Diversity of stream-living insects in northwestern Panamá

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Abstract. Data on species richness and diversity of aquatic insects are presented for 42 streams from four drainage areas in northwestern Panamá. 189 taxa were collected, many of which are undescribed species. Nearly 45% of the taxa were found in only one of the drainage areas. Diversities, as measured by alpha of the log series, and similarities, measured by number of expected species shared (NESS), were calculated for 25 sites in the four drainages. Diversities varied widely between streams and broadly overlap alpha diversities found in temperate streams. There was no significant correlation between insect diversity and altitude in the Panamanian streams. Similarity of Ephemeroptera faunas among streams showed two patterns: a relatively homogeneous mountain stream fauna in localities above 300 m elevation, and a much more heterogeneous fauna in lowland streams below this altitude. These patterns were less clear for other aquatic insect orders. The results suggest that variation among streams within a tropical region is as important as any "latitudinal gradient" between tropical and temperate streams.

Key words: Ephemeroptera, diversity indices, aquatic, insects, tropical streams, Panamá, alpha, similarity indices.

Along with the rising concern over the fate of tropical forests, there has been increasing attention to tropical freshwater ecosystems. One topic of interest has been the comparison of tropical and temperate streams in terms of diversity, community structure, and nutrient cycling. Yet, compared with the extent of knowledge of temperate streams, our understanding of tropical streams, with the exception of large rivers, is relatively poor. Even the rather basic question of how insect diversity in tropical streams compares with diversity in temperate streams has yet to be definitively answered.

In this paper I report data on aquatic insect diversity from a remote area of Central America. From April to June, 1985, I visited the Panamanian provinces of Chiriquí and Bocas del Toro and collected aquatic insects from 42 localities ranging from seepages on the rainforest floor to large rivers. The areas I visited (the continental divide region of Chiriquí and the Atlantic slope forests of Bocas del Toro) are considered "non-seasonal" (Wolda 1983a), but rainfall increases in April–early May, and mayfly emergence is higher at this time of year (Wolda and Flowers 1985). Although my primary objective was to study Ephemeroptera and collect and rear material for revisionary studies, it was also an opportunity to shed more light on the tropical vs. temperate diversity question. Accordingly, I collected all orders of aquatic insects in a consistent manner for later analysis. The re-

sults give a broader picture of aquatic insect diversity in Central America than has heretofore be available.

Direct comparisons of Neotropical and Nearctic aquatic insect diversities are scarce and their conclusions conflicting. Stout and Vandermeer (1975) compared five streams in Costa Rica and one in Colombia with several streams in the United States and found that the Neotropical streams had higher diversity and species richness. Pearson et al. (1986), studying a tropical stream in Australia, reported species richness even higher than that which Stout and Vandermeer found for the Neotropics. On the other hand, Patrick (1964) did not find the aquatic insects of the Amazon headwaters more diverse than insects of eastern U.S. rivers, and Stanford and Ward (1983) expressed the opinion that tropical aquatic insects are less diverse than their temperate counterparts. Wolda and Flowers (1985) compared light-trap samples of mayflies from a number of temperate countries with samples from Panamá and found that the Panamanian samples fell in the mid-range of the diversity values from the temperate areas. Often the results of a temperate-tropical comparison depend on the group of insects compared: some, like riffle beetles, are more diverse in the tropics (Brown 1981), while others, like Plecoptera, are more diverse in temperate streams (Zwick 1986). In terms of species richness in smaller streams, most studies to date

have not found streams in the tropics to be more diverse (Covich 1988).

Study Area

The streams visited in this study are located in northwestern Panamá in the provinces of Chiriquí and Bocas del Toro (Fig. 1). Streams in Bocas del Toro are on the Atlantic Slope while those in Chiriquí Province are in the headwaters of the Río Chiriquí which eventually flows into the Pacific. Collections were made from 42 sites, of which 25 provided adequate quantities of specimens for diversity analysis. Physical characteristics of these 25 sites are given in Table 1. For purposes of this study, the streams are divided into four drainage areas.

Cuenca Fortuna

This area is the catchment of the Río Chiriquí above the Proyecto Fortuna dam in the Cordillera de Talamanca. In 1977 I visited this area before construction of the dam and found a rich and diverse mayfly fauna in the river (Flowers 1979, 1987). Closure of the dam created a deep and fluctuating lake that eliminated the river insect fauna, but many species still survive in tributary streams, since the Panamanian electric authority (IRHE) purchased the entire watershed around the lake to prevent deforestation and accompanying siltation of the reservoir (Suman 1985). Principal streams visited were Quebradas Aleman (Site 8), Arena (Site 2), Honda (Site 1), and Mono (Site 4), as well as several unnamed smaller streams and forest seeps. Unnamed streams discussed further in this paper will be designated by "Fortuna [elevation]". Water temperatures ranged from 18°C in the seeps and smallest streams to 22°C in the larger streams. Stream substrates were cobble, gravel, and some large boulders. Forest seepages flowed through fallen leaves. All streams ran through primary forest or dense second growth. In 1984 a transcontinental oil pipeline was constructed between Puerto Armuelles and Chiriquí Grande; the pipe runs along the north side of the Fortuna lake, passing under a number of streams.

Palo Seco

Adjacent to Cuenca Fortuna on the Atlantic side of the continental divide is a large tract of relatively undisturbed forest, designated the Bosque Protector Palo Seco by the government of Panamá (Suman 1985). A paved road (built along with the pipeline) provides access to numerous streams. Streams sampled are unnamed tributaries of the Río Guabo and are designated here by "Palo Seco [elevation]". Stream temperatures in this area varied from 19°C to 25°C. These streams were all torrential with substrates of cobble and large boulders. The predominant vegetation was primary forest, although streambeds were unshaded at points where the pipeline road crossed them.

