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Altitudinal replacement of Ephemeroptera in a subtropical river

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Abstract

An altitudinal sampling transect was established in a subtropical mountain river to determine if replacement between two mayfly faunal components (oligostenothermal and polystenothermal) occurred. We detected three main groups: Group A, species with high abundance at higher stations, declining abruptly downstream; Group B, species with maximum abundance at lower elevations; either declining abruptly upstream or absent from higher elevations; and Group C, species with little elevational change. The physical and chemical variables did not change abruptly with altitude during our winter sampling, although the distribution of groups A and B species did. The observed distributional patterns of groups A and B do not appear to be correlated with variations in the physical and chemical variables surveyed.

Introduction

According to Illies (1969), the South American lotic entomofauna is composed of two major ecological sections: the 'oligostenothermal', or cool-adapted group and the 'polystenothermal' or warm-adapted group. The oligostenothermal species tend to inhabit cool streams and rivers in southern Argentina and Chile, as well as high mountain streams of northern Argentina. Polystenothermal species are widely distributed in the rivers of the subtropical and tropical lowlands. Illies' (1969) divisions, based mainly on Plecoptera, were meant to represent biogeographical and phylogenetic units. Pescador & Peters (1980) and Savage (1987) extended this concept to mayflies. However, Savage (1987) also included concepts of geological centers of ancestral origin, probably trying to incorporate a historical perspective and deemphasize the role of temperature. Although it was known that these two faunal components actually coexisted in some rivers, the patterns of coexistence and replacement remained unknown (Dominguez & Savage, 1987). Almost no altitudinal transects have been made on South American rivers, except for Illies' (1964) study on the invertebrate fauna of the Huallaga river, Perú. Illies collected from 4100 m down to 600 m, except for a gap between 1900 and 600 m; however, his data were only qualitative.

The Tucumán Province of northwestern Argentina, (27° S, 66° W) provides the unusual condition of both oligostenothermal and polystenothermal faunas inhabiting the same rivers, some of which fall from approximately 4500 m to 600 m in elevation. At most sites, records of the cool-adapted genera always come from above 2000 m, below 800 m. As part of an extended study on Tucumán's mayfly fauna, we established a sampling transect in order to determine the pattern of faunal turnover over most of that interval up to an elevation of 1780 m. Unfortunately it was not possible to sample higher in that river. Because water temperature is thought to be the main factor determining mayfly distributions, we expected to find a gradual replacement of one fauna by the other with declining elevation.

Study area

The Rio Cañas-Horcones (Fig. 1) is a third order stream, draining from the Mala Mala hills of the Sierras del Anconquija, which are a component of the Sierras Pampeanas orographic system. These mountains with some peaks over 5500 m of elevation, consist of metamorphic rocks, transformed from marine sediments deposited during the Precambrian-Cambrian (Aceñolaza & Toselli, 1981).

The stream begins at approximately 3500 m of elevation and drains into the Rio Los Sosa at 450 m. Stream headwaters are located in high-elevation grasslands. At 2000 m, the stream enters forests of alder (*Alnus acuminata* HBK), which at 1500–1300 m grades into deciduous forest mainly of 'Horco Cebil' (*Parapiptadenia excelsa* (Grisebach) Lillo), and at 1200–900 m, into a species rich subtropical mountain forest, the yungas, (Hueck, 1978). Our highest station (1780 m) occurred in alder forest, our lowest (620 m) in subtropical mountain forest. The river increases in size gradually from about 1 m in width with a depth of 35 cm at the first station to 4 m in width and 1 m in depth at the last station. Throughout the intervening length, the canopy is open with a substrate of rocks and sand. The size of the rocks and percentage of sand vary with the slope, but these changes are not correlated with altitude. In the low current segments, the rocks are covered with Chlorophyta.

Methods

We made a single transect, in winter (July) 1986. We chose winter to avoid unpredictable changes in the faunal composition caused by synchronous transformation of nymphs into adults, which occurs in spring and summer. We were not able to sample also in the other seasons as we wanted originally due to the particular characteristics of the river. Samples were taken every 50 m change in elevation from 1780 to 620 m of elevation. We took two subsamples at each station, one at the stream margin and the other in the main channel at a depth of 40–50 cm. Mayflies from both subsamples were placed in the same vial. We used a kicking pad net, spending the same time and effort at each location. One additional sample was taken in a small tributary at 1220 m. It was used the Spearman rank correlation coefficient = r_s [Siegel & Castellan, 1988] between numbers sampled and elevation to establish the distributional groupings.

