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The effect of riffle-scale environmental variability on macroinvertebrate assemblages in a tropical stream

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Abstract

In a tropical stream (at the Soberanía National Park, Panama), different environmental factors were quantified in riffle habitats (water characteristics: velocity, depth, turbulence, and direction; stone characteristics: surface area, sphericity, and degree of burial; and others: substrate type, and canopy cover). Characteristics of macroinvertebrate assemblages (mean density of individuals, mean taxon richness, and cumulative taxon richness in three stones at each riffle) were related to both mean values and variability of these environmental factors at riffle scale. Macroinvertebrate density was higher in shallow, fast flowing, stony riffles, with low variability in dominant substrate type. Taxon richness was also higher in shallow riffles with loose, not buried stones, and water direction more or less parallel to the bank. Environmental variability resulted as important as mean values of environmental factors to explain variation in macroinvertebrate assemblages. This is the first study, to our knowledge, that quantifies substratum variability and demonstrates its influence on macroinvertebrate assemblages in a tropical stream.

Introduction

Streams are highly variable ecosystems over space and time (Cooper et al., 1997), and this applies to the physical environment and to the structure and dynamics of stream-dwelling communities. Moreover, abiotic and biotic variation depends on the scale of observation, as has been demonstrated both in temperate (Downes et al., 1993; Boyero, 2003a) and tropical (Boyero & Bailey, 2001; Boyero & Bosch, 2002, 2004) streams.

Spatial variability or heterogeneity of the benthic environment, and its relationship with spatial variation of macroinvertebrate communities, have been examined on multiple occasions (e.g. Hart, 1978; Davis & Barmuta, 1989; Hart & Horwitz, 1991; Downes et al., 1998, 2000; Boyero, 2003c; and references in Vinson & Hawkins, 1998). However, stream ecologists have only recently began to quantify environmental variability, and this quantification has occurred mainly at riffle scale or comparable spatial scales. For example, Palmer et al. (2000) quantified the spatial distribution of sand and leaf patches in stream sites 20 m long, and demonstrated the influence of patch spatial arrangement on the abundance of chironomids and copepods. Beisel et al. (2000) quantified substratum heterogeneity at mesohabitat scale and found a relationship between assemblage characteristics and some heterogeneity measures, and Boyero (2003b) obtained similar results at a smaller spatial scale (225 cm^2 plots). Sanson et al. (1995) quantified surface roughness of stones, which represents a form of heterogeneity at a smaller scale. The influence of environmental variability on macroinvertebrate communities, however, has scarcely been explored in tropical streams, and quantification of substratum variability has not yet been performed, at any spatial scale, at these latitudes.

Given that environmental variability determines many biotic patterns in streams (Palmer et al., 1997), the variability of some environmental factors may be more relevant for macroinvertebrate assemblages than the mean values of these factors, at least at given spatial scales. In the present study, we measure various environmental factors at riffle scale in a tropical stream, and quantify both their mean values and variability. We investigate the relative role of the mean value and the variability of each factor on the density and taxon richness of stone macroinvertebrate communities.

Material and methods

The study was performed in May 2002 in a segment of the Río Frijoles, within the Soberanía National Park, Panamá. This stream has been described before by other authors (e.g. Power, 1990). The study segment was approximately 2 km long, with a mean width of 4.5 m, and was composed of alternating riffles and pools. Within the study segment, we selected 28 riffles (in a few cases, intermediate conditions between riffle and run) with an approximate length of 10 m. Channel width at the study riffles ranged from 1.7 to 7.9 m, water depth ranged from 1 to 55 cm, and current velocity ranged from approximately 0 to 84 cm/s.

Within each riffle, three individual stones randomly distributed within the riffle were lifted and washed within a 63 μm mesh hand net, so all macroinvertebrates were removed and fell into a bottle placed at the end of the net. Stone surface area was measured following Doeg & Lake (1981). Some environmental factors were recorded at 10 uniformly distributed positions within each riffle: current velocity (in m/s); water depth (in cm); surface area of the nearest stone (in cm^2); sphericity of that stone: $(bc/a^2)^{1/3}$ (a being the first axis, b the second axis and c the third axis of the stone; Gordon et al., 1992); water direction (categorized as 0: 0–10°, 1: 10–20°, 2: 20–45°); water turbulence (categorized as 0: no turbulence, 1: low degree of turbulence, 2: high degree of turbulence); canopy cover (categorized as 0: no cover, 1: cover); degree of burial of that stone (categorized as 0: no burial, 1: less than 20% of the stone buried, 2: more than 20% of the stone buried); and dominant substrate type (stones, gravel, sand, mud, bedrock, or leaf litter).