Laguna de Chiriquí

This area includes several lowland streams between Chiriquí Grande and Almirante. Streams sampled were the Río Guarumo and Quebrada Cañaza (Sites 17 and 18) in the lowlands inland from Chiriquí Grande, a stream at Miramar (Site 16) where a previous study of Ephemeroptera was conducted using a light trap (Wolda and Flowers 1985), a small stream and pool on the Isla San Cristobal, and two small streams (Sites 19 and 20) at a place known locally as Ojo de Agua on a low ridge behind the town of Almirante. All streams flowed through partly cleared areas and the predominant substrate type was cobble. Smaller streams (e.g., Miramar and Ojo de Agua I) contained large root masses from streamside trees. Water temperatures in these streams ranged from 24°C to 28°C.

Changuinola-Teribe

This large basin is drained by the Río Changuinola and its principal tributary, the Río Teribe. The Río Changuinola delta was extensively altered early this century for banana cultivation. The most productive sampling site was at Zegla (Site 25) upstream from the banana plantations at the conjunction of the Changuinola and Teribe. Collecting was also done in the Changuinola, Quebrada Bonyic, a major tributary of the Teribe (Site 21), Quebradas Sorciba (22) and Guabo (23) on the Changuinola, and in a number of small tributaries. The substrates of the rivers consisted of smooth cobble and gravel; those of the smaller streams consisted mainly of gravel, mud, and some cobble. Stream temperatures varied from 21°C to 30°C with the
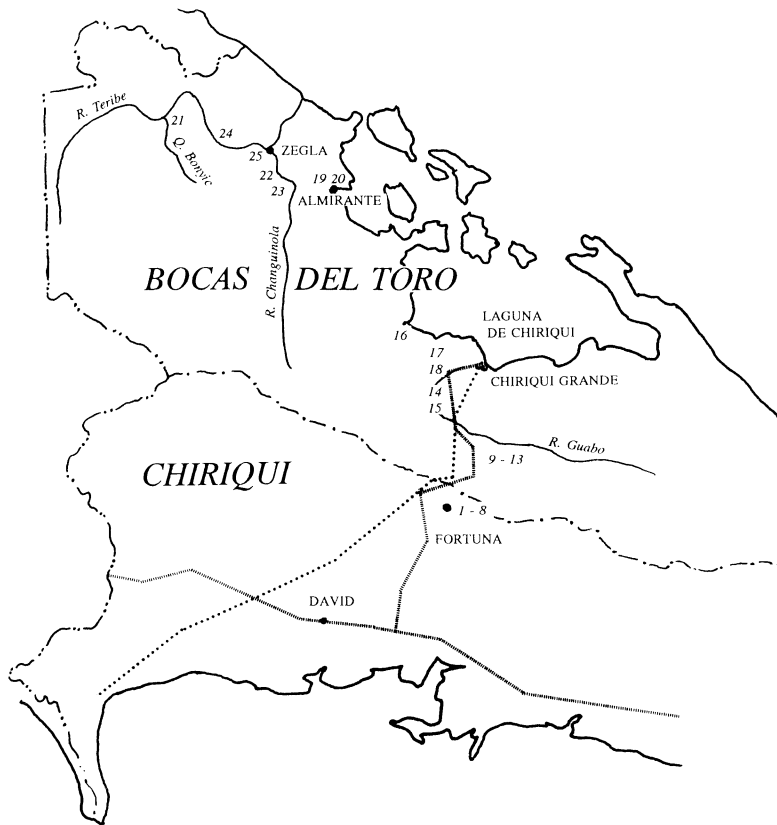
FIG. 1. Map of study area in western Panamá (redrawn from Suman 1985). ·····, oil pipeline; ——, roads; numbers refer to sites in Table 1.

highest temperatures in unshaded pasture streams in the lowlands around Zegla.

Methods

Samples were collected using a handscreen (1.5-mm mesh openings) and dipnet (1-mm mesh opening). At each site at least 3 min were spent disturbing the substrate in riffle areas. To prevent build-up of debris and loss of organisms, the 3 min were broken into 20-s periods: approximately 1 m² of substrate upstream from the net was kicked up for 20 s; the net contents were dumped into a pan and all the insects picked out; and the procedure was repeated until the 3-min total had been reached. At sites where habitats besides riffles were present, additional sampling was done, roughly one extra minute for each type of habitat. No attempt was made to compare faunas from different sub-

strates at a single site. At sites crossed by roads, all collecting was done upstream from rights-of-way (where vegetation was kept cut back). This protocol exceeds, in terms of amount of bottom substrate sampled, the recommended sampling efforts of the EPA rapid bioassessment protocol (Plafkin et al. 1989), the recommendations of Hilsenhoff (1982) for using biotic indices, and the 40-rock sample Stout and Vandermeer (1975) recommended as a minimum for an adequate assessment of species richness in tropical streams. All insects were preserved in alcohol and transported to Florida A&M University where they were identified to species or separated as far as possible into morpho-species. Ephemeroptera were identified using collections at the University; Coleoptera were identified by Dr. Paul J. Spangler, National Museum of Natural History; Plecoptera were identified by Dr. Bill Stark, Mississippi State University,

TABLE 1. Physical characteristics of 25 collecting sites in northwestern Panamá.