Results and discussion

We collected nymphs of 10 mayfly species from 3 different families (Table 1). Of these, one species (*Baetodes* sp. 2) occurred at only one station (770 m) and another (*Baetis* sp. 4) at only two stations (820 and 720 m).

The remaining species appear to form 3 distributional groups

Group A. Species with maximum abundance at higher elevations, declining abruptly downstream (*Baetis* sp. 1 [$r_s = 0.599$, $p < 0.002$] and *Baetis* sp. 2 [$r_s = 0.776$, $p < 0.001$]).

Group B. Species with maximum abundance at lower elevations, either declining abruptly upstream (*Thraulodes consortis* Dominguez [$r_s = -0.659$, $p < 0.001$] and *Dactylobaetis* sp. 1 [$r_s = -0.725$, $p < 0.001$]) or absent from higher elevations (*Leptohyphes* sp. 1 [$r_s = -0.606$, $p < 0.002$] and *Baetis* sp. 3 [$r_s = -0.653$, $p < 0.001$]).

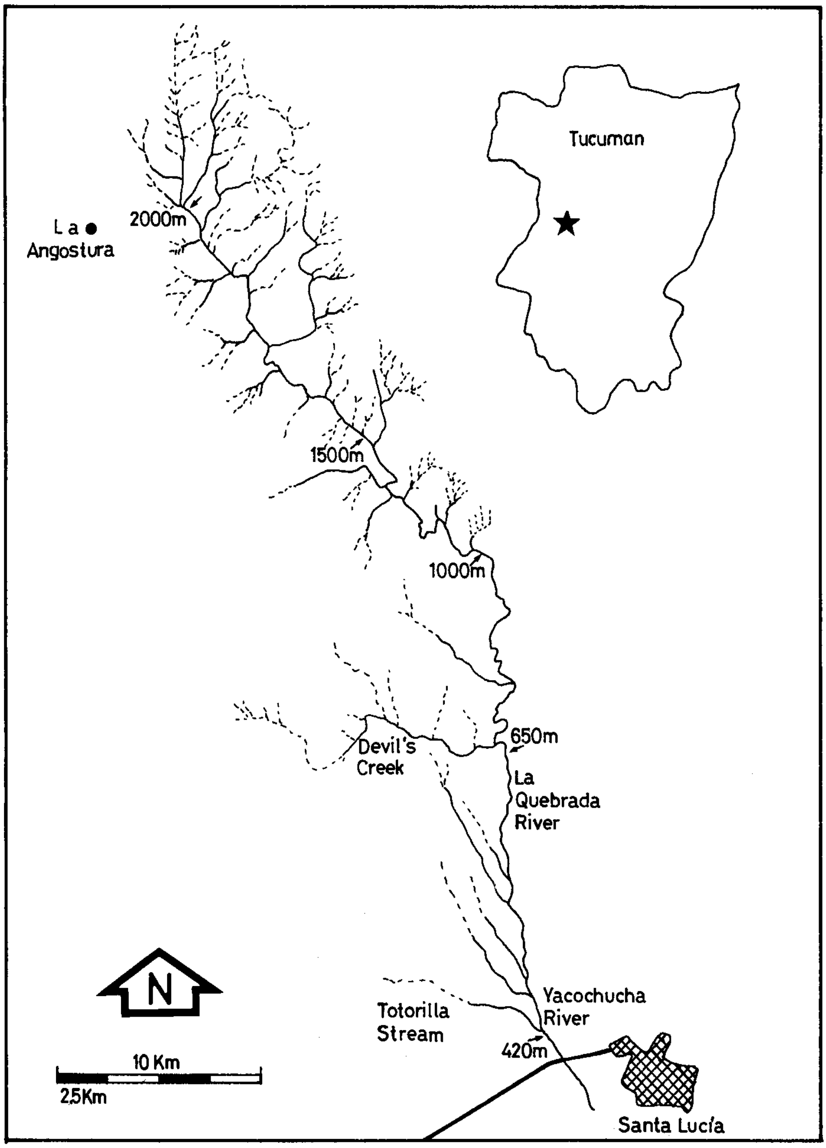

Fig. 1. Map of the Cañas Horcones River System. Star: location of the study area in Tucumán province.

Group C. Species with little elevational change in abundance (*Baetodes* sp. 1 [$r_s = -0.064$, $p > 0.05$] and *Meridialaris tintinabula* Pescador & Peters [$r_s = 0.242$, $p > 0.05$]).