We calculated the mean and variability of each of these riffle-scale environmental factors. Mean values were calculated as the average, for quantitative variables (current velocity, water depth, and stone sphericity), or the mode, for qualitative variables (all other variables; substrate type was here considered only as 'mainly sand', 'mainly cobbles', and 'others'). Variability of these environmental factors was calculated by the coefficient of variation (CV), for quantitative variables, and by the Shannon diversity index, for qualitative variables. The CV (standard deviation/mean) adjusts the sample variance by the mean and thus is a better comparative measure of variability than the variance itself (Palmer et al., 1997). The Shannon index has been previously applied to measure environmental variability (e.g. Beisel et al., 2000).

In the laboratory, samples were processed and macroinvertebrates were identified to the lowest taxonomic level possible, using available literature (Roldán, 1988; M. Springer, unpublished taxonomic keys). For each riffle, assemblage structure was described by the following variables: (1) mean density: average value of density in the three stones (being density calculated as the number of individuals per m^2); (2) mean taxon richness: average number of taxonomic groups in the three stones, being richness estimated by rarefaction (based on Magurran, 1988) to eliminate the effect of differences in the number of individuals; and (3) cumulative richness: total number of taxonomic groups found in the three stones, also estimated by rarefaction.

Variables were tested for normality using the Kolmogorov–Smirnov test, for homocedasticity using the Bartlett test, and for correlations between means and variances (using Statistica 5.5, StatSoft, Inc.). Variables which not attained the normality or homocedasticity assumptions were log-transformed, although the ANOVA is quite robust against these violations (Lindman, 1974); this is not the case when correlations between means and variances exist (Lindman, 1974), but they were not found in any case.

Given the low number of samples within each riffle, a one-way ANOVA was used to test if variation among samples within a riffle was higher than variation among riffles (for mean density, mean richness and cumulative richness, all log-transformed).

Relationships between each assemblage characteristic (mean density, mean richness and cumulative richness) and the mean and variability of the environmental factors were examined by stepwise regression models (backward direction), performed with JMP 4.0.1 (SAS Institute, Inc.). The probability to enter and the probability to remove a variable were 0.250 and 0.100, respectively. In each model, the assemblage characteristic was the dependent variable, and all the environmental factors were the independent variables or predictors. The categorical predictors (modes of qualitative variables) were included in the model as dummy variables (therefore, one dummy variable when only two categories were present, e.g. canopy cover; two dummy variables when three categories were present, e.g. water turbulence; etc).

Results

Forty-nine taxonomic groups of macroinvertebrates were found (Table 1), belonging to the Ephemeroptera, Plecoptera, Trichoptera, Coleoptera, Heteroptera, Odonata, Lepidoptera, Hydracarina, Hirudinea, and Mollusca. The total number of individuals found in the 84 sampled stones was 860. The number of individuals per stone ranged from 1 to 111 individuals (mean$\pm$SE $= 10.2 \pm 1.6$), the density ranged from 43.8 to 7192.5 individuals per m^2 (669.0 ± 1.2), and taxon richness ranged from 1 to 16 taxa per stone (5.3 ± 0.4), and from 4 to 23 taxa per riffle (11.2 ± 0.9). The assemblage characteristics and environmental factors recorded at each riffle are summarized in Figure 1.

The one-way ANOVAs showed that variation among riffles was higher than variation within riffles for all the assemblage characteristics: mean density ($F_{27,56} = 13.17$, $p < 0.0001$), mean richness ($F_{27,56} = 3.08$, $p = 0.0002$), and cumulative richness ($F_{27,56} = 4.88$, $p < 0.0001$).