Stream	Elev.	Width	Temp. (°C)	Substr.	Banks	Sampling date(s)
Cuenca Fortuna						
1 Queb. Honda	1076 m	3–10 m	18.5	C, **B**	forest	15, 17, 25-V-1985
2 Queb. Arena	1068 m	3–10 m	22	G, C	forest	9-V-1985, 4-VI-1985
3 Fortuna 1121	1121 m	1–3 m	19	G, C	forest	2-VI-1985
4 Queb. Mono	1068 m	3–10 m	18.5	C	forest	1-VI-1985
5 Fortuna 1197	1197 m	1–3 m	18.5	C, **B**	forest	30-V-1985
6 Fortuna 1100	1091 m	1–3 m	—	C, B	forest	15, 19-V-1985
7 Fortuna 1182	1182 m	3–10 m	19	C, B	forest	7-V-1985
8 Queb. Aleman	1190 m	1–3 m	18	C	forest	11, 23-V-1985
Palo Seco						
9 Palo Seco 970	970 m	<1 m	19	C, **B**	forest	10-V-1985
10 Palo Seco 818	818 m	1–3 m	20.5	C	forest	10-V-1985
11 Palo Seco 576	576 m	3–10 m	21.5	C, B	forest	3-VI-1985
12 Palo Seco 549	549 m	3–10 m	22.5	C, B	forest	25-V-1985
13 Palo Seco 515	515 m	3–10 m	25	C	forest	14, 29-V-1985
14 Palo Seco 333	333 m	1–3 m	—	G, C	forest	24-V-1985
15 Río Guabo	150 m	>10 m	24.5	S, C	forest	16-V-1985
Laguna de Chiriquí						
16 Miramar	0 m	1–3 m	25	C, Lv, Rt	F, P	2-V-1985
17 Río Guarumo	76 m	>10 m	27	G, C	pasture	28-V-1985
18 Queb. Cañaza	90 m	3–10 m	26	F, G	pasture	16, 19, 24-V-1985
19 Ojo de Agua I	150 m	<1 m	24.5	C	pasture	4-V-1985
20 Ojo de Agua II	150 m	1–3 m	25	C, R	pasture	4-V-1985
Changuinola–Teribe						
21 Queb. Bonyic	±25 m	3–10 m	24.5	C	forest	25-IV-1985
22 Queb. Sorciba	80 m	1–3 m	29	G, C	pasture	27-V-1985
23 Queb. Guabo	100 m	3–10 m	21	C, B	forest	27-V-1985
24 Río Teribe, Charagres	±20 m	>10 m	25	S, C	F, P	23-V-1985
25 Río Teribe, Zegla	±15 m	>10 m	26	G	pasture	20, 25-V-1985

Substr. (substrate): F = fine particulates, S = sand, G = gravel, C = cobble, B = boulders, R = bedrock, Lv = leaf packs; Rt = root masses; dominant substrate indicated in bold. Banks (=dominant riparian vegetation): F = forest, P = pasture.

and the remaining groups were determined as far as possible to morpho-species using available literature as a guide.

The 25 sites selected for diversity and similarity analyses were those that yielded 30 or more specimens of aquatic insects during the sampling procedure. This cut-off removed a number of "non-standard" localities such as seepages, very small streams, sites that were dry until just before they were visited, and the Río Changuinola itself, which was too swift and deep to allow representative sampling. Diversity was calculated for total aquatic insects and for Ephemeroptera alone using Fisher's alpha of the log series (Wolda 1981). This index is free of two important limitations of the Shannon-Weaver, Simpson's, and other better known diversity indices: alpha is independent of sample size and it does not give excessive weight to the most common species in a sample (Wolda 1983b). Similarity between sites for Ephemeroptera was calculated using the Normalized Expected Species Shared (NESS) measure, a generalization of the Morisita index (Wolda 1983a). This generalization was originally developed by Grassle and Smith (1976) and overcomes a limitation of the Morisita and some other similarity indices: the excessive weight given to the most common species. The Grassle and Smith measure is based on comparing the number of

TABLE 2. Aquatic insect taxa collected in northwestern Panamá, showing occurrences in the four drainages visited. CF = Cuenca Fortuna; PS = Palo Seco; LC = Laguna de Chiriquí; CT = Changuinola–Teribe.