No significant change was found in the coefficient when the tributary sample (station 12) was excluded.

Within the Leptophlebiidae, *M. tintinabula* is a typically cool-adapted species, inhabiting rivers of the Patagonian plains, and extending northward at higher elevations in the Andes. It is interesting that *M. tintinabula* (Fig. 2) showed no significant elevational pattern in the portion of the stream investigated. In contrast the other leptophlebiid, *T. consortis*, clearly a lowland species from the tropics and subtropics, increasingly uncommon at higher elevations and latitudes. These two genera have been thought to be phylogenetically distant, although this is now in doubt (Savage, 1987; Flowers & Dominguez, 1991). In our

Table 1. Species composition and abundance at each of the 25 stations.

Taxon	Station numbers																								
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Meridialaris tintinabula	45	10	27	28	15	12	31	24	37	32	60	5	55	17	39	34	40	29	45	20	30	4	10	3	0
Thraulodes consortis	0	3	1	0	1	0	3	1	0	5	1	33	2	2	4	4	5	2	1	2	17	4	9	25	19
Beatodes sp. 1	1	1	2	8	3	0	3	2	6	3	0	0	4	1	2	5	4	3	5	4	0	3	2	0	3
Baetis sp. 1	38	7	2	2	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0
Baetis sp. 2	6	4	17	24	8	11	13	5	3	0	1	4	1	2	1	1	1	2	3	1	0	3	0	0	0
Dactylobaetis sp. 1	0	0	0	2	2	2	4	3	1	19	1	0	1	0	5	6	5	8	16	13	5	19	9	15	11
Leptohytes sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2	1
Baetis sp. 3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	1	2	4	0	2
Baetis sp. 4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2	0	0
Baetodes sp. 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Total number/samples	90	25	49	64	29	25	54	35	47	59	63	45	63	22	51	50	55	46	71	40	56	37	36	45	36
Species/sample	4	5	5	5	5	3	5	5	4	4	4	4	5	4	5	5	5	6	6	5	6	8	6	4	5

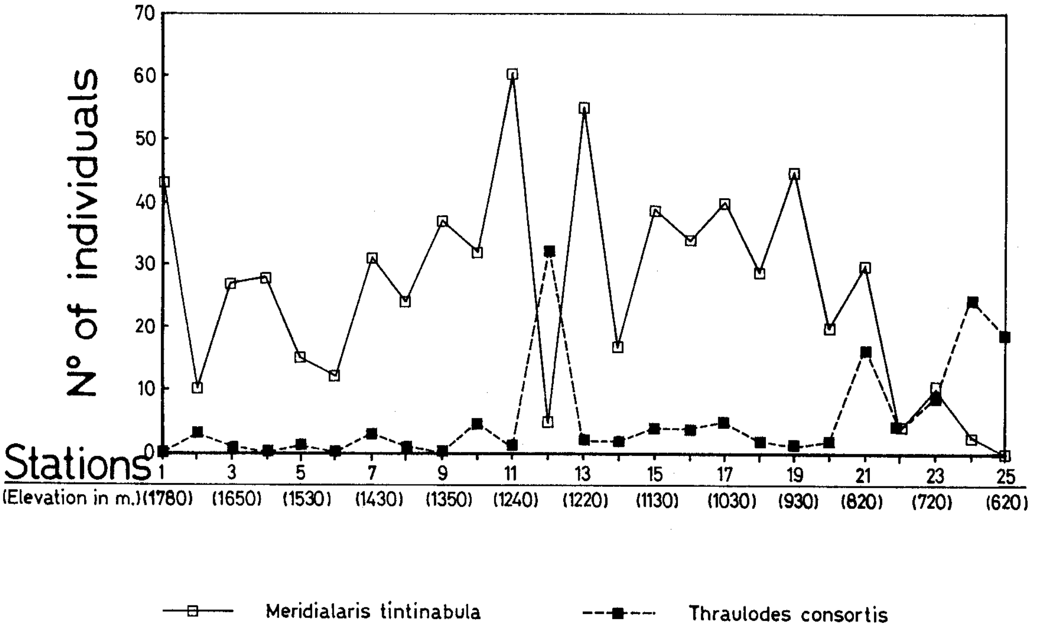

Fig. 2. Abundance of two species of Leptophlebiidae, *Meridialaris tintinabula* Pescador & Peters and *Thraulodes consortis* Dominguez, along the altitudinal gradient.

study no significant pattern of replacement was detected between these two leptophlebiid species ($r_s = -0.385$, $p > 0.05$). However we observed an unusual pattern in the additional sample taken from a tributary at 1220 m (station 12), only 3 m above its junction with the main river (where sample 13 was taken) and with all measured physical parameters identical between the samples taken in winter (see Table 2). The numerical relationships were totally inverted (Fig. 2), with 33 individuals of *T. consortis* at station 12 (1 and 2 in stations 11 and 13, respectively) and 5 specimens of *M. tintinabula* (60 and 55 in stations 11 and 13).

