
Elmidae sp. 3	X	X					X			
Polycentropodidae sp. 1	X	X						X		
Elmidae sp. 14		X			X	X				
Polycentropodidae sp. 2		X	X							X
Leptophlebiidae sp. 5	X					X		X		
Psephenidae sp. 3			X		X				X	
Elmidae sp. 10				X	X			X		
Tabanidae (?) sp. 1			X				X	X		
Philopotamidae sp. 4					X	X		X		
Phoridae (?) sp. 1							X	X	X	
Perlidae sp. 3						X			X	X
Hydroptilidae sp. 8								X	X	X
Psephenidae sp. 4	X	X								
Ceratopogonidae sp. 1	X	X								
Helicopsychidae sp. 4	X		X							
Hirudinea sp. 1	X			X						
Perlidae sp. 4	X				X					
Glossosomatidae sp. 2		X		X						
Helicopsychidae sp. 1		X		X						
Dolichopodidae (?) sp. 1		X		X						
Philopotamidae sp. 1	X					X				
Gyrinidae sp. 1			X		X					
Tipulidae sp. 3			X		X					
Hydrophilidae sp. 1		X					X			
Gripopterygidae sp. 2			X			X				
Naucoridae sp. 2				X	X					
Elmidae sp. 17				X		X				
Odontoceridae sp. 2				X						X
Gyrinidae sp. 2					X				X	
Pyralidae sp. 1						X		X		
Hydropsychidae sp. 5					X					X
Leptohyphidae sp. 8							X	X		

APPENDIX. Continued.

	Streams									
	1	2	4	6	7	3	5	8	9	10
Leptohiphidae sp. 6							X	X		
Blephariceridae sp. 1								X		X
Ceratopogonidae sp. 6	X									
Elmidae sp. 4	X									
Hydrophilidae (?) sp. 3	X									
Tipulidae sp. 6	X									
Hydrophilidae (?) sp. 4		X								
Leptoceridae sp. 8		X								
Leptoceridae sp. 7		X								
Odontoceridae sp. 3		X								
Elmidae sp. 15		X								
Gastropoda sp. 1		X								
Perlidae sp. 7		X								
Leptoceridae sp. 9			X							
Calamoceratidae sp. 2				X						
Ceratopogonidae sp. 4				X						
Ceratopogonidae sp. 5				X						
Elmidae sp. 11				X						
Elmidae sp. 8				X						
Elmidae sp. 9				X						
Helicopsychidae sp. 3				X						
Leptoceridae sp. 5				X						
Odontoceridae sp. 4				X						
Empididae (?) sp. 3				X						
Odontoceridae sp. 1				X						
Tipulidae sp. 4				X						
Ecnomidae sp. 1					X					
Ceratopogonidae sp. 7					X					
Hydrophilidae sp. 2					X					
Ephydriidae (?) sp. 1					X					
Anomalopsychidae sp. 1						X				
Elmidae sp. 16						X				
Tipulidae sp. 5						X				
Ceratopogonidae sp. 8							X			
Perlidae sp. 8							X			
Leptoceridae sp. 6							X			
Empididae (?) sp. 4							X			
Ephydriidae (?) sp. 2							X			
Hydropsychidae sp. 9								X		
Leptophlebiidae sp. 7									X	
Hydropsychidae sp. 6									X	
Gripopterygidae sp. 6									X	
Leptoceridae sp. 11										X
Elmidae sp. 18										X
Empididae sp. 2										X
Hydropsychidae sp. 8										X
Hydrobiosidae sp. 2										X
Gastropoda sp. 2										X
Hydroptilidae sp. 3										X
Gripopterygidae sp. 3										X
Baetidae sp. 4										X
Leptohiphidae sp. 7										X
Baetidae sp. 6										X
Hydropsychidae sp. 7										X
Leptoceridae sp. 10										X
Total spp.	71	80	74	74	77	42	57	67	67	52