	Drainage basin					Drainage basin			
	CF	PS	LC	CT		CF	PS	LC	CT
Ephemeroptera					Baetidae C	x	x		
Traverella A			x	x	Baetidae D	x			
"T." bradleyi				x	Baetidae E		x	x	
"T." primana	x	x		x	Baetidae F		x	x	
Hagenulopsis A		x	x	x	Baetidae G			x	x
Hagenulopsis B				x	Baetidae H		x		x
Atopophlebia fortunensis	x		x		Baetidae I				x
Farrodes A	x	x	x	x	Baetidae J			x	
Farrodes B				x	Leptohyphes A		x	x	x
Farrodes C				x	Leptohyphes B		x	x	x
Terpides	x				Leptohyphes C	x		x	x
Thraulodes A		x	x	x	Leptohyphes D	x	x	x	x
Thraulodes B			x	x	Leptohyphes E	x			
Thraulodes C	x				Leptohyphes G	x			x
Thraulodes D	x				Leptohyphes J	x			x
Thraulodes E	x	x			Leptohyphes L			x	
Thraulodes F		x	x		Leptohyphes K		x	x	x
Thraulodes G	x				Leptohyphes N		x	x	
Thraulodes H	x				Leptohyphes O				x
Thraulodes I				x	Haplohyphes	x	x		
Ulmeritus			x		Tricorythodes A	x	x	x	x
Genus A nr. Thraulodes		x			Tricorythodes B	x		x	
Genus B nr. Thraulodes		x	x	x	Tricorythodes C			x	x
Moribaetis ellenae	x	x	x		Tricorythodes D			x	x
Moribaetis maculipennis	x	x			Tricorythodes E	x			
Moribaetis salvinii	x	x	x		Tricorythodes F	x			x
Moribaetis macaferti		x			Tricorythodes G			x	
Baetodes velmae	x	x			Tricorythodes H			x	x
Baetodes tritus	x	x			Tricorythodes I				x
Baetodes "tritus"-ally			x		Epeorus		x		
Baetodes A		x	x		Euthyplocia hecuba			x	x
Baetodes B			x		Plecoptera				
Baetodes C	x	x			Anacroneuria A	x	x		
Baetodes D	x	x			Anacroneuria B	x	x	x	x
Baetodes E			x		Anacroneuria C	x	x	x	
Baetodes F		x			Anacroneuria D				x
Dactylobaetis A		x	x	x	Anacroneuria E		x		
Dactylobaetis B		x	x	x	Anacroneuria F		x		
Dactylobaetis C	x	x	x		Diptera				
Dactylobaetis D	x	x			Simuliidae A	x	x	x	
Dactylobaetis E	x	x			Simuliidae B	x	x	x	x
Dactylobaetis F				x	Simuliidae C			x	
Guajirolus			x		Simuliidae D	x	x	x	
Cloeodes A		x	x	x	Tipulidae	x	x	x	
Cloeodes B	x	x	x		Chironomidae	x	x	x	x
Baetis A	x				Atherix	x			
Baetis B	x	x			Blepharoceridae	x	x		x
Baetis C		x		x	Dixidae	x			
Paracloeodes A		x	x		Culicidae				x
Paracloeodes B			x		Ceratopogonidae				x
Baetidae A			x						
Baetidae B	x		x						

TABLE 2. Continued.

	Drainage basin			
	CF	PS	LC	CT
Coleoptera				
Psephenidae	x	x	x	x
Psephenops			x	
Anchytarsus palpalis	x		x	
Anchytarsus A	x	x	x	x
Neocylloepus			x	x
Microcylloepus			x	
Heterelmis	x		x	x
Macrelmis	x	x	x	x
Phanocerus			x	x
Pseudodisersus goudotii	x		x	
Disersus longipennis	x	x	x	
Disersus uncus	x			
Hexanchorus	x	x	x	x
Cylloepus	x	x	x	
Neoelmis		x		
Austrolimnius	x			
Xenelmis	x			
Elmidae ?		x	x	x
Copelatus A	x			
Copelatus B	x			
Agametrus	x			
Limnichiidae				x
Hydrophilidae		x		
Trichoptera				
Chimarra	x	x	x	x
Helicopsychidae	x	x	x	x
Polyplectropus	x		x	
Phylloicus	x		x	
Hydropsychidae A			x	
Hydropsyche		x		
"*Potamyia*"		x	x	x
Cheumatopsyche	x	x	x	x
Leptonema	x	x	x	
Smicridea		x	x	x
Lepidostomatidae	x			
Dolophilodes	x			
Glossosomatidae	x	x		x
Polycentropus	x	x		x
Atopsyche A	x	x		
Atopsyche B		x		
Leptoceridae		x		x
Hydroptilidae	x		x	x
Oecetis	x			
Alisotrichia			x	
Nectopsyche	x		x	
"*Macronema*"			x	
Cyrnellus	x			
Parapsyche		x		

	Drainage basin			
	CF	PS	LC	CT
Xiphocentron				x
Wormaldia		x		
Odonata				
Coenagrionidae A	x	x	x	x
Coenagrionidae B	x			
Coenagrionidae C			x	
Coenagrionidae D	x			
Megalopodagrionidae A	x	x	x	x
Megalopodagrionidae B	x	x		
Megalopodagrionidae C			x	x
Megalopodagrionidae D	x			
Megalopodagrionidae E	x			
Libellulidae A			x	x
Libellulidae B			x	
Libellulidae C		x	x	x
Libellulidae D	x	x		
Libellulidae E			x	x
Gomphidae A			x	
Gomphidae B	x		x	
Gomphidae C			x	
Gomphidae D			x	
Calopterygidae A				x
Calopterygidae B	x	x		
Calopterygidae C	x			
Polythoridae	x		x	x
Lestidae	x			
Lestidae B	x			
Hemiptera				
Rhagovelia A		x	x	
Rhagovelia B	x			
Rhagovelia C				x
Rhagovelia D	x			
Rhagovelia E	x			
Rhagovelia F	x	x		
Rhagovelia G			x	
Hebridae			x	
Naucoridae:Cryphocorinae	x	x	x	x
Naucoridae:Limnocorinae	x	x		x
Belostomatidae		x		
Notonectidae	x			
Gerridae				x
Megaloptera	x	x	x	x
Lepidoptera				
Pyralidae A			x	
Pyralidae B	x	x	x	x
Pyralidae C	x			
Pyralidae D	x			

species shared in random samples of size *m* re- peatedly drawn from two populations. With a large number of repeated drawings, this num- ber will approach a fixed value which is the basis for NESS (Grassle and Smith 1976). When the parameter $m = 1$, NESS is equal to the Mori- sita index, but at larger values of *m*, less weight is given to the most common species. Because of the way NESS is calculated, *m* must be less than half the number of individuals in the smallest sample of a dataset, and empty datasets are not allowed. Like alpha of the log series, NESS is independent of sample size (Wolda 1983a). NESS values can range between 0 (no species in common between sites) to 1 or some- what greater than 1 (samples taken from the same site have an expected NESS value of 1, with a probabililty of the actual value of NESS being >1). For Ephemeroptera, NESS was cal- culated using values for *m* of 1, 8, and 18. The largest *m* that could be used for the Ephemer- optera at all sites was 8, since only 18 mayflies were collected from Site 22. When Site 22 was excluded from the dataset, *m* could be raised to 18; the similarity matrix was recalculated using this higher *m*.

