

## Structure of water mite taxocoenoses in two northwestern Argentinean subtropical sub-catchments

HUGO R. FERNÁNDEZ\*

*Facultad de Ciencias Naturales e Instituto Miguel Lillo, Universidad Nacional de Tucumán, Argentina*

*\*Present Address: Flathead Lake Biological Station, The University of Montana, Polson, Montana 59860-9659 USA. E-mail: hugof@selway.umt.edu*

### Abstract

Hydrachnidia water mites were examined in eight streams with similar chemistry from two sub-catchments that did not differ with respect to precipitation predictability ( $P > 0.05$ ). This study describes the structure of this taxonomic segment of the invertebrate community as species diversity, relative abundance, and composition. Twenty-two water mite species were found in this study. Following rarefaction to sub-samples of 170 individuals, expected richness for these eight subtropical streams was lower ( $E < 16$ ) than found for a tropical stream ( $E = 23$ ). Species composition and the log-normal distribution of species were similar in the two sub-catchments. However, richness and diversity show significant differences between the two sub-catchments ( $P < 0.05$ ). The results suggest that similar seasonal rainfall pattern (contingency  $> 65\%$ ) does not guarantee similar patterns of diversity and richness in neighboring sub-catchments.

**Key words:** benthic, stream, diversity, richness, predictability, constancy, contingency

### Introduction

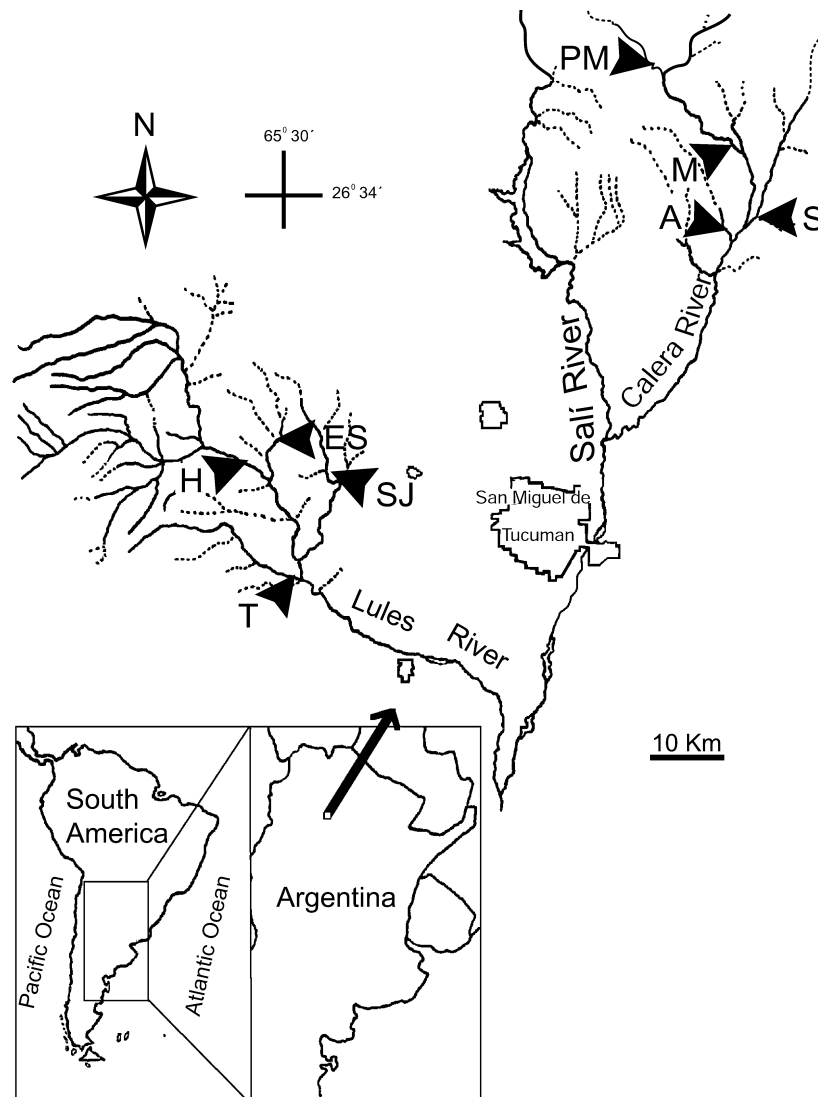
Some knowledge of the northwestern Argentinean water mites (Figure 1) would add one more piece to the incomplete puzzle of the Neotropical river ecology, especially with regard to the streams in many regions that have received little or no attention (Covich 1988). Despite of their abundance and ubiquity, Hydrachnidia (the true water mites) have often been neglected in aquatic ecology studies because of their small size, taxonomic problems, and general difficulty in identification (Proctor & Pritchard 1989). Thus, we still lack basic information on water mite ecology (see reviews by Di Sabatino *et al.* 2000, 2002). In the Neotropical region, some ecological information about the taxocoenotic structure and trophic relationships of Hydrachnidia can be found from tropical (Böttger 1980) as well as subtropical (Matveev *et al.* 1989) and temperate areas (Ferradás *et al.* 1987; Balseiro 1992).