Table 2. Physical and chemical data for 25 sampling stations in winter, 1986.

Factor	Station 1	2	3	4	5	6	7	8	9	10	11	12	13
Elevation	1780	1700	1650	1600	1530	1480	1430	1380	1350	1300	1240	1220	1220
Air T. °C	7	10	10	9	11	11	10	7	7	8	10	8	8
H_2O T. °C	8	9	9	9	9	9	9	9	9	9	9	9	9
pH	6.8			6.4	6.8	6.5	6.8	6.5	6.5	6.5	6.5	6.4	6.4

Factor	Station (cont.) 14	15	16	17	18	19	20	21	22	23	24	25
Elevation	1180	1130	1080	1030	980	930	880	820	770	720	670	620
Air T. °C	9	9	9	9	11	11	11	8	11			
H_2O T. °C	9	9	10	10	9	10	10	9	9			
pH	6.5	6.5	6.5	6.5	6.5	6.5	6.5	6.5	6.5	6.5	6.5	6.5

In the Baetidae, the situation is more complex, due to insufficient knowledge on the systematics and distribution of this family. *Dactylobaetis* sp. 1 (Fig. 3) follows broadly the tendency of *T. consortis* (Fig. 2). *Baetis* sp. 2 (Fig. 3) diminishes gradually downstream and maintains a presence at low elevations. In contrast, *Baetis* sp. 1 occurred at the uppermost station but disappeared totally by stations 5 (1530 mm) except for a brief reappearance at the tributary station 12. Nearly the opposite patterns occurred in *Baetis* sp. 3, which appears for the first time at station 18 (980 m) and was collected at most of the remaining downstream stations.

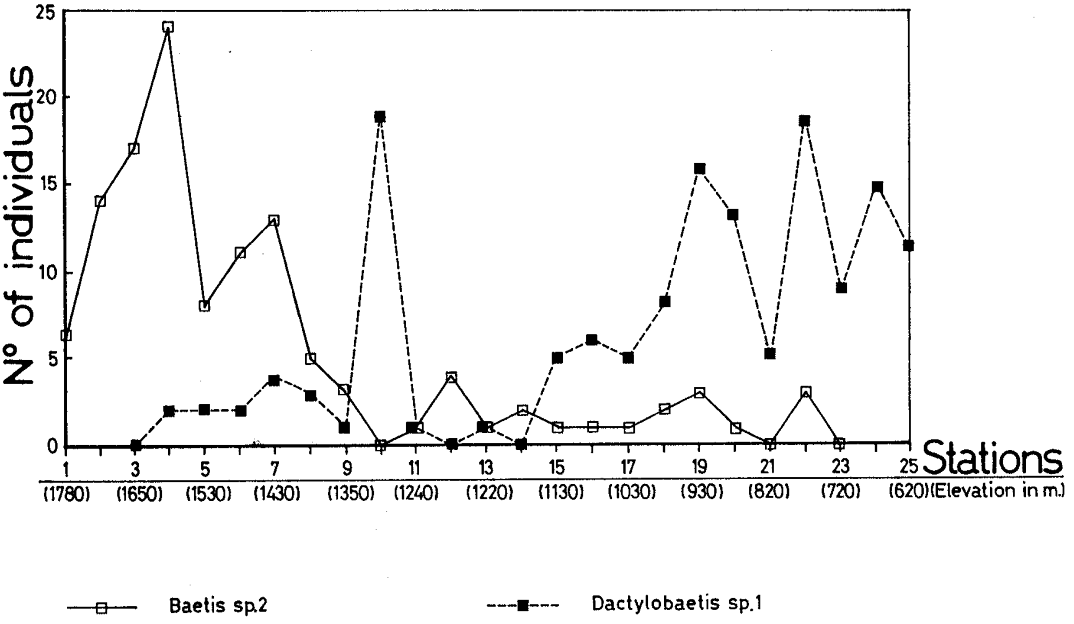

Fig. 3. Abundance of two species of Baetidae, *Baetis* sp. 2 and *dactylobaetis* sp. 1, along the altitudinal gradient.