Because individuals of other insect orders were taken in much lower numbers than were Ephemeroptera, it was only possible to use NESS with $m = 1$ (i.e., the Morisita index) for these groups. Similarities were calculated for Tri- choptera plus Odonata and Coleoptera plus Ple- coptera. Orders were combined in this fashion to eliminate empty datasets. Even so, it was nec- essary to delete four localities from the analysis of Coleoptera plus Plecoptera since samples from these had less than the 3 individuals necessary for the NESS formula to function, even at *m* = 1.

Results

Table 2 lists taxa collected from all 42 sites and their occurrence in the four drainage ba- sins. Almost 45% of the taxa were found only in one basin. Although nymphal Ephemerop- tera are probably the best known of any Central American immature insects, most of the nymphs from this area of Panamá could not be identified to species, and taxonomy of the larvae of other aquatic orders from this region is almost non- existent. Diversities of aquatic insects and may- flies for the 25 selected sites, along with their altitudes, are shown in Table 3. Highest total aquatic insect diversity occurred at Miramar ($\alpha = 25.87$), followed by Ojo de Agua I ($\alpha = 22.83$). Lowest insect diversity ($\alpha = 5.33$) was found in Fortuna 1197. Ojo de Agua I also had the highest mayfly diversity ($\alpha = 9.21$) and Fortuna 1197 had the lowest ($\alpha = 1.04$). Miramar and Ojo de Agua I are both at rather low altitudes in the Laguna de Chiriqui drainage; however, both streams contain species more characteristic of higher elevations. Miramar is a particularly dra- matic example of the overlap between montane and lowland faunas. The stream runs down a steep mountainside and crosses a flat sea-level plain that is only a few hundred yards wide. At the juncture of the mountain and the plain, it is possible to collect nymphs of the typically torrential mayflies *Moribaetis* and *Baetodes* along with lowland species of *Thraulodes* and *Euthy- plocia*.

Stream samples taken during this study showed differences when compared with the light-trap data of Wolda and Flowers (1985). Nymphs of the leptophlebiid mayfly *Hagenu- lopsis* were abundant in net samples but no adults were taken at light: adult *Hagenulopsis* swarm in the morning (e.g., 9 a.m. on the morning I visited), not at dusk. Another difference be- tween net and light samples was that nymphs of *Leptohyphes* in the Miramar stream were no- where near as abundant as light-trap samples of adults would lead one to expect.

Neither diversity nor species richness of the total aquatic insect fauna was significantly af- fected by altitude. Regression of alpha on alti- tude gave a slope close to zero.

Between-site similarities calculated by NESS for Ephemeroptera are shown in Figures 2 and 3. Figure 2 gives similarities when $m = 1$ and NESS is identical to the Morisita index. When *m* is raised to 8 (Fig. 3), more weight is given to rare species and more cells in the upper left of the matrix show similarities greater than 0.50. At this higher *m*, the homogeneity of the moun- tain stream insect fauna in Cuenca Fortuna and Palo Seco becomes more apparent. Increasing *m* still further to 18 (not shown) produced only slight changes in that five additional cells in the Fortuna–Palo Seco area of the matrix rose above 0.05.

Figure 4 shows similarity matrices for the study sites using Trichoptera and Odonata. Low numbers at several sites limited the analysis to

TABLE 3. Diversity of samples of Ephemeroptera and aquatic insects at 25 collecting sites.