The stepwise regression models relating macroinvertebrate assemblages with the environmental factors were highly significant in all cases: mean density, adjusted $r^2 = 0.58$, $F_{7,27} = 6.22$, $p = 0.0006$; mean richness, adjusted $r^2 = 0.58$, $F_{7,27} = 6.33$, $p = 0.0005$; cumulative richness, adjusted $r^2 = 0.67$, $F_{8,27} = 7.83$, $p = 0.0001$. Seven environmental variables were related to mean density and mean richness, and eight variables were related to cumulative richness (Table 2). Mean density was mostly related to mean water depth, variability of substrate type, and mean current velocity. Density was higher with low water depth, high current velocity, and low variability in substrate type. Both mean and cumulative taxon richness were mostly related to mean water depth, mean water direction, and mean and variability of stone burial. Richness was also higher with low water depth, flow more or less parallel to the bank, and most stones not buried, lying on the stream bottom.

Discussion

Our results indicate that variation in macroinvertebrate assemblages in our tropical stream is, at the riffle scale, mediated by both mean values and variability measures of environmental factors. Riffle-scale variation in macroinvertebrate density was related to four measures of mean environmental characteristics and three measures of variability. Variation in mean richness was explained by three mean environmental characteristics and two values of variability; and finally, cumulative richness was related to three mean and four variability values. This indicates that variability is as important as mean environmental parameters in order to understand macroinvertebrate patterns of distribution, as was pointed out by Palmer et al. (1997).

Although there are too many studies that have demonstrated an effect of environmental variability on macroinvertebrate assemblages (e.g. Beisel et al., 1998; Lance et al., 2003; and see references in the Introduction), these studies are very scarce in tropical streams (but see Flecker, 1997). Similarly, studies that quantify environmental variability in streams are now common (e.g. Sanson et al., 1995; Minshall & Robinson, 1998; Beisel et al., 2000;

Table 1. Total number of individuals of each taxonomic group found on 84 stones in riffles of the Río Frijoles (n.i. – non-identified specimens)

Taxonomic group	# Individuals	Taxonomic group	# Individuals
Ephemeroptera		Coleoptera (cont.)	
Baetis	14		
Baetodes	66	Elmidae n.i.	25
Camelobaetidius	3	Psepheninae	45
Leptohyphes	41	Ptilodactylidae	1
Tricorythodes	88	*Gyretes*	1
Farrodes	25	Diptera	0
Euthyplocia	6	Orthocladiinae	133
Plecoptera	0	Tanypodinae	17
Anacroneuria	1	Chironominae	36
Trichoptera	0	Chironomidae n.i.	35
Smicridea	29	*Simulium*	12
Hydropsychidae	122	Ceratopogonidae	2
Polycentropus	15	*Maruina*	2
Polyplectropus	9	Psychodidae	17
Mayatrichia	3	Tabanidae	1
Hydroptilidae	6	Heteroptera	0
Glossosomatidae	7	*Potamocoris*	8
Chimarra	7	Odonata	0
Wormaldia	2	Megapodagrionidae	1
Marilia	1	Zygoptera	4
Limnephilidae	1	Lepidoptera	0
Leptoceridae	1	Pyralidae	19
Helichopsychidae	1	Hydracarina	0
Phylloicus	1	Hydracarina n.i.	26
Trichoptera n.i.	4	Hirudinea n.i.	0
Coleoptera	0	Hirudinea n.i.	5
Heterelmis	6	Mollusca	0
Hexacylloepus	1	Planorbiidae	2
Xenelmis	1	Gastropoda n.i.	1
Phanocerus	1	Bivalvia n.i.	5

Palmer et al., 2000; Boyero, 2003b) but, to our knowledge, this is the first study that quantifies substratum variability and demonstrates its influence on macroinvertebrate assemblages in a tropical stream.

In our study stream, numbers of individuals were higher with low water depth, low substrate type variability, and high current velocity. These factors indicate that higher macroinvertebrate densities may be related to shallow, fast-flowing, stony riffles, which had been previously found to harbour high abundances of macroinvertebrates, compared to other types of habitat, e.g. pools (Brown & Brussock, 2001) or bedrock riffles (Robson & Chester, 1999). The low variability of dominant substrate types does not imply necessarily low substrate heterogeneity, but rather it means that the same type of substrate (e.g. stones) was dominant throughout the whole riffle. In fact, stony riffles usually contain different substrate sizes, from cobbles to sand, and thus can be considered as heterogeneous habitats.