Conclusions

Many factors can affect the distribution of benthic animals along altitudinal gradients. water temperature is believed to be one of the most important (Ward & Stanford, 1982). In this preliminary study, the physical and chemical variables measured (air temperature, water temperature and pH) (Table 2), did not change abruptly in winter although the fauna did so. According to Ward & Berner (1980), several physical and chemical variables including water temperature, pH and total dissolved salt, changed radically over the entire year with altitude in a Colorado (USA) mountain stream. Nevertheless, they found a general pattern of addition of species in the downstream direction without loss of those present at higher elevations, except for a sharp faunal break in the lower foothills at an elevation between 1750–1600 m. We had less species in the Cañas-Horcones river, but we found also a faunal break at an altitude of 770–670 m. However, it is very difficult to compare rivers that differ greatly in faunal and ecological conditions.

At this point, it appears that neither water temperature nor altitude alone determines the distribution of mayfly fauna components along an altitudinal gradient in the Tucumán area. This is evidenced by the radical change of the fauna between stations 12 and 13 (Fig. 2, Table 1), despite the similar physical conditions in winter. Furthermore, Dominguez in Dominguez & Savage (1987) working in the neighboring Sierras de Medina and de Burruyacu, found *Thraulodes* and *Farrodes*, two supposedly warm-adapted genera, to be abundant at 1550 m in the absence of cool-adapted genera. Thus, the distinction between cool-adapted and warm-adapted South American aquatic entomofaunas may result more from past history than from current ecological traits.

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References

Aceñolaza, F. G. & A. J. Toselli, 1981. Geología del Noroeste Argentino. Publ. esp. Fac. Cienc. Naturales. Univ. Nac. Tuc. N° 1287; San Miguel de Tucumán 1–212.

Dominguez, E. & H. M. Savage, 1987. Two new species of *Farrodes* from Continental South America with comments on the distribution of faunal components in Argentina (Ephemeroptera:Leptophlebiidae). Stud. Neotrop. Fauna Envir. 22: 43–52.

Dodds, G. S. & F. L. Hisaw, 1925. Ecological studies on aquatic insects. IV. Altitudinal range and zonation of mayflies, stoneflies and caddisflies in the Colorado Rockies. Ecology 6: 380–390.

Flowers R. W. & E. Dominguez, 1991. Preliminary cladistics of the *Hermanella* complex (Ephemeroptera:Leptophlebiidae). Proc. VI Int. ephemeroptera Conf. Granada, Spain: 49–62.

Hueck, K., 1978. Los bosques de Sudamérica. Ecología, composición e importancia económica. Soc. Alemana Coop. Tec. (GTZ), Eschborn. 476 pp.

Hynes, H. B. N., 1970. The ecology of running waters. Univ. Toronto Press, Toronto.

Illies, J., 1964. The invertebrate fauna of the Huallaga, a Peruvian tributary of the Amazon River, from the sources down to Tingo Maria. Verh. Int. Ver. Limnol. 15: 1077–1083.

Illies, J., 1969. Biogeography and ecology of Neotropical freshwater insects, especially those from running waters. In Fittkau *et al.* (eds), Biogeography and Ecology in South America. Dr W. Junk, The Hague. Vol 2: 685–707.

Pescador, M. L. & W. L. Peters, 1980. Phylogenetics relationships and zoogeography of cool-adapted Leptophlebiidae Ephemeroptera) in Southern South America. Adv. Ephemeroptera Biol. Flanagan J. F. & K. E. Marshall (eds): 43–56.

Savage, H. M., 1987. Biogeographic classification of the Neotropical Leptophlebiidae (Ephemeroptera) based upon geological centers of ancestral origin and ecology. Stud. Neotrop. Fauna Envir. 22: 199–222.

Siegel, S. & N. J. Castellan, Jr. 1988. Nonparametric statistics for the behavioral sciences. 2nd edn. McGraw-Hill, New York.

Ward, J. V. & L. Berner, 1980. Abundance and altitudinal distribution of Ephemeroptera in a Rocky Mountain stream, In J. F. Flanagan & K. E. Marshal (eds), Advances in Ephemeroptera Biology. Plenum Publ. Corp., New York: 169–177.

Ward, J. V. & J. A. Stanford, 1982. Thermal responses in the evolutionary ecology of aquatic insects.