	Alt.	Ephemeroptera			Total Insecta		
		N[a]	s[b]	$\alpha \pm$ SD	N[a]	s[b]	$\alpha \pm$ SD
Cuenca Fortuna							
1 Queb. Honda	1076 m	50	10	3.78 ± 1.19	138	40	18.88 ± 2.99
2 Queb. Arena	1068 m	139	23	7.87 ± 1.64	239	43	15.29 ± 2.33
3 Fortuna 3700	1121 m	37	13	7.16 ± 1.98	59	27	19.21 ± 3.70
4 Queb. Mono	1068 m	161	9	2.07 ± 0.69	205	23	6.64 ± 1.38
5 Fortuna 3950	1197 m	48	4	1.04 ± 0.52	68	14	5.33 ± 1.43
6 Fortuna 3600	1091 m	47	9	3.32 ± 1.10	75	18	7.49 ± 1.77
7 Fortuna 3900	1182 m	73	9	2.71 ± 0.90	108	22	8.34 ± 1.78
8 Queb. Aleman	1190 m	164	16	4.40 ± 1.10	257	40	13.26 ± 2.10
Palo Seco							
9 Palo Seco 3200	970 m	152	12	3.06 ± 0.88	213	32	10.44 ± 1.84
10 Palo Seco 2700	818 m	128	14	4.02 ± 1.07	165	27	9.16 ± 1.76
11 Palo Seco 1900	576 m	115	10	2.64 ± 0.83	152	26	9.00 ∓ 1.77
12 Palo Seco 1800	549 m	132	12	3.22 ± 0.93	164	24	7.73 ± 1.58
13 Palo Seco 1700	515 m	368	18	3.97 ± 0.94	523	44	11.44 ± 1.72
14 Palo Seco 1100	333 m	63	14	5.56 ± 1.49	73	20	9.06 ± 2.03
15 Río Guabo	150 m	61	9	2.93 ± 0.97	88	24	10.85 ± 2.22
Laguna de Chiriquí							
16 Miramar	0 m	207	24	7.04 ± 1.49	361	70	25.87 ± 3.09
17 Río Guarumo	76 m	182	14	3.54 ± 0.95	236	34	8.25 ± 1.56
18 Queb. Cañaza	90 m	206	20	5.48 ± 1.22	263	34	10.39 ± 1.78
19 Ojo de Agua I	150 m	56	18	9.21 ± 2.17	103	39	22.83 ± 3.66
20 Ojo de Agua II	150 m	54	9	3.10 ± 1.03	73	17	6.95 ± 1.69
Changuinola–Teribe							
21 Queb. Bonyic	±25 m	71	17	7.10 ± 1.72	149	31	11.89 ± 2.14
22 Queb. Sorciba	80 m	18	8	5.56 ± 1.96	43	19	12.98 ± 2.98
23 Queb. Guabo	100 m	55	8	2.59 ± 0.91	84	22	9.68 ± 2.06
24 Río Teribe, Charagres	±20 m	127	8	1.90 ± 0.67	164	20	5.96 ± 1.33
25 Río Teribe, Zegla	±15 m	371	18	3.96 ± 0.93	550	34	8.00 ± 1.37

[a] Number of individuals; [b] number of species or morphospecies.

$m = 1$ (the Morisita index). Figure 4 suggests that for these two orders, faunas above 300 m are slightly less homogeneous and faunas below this level are slightly more so, compared with the Ephemeroptera. Data on Plecoptera and Coleoptera (not shown) did not give meaningful results with NESS owing to low numbers collected and the number of sites that could not be included.

Discussion

As the insect fauna of northwestern Panamá becomes better known, the apparent high level of endemicity and undescribed species found in this study will almost surely decrease. Two insect groups that may have been significantly under-collected are hydroptilid caddisflies and Chironomidae. Hydroptilidae were abundant at lights in the lowlands, and in the Rio Teribe large numbers of empty pupal cases drifted in the current. However, collecting larvae of this family can be difficult, even in streams where light trapping indicates they should be abundant (Dr. Steven Harris, University of Alabama, personal communication). Chironomidae, which also can be very abundant in tropical streams (e.g., Bishop 1973, Boon et al. 1986), were infrequently taken during this study. In part, this may have been due to bias caused by using nets that allowed small larvae to escape through the relatively coarse mesh. On the other hand, light trapping during this study produced relatively few adult chironomids.
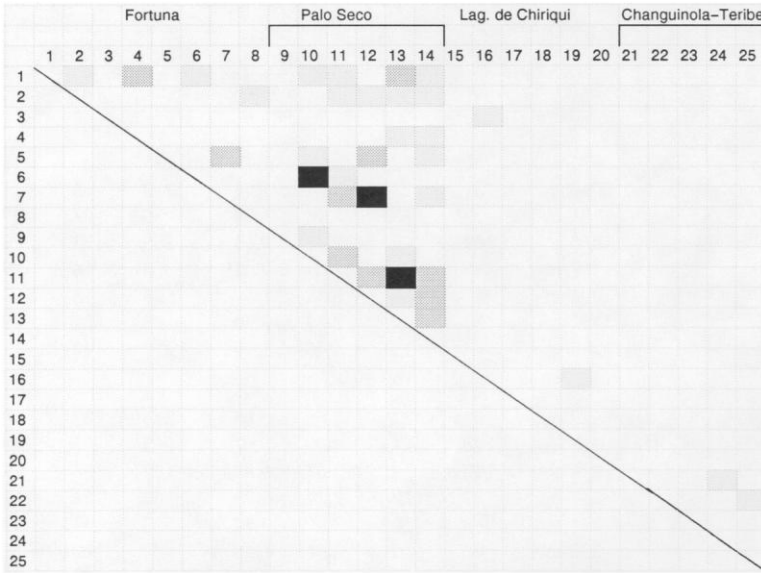
FIG. 2.   Between-site similarity matrix for Ephemeroptera at $m = 1$. White cells, <0.50; light grey cells, 0.50–0.69; dark grey cells, 0.70–0.89; black cells, >0.90. Sites are numbered as in Table 1.

Overall, the sampling method used here produced data consistent with that from other tropical stream studies in terms of species richness. Numbers of taxa collected from the 25 streams in Table 2 are comparable to the total taxa (44) actually collected by Stout and Vandermeer (1975) in their Costa Rican streams; it should be noted that their maximum richness of 132 species, sometimes quoted in the literature, is a theoretical maximum calculated from species-sample curves. Similarly, the high richness reported from Yuccabine Creek in Australia by Pearson et al. (1986) was for cumulative data taken over a year, which undoubtedly gave a more realistic picture of a biota's richness and diversity.