Richness was also higher in shallow riffles, mostly with loose stones lying on the bottom. These stones have larger surfaces available to harbour macroinvertebrates, mostly on their

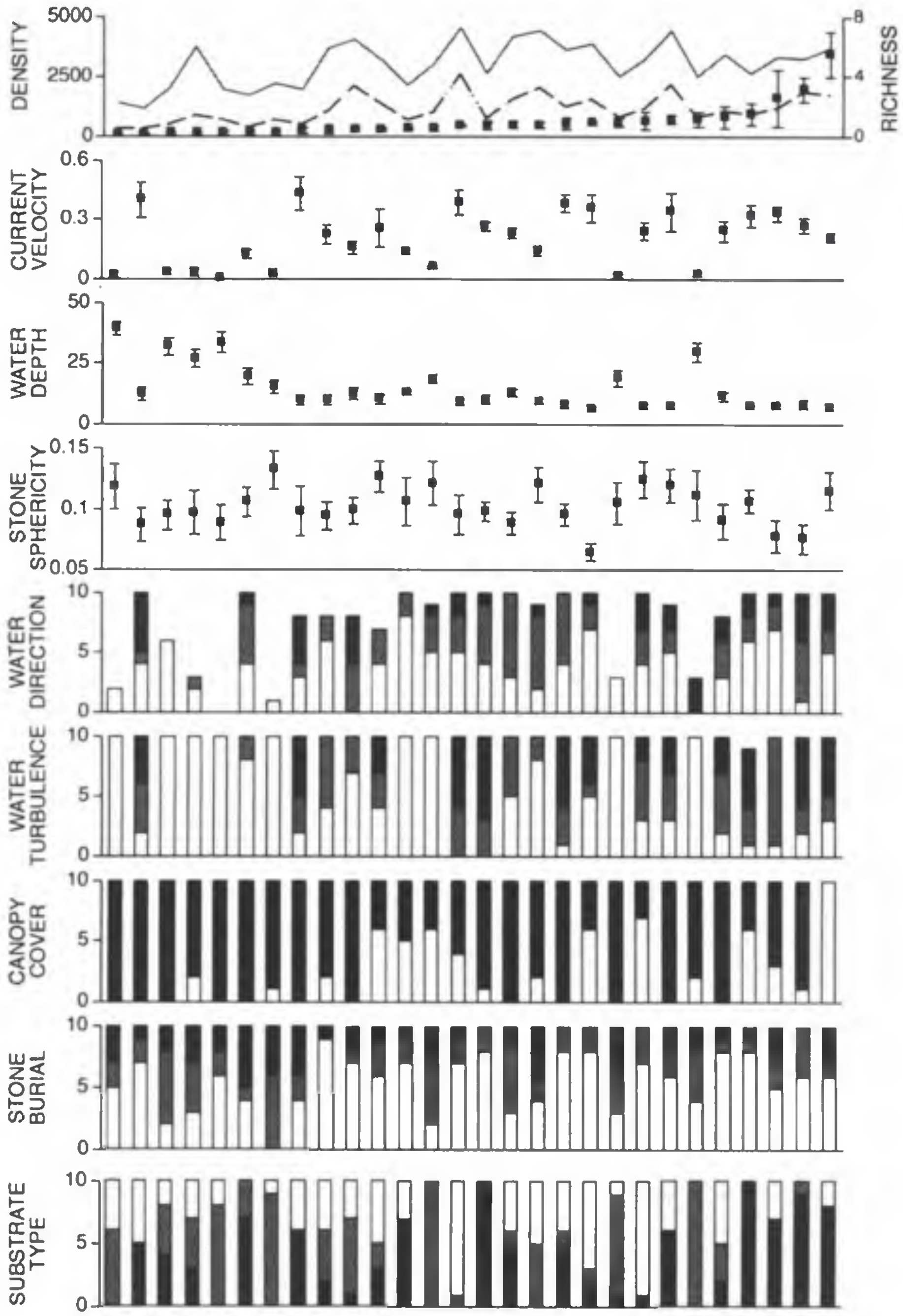

Figure 1. (Variability (mean ± SE for continuous variables, and counts for categorical variables) of the assemblage characteristics and environmental factors recorded at each of the 28 sampled riffles in the Río Frijoles. From up to down: density (number of individuals per m^2, represented by points), mean richness (mean number of taxa per stone, represented by the broken line), and cumulative richness (number of taxa per riffle, represented by the solid line); current velocity (in m/s); water (in cm); stone sphericity (index calculated from the three stone axes); water direction (white: 0–10°, grey: 10–20°, black: 20–45°; incomplete bars denote lack of data because water was not moving at that point); water turbulence (white: no turbulence, grey: low degree of turbulence, black: high degree of turbulence); canopy cover (white: no cover, black, cover); stone burial (white: no burial, grey: less than 20% of the stone buried, black: more than 20% of the stone buried); dominant substrate type (black: sand, grey: stones, white: others).