The physical forces that define stream morphology influence the benthic community, but relevant structural elements will vary as a function of scale. The hierarchical approach has been especially useful in describing stream structure (Frisell *et al.* 1986, Fisher 1997). At the catchment level, the physical pattern is determined by the floods, which can be considered the relevant structural element (Resh *et al.* 1988). In natural systems, diversity is correlated with the spatial and temporal heterogeneity (Turcotte & Harper 1982, Stanford & Ward 1983, Huston 1994). Spatial heterogeneity reflects the physical structure of the environment while temporal heterogeneity reflects the regularity or constancy of one or several climatic variables. Temporal heterogeneity can be measured from the predictability of the climatic variables that influence the stream structure and therefore the benthic community. In a study on Ecuadorian rivers, Jacobsen *et al.* (1997) suggested

that spates regime and maximum temperature gradient might determinate the richness of stream invertebrate communities. In their study of a South American tropical stream, Turcotte and Harper (1982) found that streams are controlled by a regularly recurrent event in areas with dry and wet seasons. Thus, if there are no differences in the predictability of one structurally important element (spates) in two watersheds, we will expect similar richness and diversity patterns of the taxocoenosis considered.

The temporal pattern and volume of precipitation allow us to describe the forces that determine the structure of the streams in the area of interest. This pattern may be described by the parameters defined by Colwell (1974, see analysis of data), and can be analyzed with regard to its influence on the water mite taxocoenotic structure in two neighboring sub-catchments.

This study compared the taxocoenotic water mite structure (richness and diversity) from two neighboring streams with similar annual precipitation regimes.



**FIGURE 1.** Location of sampling sites in Lules and Calera subcatchments. Insets are continental map and regional map showing sampling area. (References: A, Artaza, ES, El Siambon, H, de la Hoyada, M, Medina, PM, Padre Monti, S, Sunchal, SJ, San Javier, T, Las Talitas.)

## Materials and Methods

### Study sites

Two adjacent sub-catchments (Lules river at 26° 47' S, 65° 28' W and Calera river at 26° 27' S, 65° 57' W) within the Salí-Dulce drainage, a 14,130 km<sup>2</sup> catchment in northwestern Argentina (Tucumán province) were studied (Figure 1). Four streams representing a range of stream segments (*sensu* Frisell *et al.* 1986) were sampled within each sub-catchment. Elevation ranged from 900 m to 1,000 m above sea level. The Lules and Calera sub-catchments (SC<sub>1</sub> and SC<sub>2</sub>, respectively) are located in an area with a subtropical climate (Figure 1), with nearly all of the annual precipitation falling between November and March (> 80% from December to January; Table 2). River discharge has a single maximum, typical of a monsoonic rainfall regime (Villalba *et al.* 1992). Precipitation during winter is < 5 mm per month.

The streams are running through a low subtropical mountain forest dominated by deciduous trees ("yungas" phytogeographical province). Although these trees reach considerable size, they are generally not adjacent to the stream during winter because the active stream channel is > 25 m wide (higher water during summer fills this channel). The stream substrate is heterogeneous, consisting mainly of pebbles, cobbles and boulders. The sites consisted mainly of riffles, without aquatic macrophytes or macroalgae (except some cases of *Cladophora sp.*). Preliminary chemical analyses indicate moderately soft waters in both sub-catchments, with 60-180 mg l<sup>-1</sup> bicarbonate and an average conductivity of 300 µS cm<sup>-1</sup>. These analyses indicate the waters had low Nitrate-N (< 2 mg l<sup>-1</sup>) and Phosphate-P (< 0.20 mg l<sup>-1</sup>) concentrations, and high dissolved O<sub>2</sub> concentrations (> 6 mg l<sup>-1</sup>). Principal Components Analysis confirmed that between-site variation in chemistry (ionic, conductivity and nutrients) was low (Fernández, unpublished data).