Although alpha diversity is independent of sample size, data from this study show how local environmental conditions can affect diversity estimates directly through their effects on communities, or indirectly by limiting the sampling effort of the researcher. Ojo de Agua I and II (Sites 19 and 20) are two small streams running along opposite edges of a small pasture. Ojo I, a relatively slow stream shaded by large trees, had the highest mayfly diversity and the second highest aquatic insect diversity, while Ojo II, a torrential stream of small pools and solid rock flumes with little shade, had low val-

ues for both mayfly and insect diversities. A second example involves the two sites on the Rio Teribe (Sites 24 and 25). At Charagres (24) the river was wide with a deep channel; only a relatively small proportion of the bottom was accessible to net sampling. At Zegla, less than 3 km downstream and at the mouth of the river, the water flowed over a series of shallow gravel bars as a result of an unusual lack of rain during the dry months of 1985 (A. González, personal communication), and almost all of the river could be reached by wading. During a year of normal rainfall, the river at Zegla is much higher, which would restrict sampling efforts and thus probably yield lower diversity estimates.

To put these diversity values in broader context, Table 4 compares alpha diversities for total aquatic insects of several tropical and temperate streams. All data from streams outside Panamá are for immature forms collected in a manner comparable to the method used in my study. Values for the most diverse, mid-range, and least diverse streams in this study are shown, as well as values from both the literature and some other tropical collections I have made. Because raw numbers of insects per collection, rather than densities, are needed to calculate alpha, relatively few published studies could be used in this comparison, and the studies used here may
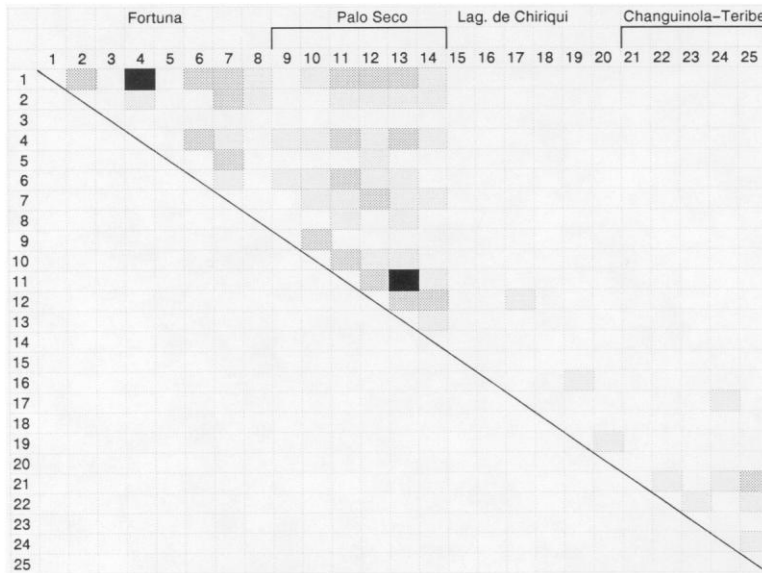
FIG. 3. Between-site similarity matrix for Ephemeroptera at $m = 8$. Numbers and symbols as in Figure 2.

not show the full range of diversities of temperate insect faunas. While tropical streams can show high diversities, Table 4 also shows an almost complete overlap in ranges of the tropical-temperate diversities and there is no significant difference between means for tropical and temperate diversities in this sample.

Although some data suggest that tropical insect diversity is greatest at mid-elevations (Janzen 1973), long-term light trap data of Panamanian terrestrial groups show a decrease in diversity at higher altitudes (Wolda 1987), whereas stream collecting in the Blue Mountains in Jamaica showed the reverse trend (Boon et al. 1986). Collecting methods and the type and intensity of human disturbance may affect the results of these diversity-altitude studies (Wolda 1987). Although no altitudinal gradient in the Panamá streams can be inferred from the diversity or species richness data in my study, replacement of mayfly species within genera was evident as I traveled between the upper and lower altitudes. A transition point appeared to be at around 300 m and this change is reflected in the similarity matrices (Figs. 2, 3) which show a lack of any significant similarity in the upper right cell quadrant where Laguna de Chiriquí and Changuinola Teribe sites intersect with Fortuna and Palo Seco sites.

Hynes (1971) studied a river in Trinidad and

recognized a "rhithron-potamon" break below 30 m. He noted that this dividing line was considerably lower than similar divisions proposed in other studies. However, Hynes's data also show a second "boundary" near 245 m, where 12 "low elevation" taxa first appear in his samples. Interestingly, half of these taxa were mayflies of the Baetidae and Tricorythidae, families that were well represented in the lowland streams in Panamá. That second "boundary" in Hynes's Trinidad data may be analogous to the 300 m montane-lowland boundary suggested by my study.