Table 2. Mean value (*M*) and variability (*V*) of the environmental factors that are related to macroinvertebrate assemblage characteristics (mean density of individuals, mean taxon richness, and cumulative taxon richness) at riffle scale, explored through stepwise regression models

Variables in the model	$F_{1,27}$	p	Sign
Mean density			
M water depth	20.50	0.0002	–
V substrate type	15.60	0.0008	–
M current velocity	9.05	0.0070	+
M stone sphericity	8.77	0.0077	–
V canopy cover	4.70	0.0424	+
V current velocity	4.63	0.0439	–
M canopy cover	4.62	0.0440	–
Mean richness			
M water depth	23.60	<0.0001	–
M water direction (0 & 1–2)	15.40	0.0008	–
M stone burial (0–1 & 2)	6.74	0.0173	–
V stone burial	6.57	0.0186	–
M stone burial (1–2)	5.78	0.0261	–
V current velocity	5.59	0.0283	–
M water direction (0–1)	4.72	0.0421	–
Cumulative richness			
M water depth	32.8	<0.0001	–
M water direction (0 & 1–2)	17.5	0.0005	–
M stone burial (0–1 & 2)	11.00	0.0037	–
V stone burial	10.20	0.0048	–
M water direction (0–1)	7.27	0.0143	–
V substrate type	6.69	0.0181	+
V current velocity	6.27	0.0216	–
V canopy cover	3.78	0.0668	+

The r^2, F and p-value of the whole models are given in the text, while F and p-values of each variable and the sign of the relationship (positive or negative) are shown here. Categorical variables were included as one or more dummy variables in the model (e.g. mean stone burial, which categories were 0, 1, and 2, was included as two dummy variables: 0–1 & 2, and 1–2).

underside, which is usually the habitat preferred by many taxa. The low water depth is usually associated with the dominance of stones in the substrate. Also, the fact that richness was higher when water direction is mostly parallel to the bank may indicate the presence of not very large stones, which could have produced a higher deviation in water direction.

Variability of substrate type positively affected cumulative taxon richness, that is, riffles with more types of dominant substrate harboured more taxa. For example, stony riffles with patches of leaf litter and/or bedrock may contain taxa that are not present in riffles only dominated by stones, e.g. *Simulium* is usually found on bedrock surfaces, while shredder taxa as the Leptoceridae or the Pyralidae use to dwell in leaf litter.

Density and richness were higher when canopy cover was more variable, that is, when both open and shaded sites occurred in the same riffle. Mean canopy cover also influenced density, in this case negatively, that is, numbers of invertebrates were higher in more open riffles. This could be related to the higher growth of periphyton in sun-exposed sites, which serves as food for grazer taxa, as can be many taxa present in the Río Frijoles (e.g. Baetidae, Elmidae, Hydroptilidae, Helicopsychidae, Mollusca). Some studies have found that periphyton growth is related to higher macroinvertebrate densities and richness (e.g. Towns, 1981). Zimmerman & Death (2002) found no differences in density and richness with periphyton growth, but high differences in taxonomic composition, finding grazers and generalist taxa in open sites, while in shaded sites, the more abundant taxa were others commonly found in forest streams.

Further work is needed in order to explore the relationships between environmental variability and macroinvertebrate assemblages at multiple spatial scales at tropical latitudes. Streams are extremely heterogeneous systems at multiple scales, ranging from millimetres to tens of kilometers (Cooper et al., 1997), and thus variability can be detected and quantified at a whole range of scales. The patch and the riffle are probably among the most relevant scales to detect macroinvertebrate variation (Boyero, 2003a), given that environmental variability at these scales may affect individuals in their search for resources and their movement patterns (Boyero, 2003b).

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