### Sampling of water mites

Water mites were sampled quantitatively at 8 stations (Figure 1), 4 in each sub-catchment (SC), during the winter of 1991 using a Surber sampler (area 900 cm<sup>2</sup> and 200 µm mesh size). The substratum within the Surber sampler was stirred to a depth of about 5 cm. Two random sample units were collected near mid-stream at each site and pooled together into a single sample unit (area = 1,800 cm<sup>2</sup>) to reduce the variability.

### Analysis of data

Temporal patterns were expressed as Predictability (P), Constancy (C), and Contingency (M) (Colwell, 1974), which are non-parametric measures of data expressed as temporal series of nominal or metric data (Atmar, 2001). Predictability is a measure of the pattern produced by a periodic phenomenon and is determined by one of the other components (C, M) or by a combination of both. The constancy is the inverse measure of the amplitude variation, being at maximum when the state is the same for all classes of time. Contingency represents the magnitude in which the time determines the state, being at maximum when a strong seasonal pattern is present.

Data on total monthly precipitation of 10 years (starting in 1977) at two stations located approximately in the geographic center of each sub-catchment (close stations T and M in Figure 1) were used. Precipitation classes were arranged following various authors as log<sub>2</sub> precipitation to address the correlation between means and standard deviations (Table 3). The predictability index may be calculated for any cyclic phenomena that can be scored for at least two states over at least two time periods or phases of the cycle, for as many cycles as possible. The equation for uncertainty with respect to time or  $H(x)$  is:

$$H(x) = -\sum \frac{x_j}{z} \log \frac{x_j}{z}$$

Where

$x_j$  = columns totals

$z$  = grand total

Uncertainty with respect to state or  $H(y)$  is:

$$H(y) = -\sum \frac{y_i}{z} \log \frac{y_i}{z}$$

Where

$y_i$  = row total.

Uncertainty with respect to interaction of time and state is:

$$H(xy) = -\sum \sum \frac{N_{ij}}{z} \log \frac{N_{ij}}{z}$$

Where

$N_{ij}$  = be the number of cases for which phenomenon was in state  $i$  at time  $j$  of cycle.

Constancy will be:

$$C = 1 - \frac{H(y)}{\log s}$$

Where

$s$  = number of states.

Contingency will be:

$$M = \frac{H(x) + H(y) + H(xy)}{\log s}$$

#### *Structure of the taxocoenosis*

To analyze the structure of the taxocoenosis at the two sub-catchments, the data were adjusted to the theoretical distribution models of abundance and richness of species as representative of its organization (Ludwig & Reynolds 1988). For this, the data were analyzed empirically through the species-abundance curve (Figure 2). I fit a log-normal distribution to the species abundance data and calculated an expected distribution and the goodness of fit was determined by a  $\chi^2$  - test (Magurran 1989). If the test confirms the adjustment, I calculated the  $\lambda$  parameter as a measure of diversity from the estimated value of richness, ( $R_t$ ) in the normal logarithmic curve (Ludwig & Reynolds 1988).

The  $\lambda$  parameter is defined as:

$$\lambda = R_t / S$$

Where

$R_t$  = total richness expected.

$S$  = standard deviation.

#### *Diversity of the water mite assemblages*

Two non-parametric indices were used to test the heterogeneity in each sub-catchment and to compare them. These indices represent alternative descriptions of the species-abundance relationship in communities (Ludwig & Reynolds 1988) as a measure of taxocoenosis structure.

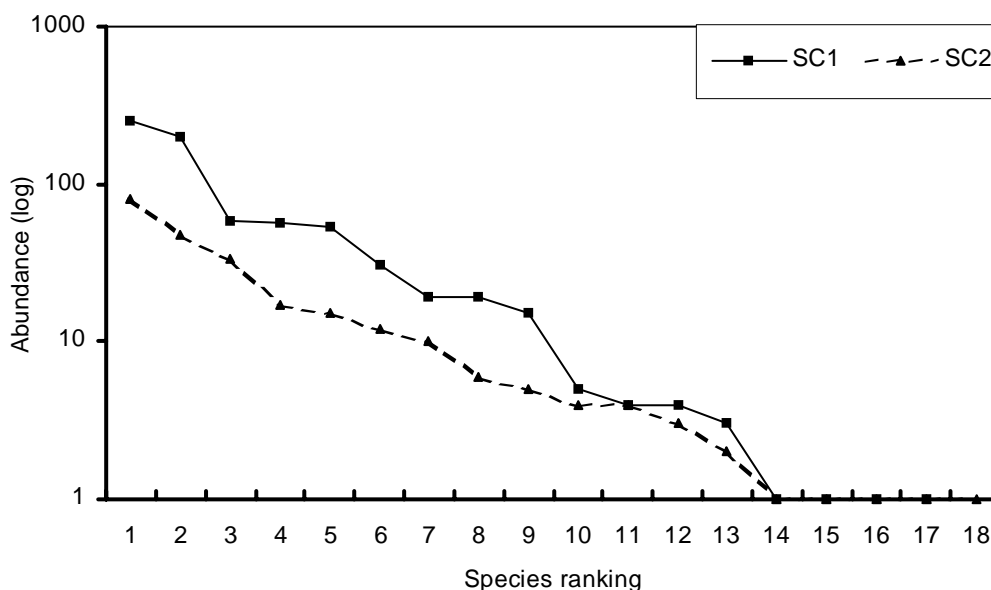
The Berger-Parker index ( $d$ ) defined as:

$$d = N_{max} / N$$

where

$N_{max}$  = number of individuals of the most abundant species in the sample.

$N$  = total abundance.



**FIGURE 2.** Taxocenoses structure as dominance-diversity curves.

Unlike other indices of dominance, the Berger-Parker index is a richness-independent (Magurran 1989) measure in which the reciprocal value ( $1/d$ ) is known as proportional reciprocal abundance of the most frequent species.

As dominance/evenness index, the Shannon and Wiener index was used according to Hurlbert (1971):

$$\sum_{i=1}^R p_i \log p_i$$

Where

$p_i$  = the proportion of individuals in the  $i^{\text{th}}$  species ( $n_i/N$ ).

$R$  = number of species

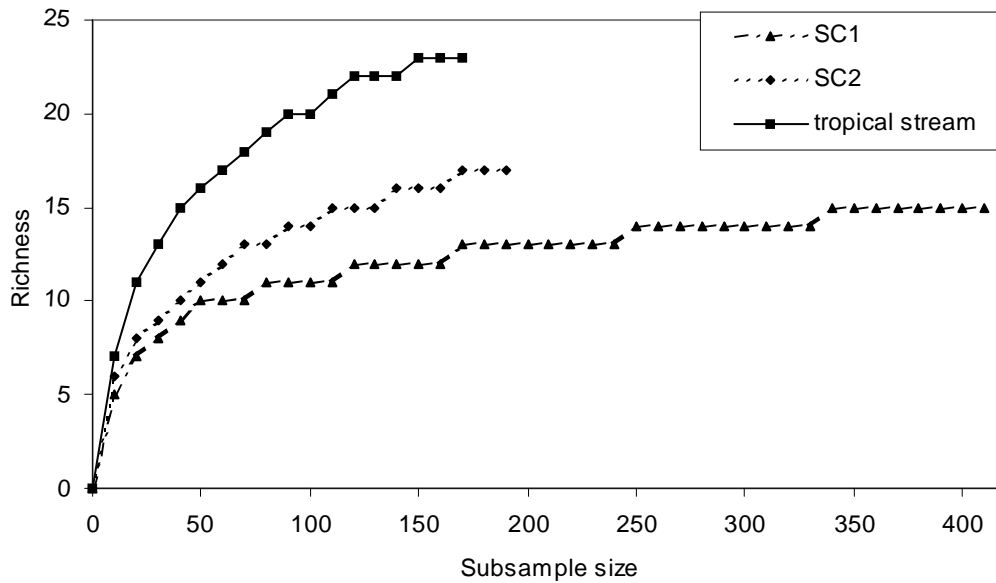
The Shannon and Wiener index was calculated to assess the species diversity in each sub-catchment (SC<sub>1</sub> and SC<sub>2</sub>).

The variance was calculated with the equation proposed by Magurran (1989):

$$\text{Var}H' = \frac{\sum p_i (\ln p_i)^2 - (\sum p_i \ln p_i)^2}{N} + \frac{R-1}{2N^2}$$

Results were compared using a  $t$ -test,  $\alpha = 0.05$  (Magurran 1989), with the hypothesis  $H_0$ : There are no differences in species diversity between the water mite taxocoenosis of the two sub-catchments.

Richness is estimated with rarefaction, where the number of species expected for each sample assumes all samples would be of equal size (Hurlbert 1971; Magurran 1989):



**FIGURE 3.** Richness as rarefaction of two subtropical subcatchments (SC<sub>1</sub> and SC<sub>2</sub>, Argentina) and one tropical stream (Guatemala).

$$E(S_n) = \sum_{i=1}^R \left[ 1 - \frac{\binom{N - N_i}{n}}{\binom{N}{n}} \right]$$

Where

$E(S_n)$  = the expected number of species in a random subsample of  $n$  individuals.

$N$  = total number of individuals.