Between-site similarities of Panamá streams, as measured by the Ephemeroptera fauna, are relatively low, especially at lower elevations. Streams in the Cuenca Fortuna and Palo Seco drainages (all above 300 m, upper left of the matrices) show evidence of having a homogeneous mayfly fauna. This evidence becomes more pronounced as m increases from 1 to 18, reflecting the increasing contribution of the rare species to the similarity estimates. This intermediate-altitude fauna is characterized by nymphs of *Moribaetis*, *Baetodes* (especially *B. velmae*), and *Camelobaetidius* (=*Dactylobaetis*, McCafferty and Waltz 1990). These mayfly nymphs are well adapted to the fastest currents found in this region, and can be found clinging to faces of large boulders or even the vertical sides
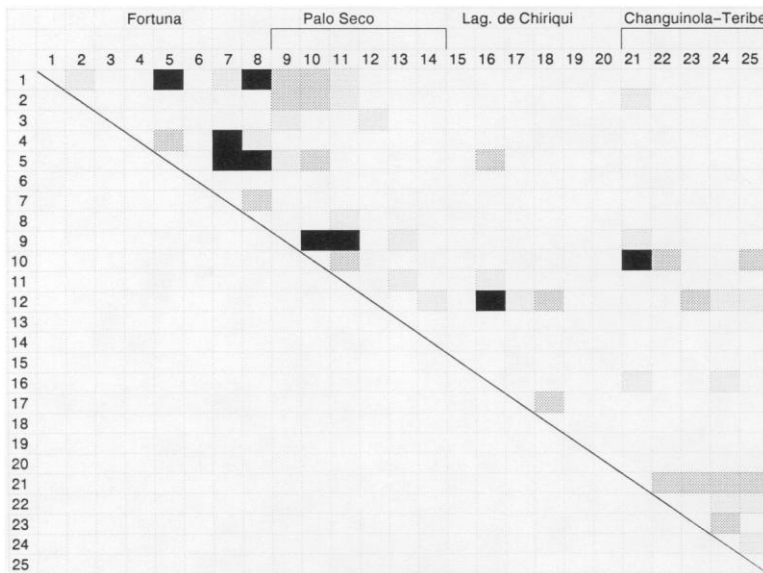
FIG. 4.   Between-site similarity matrix for Trichoptera + Odonata at $m = 1$. Numbers and symbols as in Figure 2.

of waterfalls. In more sheltered areas, large *Thraulodes* nymphs and several species of *Leptohyphes* are typically encountered. Lowland streams (Changuinola-Teribe and Laguna de Chiriquí sites) typically had a great variety of small Baetidae species, many of which were found in only one or two streams. There is no evidence of higher similarity within the Atlantic slope (Palo Seco, Laguna de Chiriquí, Changuinola-Teribe) and Pacific slope (Cuenca Fortuna) drainages than between them; this result is not unexpected, given that the continental divide in the study area is only a few meters above Quebrada Arena (Site 2) and presents no barrier to flying adults.

The measures of alpha and beta diversity used here are relatively untested in freshwater ecosystems (although Shepard 1984 used alpha of the log series in a study of stream insects in Idaho, and NESS was developed for marine ecosystems) but their excellent performance with terrestrial faunas (Wolda 1981, 1983a, 1983b) as well as general dissatisfaction with better known diversity measures (Resh 1988) suggests that NESS and alpha of the log series may have a place in freshwater ecology. However, future studies in which NESS is to be used should be carried out keeping in mind the limitations of using a high m: an adequate number of indi-

viduals of the taxa being compared must be present in every sample. If m is to be 20, every sample must have at least 41 individuals. For this reason, NESS may not be suitable for short-

TABLE 4.   Diversity of some tropical and temperate samples of immature aquatic insects. Sites are listed by decreasing diversity.

Locality	alpha
Panama—Miramar[a]	25.87
Idaho—Big Smoky Creek[b]	14.89
Costa Rica—Río San Josecito (700 m)[c]	11.21
Panama—Queb. Cañaza[a]	10.39
Ecuador—Río Matadero trib. (3300 m)[d]	9.08
Costa Rica—Río San Lorenzo[c]	8.44
New York—Susquehanna River[c]	8.10
Costa Rica—Río Puerto Viejo (50 m)[c]	7.95
Florida—Withlacoochee River[e]	7.90
Japan—River Kaunnai[f]	5.95
Panama—Fortuna 1197[a]	5.33
Indiana—Black Creek[g]	3.89
Peru—Río Huallaga (1900 m)[h]	3.65
Peru—Río Huallaga (3600 m)[h]	1.87
Idaho—Portneuf River[b]	1.84

[a] Present study; [b] Shepard (1984); [c] Flowers, unpublished data; [d] Turcotte and Harper (1982a, 1982b); [e] WAR (1990); [f] Okazawa (1975); [g] McCafferty (1978: maximum value); [h] Illies (1969).

term studies of less common taxa. However, this limitation will be less important in long term studies and, with the development of aquatic field stations in Costa Rica and elsewhere, such studies will be much easier to conduct in future years.

This study, while not denying that individual tropical streams can be highly diverse in insect life, nevertheless further undermines the "diversity gap" that some have reported to exist between "temperate" and "tropical" stream ecosystems, and highlights the variation found among streams within a tropical region. This variation, when more thoroughly documented, may swamp any "latitudinal gradient" in aquatic insect diversity. The generally low similarity between sites in Panamá mirrors low estimates obtained by Patrick (1975) when she compared biotas of 15 North American streams.

These results add weight to what seems to be a growing belief among aquatic biologists that patchiness of resources and local conditions are more important than latitudinal gradients in explaining the structures of aquatic insect communities. This should not be unexpected. The vast difference between diversities of temperate and tropical terrestrial insects, so often noticed by entomologists, is variously attributed to the structural complexity of tropical vegetation (Klopfer and MacArthur 1961), or the radiation of angiosperms and their attendant pollinators, herbivores, and seed dispersers (Regal 1977). The recent estimates of huge numbers of tropical insect species in rainforest canopies is probably a function of the fine-grainness and botanical species richness of the canopy habitat (Erwin 1988). Such complexity is lacking in tropical stream ecosystems where the primary producers are algae. Both temperate and tropical stream biotas are based on the same basic food sources of detritus and periphyton (Patrick 1975), and while fresh tropical forest leaves may have driven an explosion in the diversity of terrestrial insects, the breakdown products of these same leaves in running water has not had an analogous effect on aquatic insects.

Acknowledgements

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