$N_i$  = number of individuals of species  $i$ .

$n$  = value of subsample size ( $n$  individuals) chosen for standardization, selected at random.

Estimates of  $E(S_n)$  from the curves (Figure 3) can be used to make comparisons and to test the hypothesis from the calculated variance with  $\infty$  degrees of freedom (Magurran 1989). Results (Table 5) were compared using a  $t$ -test for a subsample of 170 individuals (corresponding to the smallest sample size measured) with the hypothesis  $H_0$ : There are no differences in species richness between the water mite taxocoenoses of the two sub-catchments.

The expected values for Argentinean streams were compared with the richness index calculated for taxocoenosis of a tropical stream in Guatemala (Río Lima, Cobán,  $N = 200$  indiv. /  $0.22 \text{ m}^2$ ,  $R = 24$  species; Böttger 1980). This comparison also used a sample size of  $n=170$  individuals (Figure 3, Ludwig & Reynolds 1988).

**TABLE 1.** Species composition and abundance of water mites in the two subcatchments studied, Aug 29-30, 1991.

Species	SC1					SC2				
	R. San	R. El	R. de la	R. de	total	R. Villa	R. de	Arroyo.	R. El	total
	Javier	Siambon	Hoyada	las Tablas		P. Monti	Medina	Artaza	Sunchal	
<i>Rhyncholimnochaes expansiseta</i>	-	17	4	10	31	-	4	-	2	6
<i>Clathrosperchon punctatus</i>	-	-	-	4	4	1	15	1	-	17
<i>Torrenticola columbiana</i>	4	130	7	58	199	-	69	4	7	80
<i>Neomamersa willinki</i>	-	-	-	-	-	-	1	-	-	1
<i>Protolimnesia setifera</i>	51	-	8	-	59	-	-	-	-	-
<i>Protolimnesia sorpresa</i>	-	-	-	-	-	-	-	-	1	1
<i>Protolimnesia interstitialis</i>	-	-	-	1	1	-	5	-	-	5
<i>Limnesia</i> sp.	1	-	-	-	1	-	-	-	-	-
<i>Hygrobatas plebejus</i>	-	-	-	-	-	-	1	-	-	1
<i>Atractides</i> sp.a	13	23	4	13	53	-	5	22	7	34
<i>Atractides sinuatipes</i>	21	14	6	15	56	-	3	1	11	15
<i>Atractidella porophora</i>	-	3	-	-	3	-	3	-	-	3
<i>Hygrobatella multiacetabulata</i>	-	11	4	-	15	-	-	-	-	-
<i>Dodecabates dodecaporus</i>	179	29	16	28	252	21	26	-	-	47
<i>Tetrahygrobatella argentinensis</i>	-	2	17	-	19	-	12	-	-	12
<i>Corticacarus</i> sp. a	2	8	9	-	19	-	2	-	2	4
<i>Corticacarus smithi</i>	-	-	-	5	5	-	2	-	-	2
<i>Diamphidaxona yungasa</i>	-	-	-	-	-	-	1	-	-	1
<i>Frontipoda parva</i>	-	-	-	-	-	-	1	-	-	1
<i>Axonopsella</i> sp.	2	1	-	1	4	-	4	-	-	4
<i>Stygaliella tucumanensis</i>	-	-	1	-	1	-	7	1	2	10
<i>Miraxonides</i> sp.	1	-	-	-	1	-	-	-	-	-

**TABLE 2.** Subcatchment morphometrics and climatic variables.

	Río Lules, SC <sub>1</sub>	Río Calera, SC <sub>2</sub>
Subcatchment area (km <sup>2</sup> )	4,192	3,392
Order (scale 1:250,000)	5	5
Mean discharge August (m <sup>3</sup> s <sup>-1</sup> )	2.3	0.75
Quarterly (winter) critical mean discharge (m <sup>3</sup> s <sup>-1</sup> )	2.1	0.67
Dry season discharge (April-September) (m <sup>3</sup> s <sup>-1</sup> )	8.65	2.05
Mean monthly precipitation: 1990 (mm)	89	73
Mean annual precipitation (1977-1986) (mm)	1,000	620
Mean monthly precipitation August (mm)	10	5

## Results

A total of 967 individuals representing 22 species of water mite was recorded in the two sub-catchments (Table 1). The two sub-catchments shared 14 species (64 %). The species abundance data fit a log-normal distribution in both sub-catchments ( $\chi^2$ -test,  $P > 0.05$ ). This distribution is characteristic for the high number of individuals with good equitability.

The species-abundance curves (Figure 2) are very similar for the two sub-catchments. However, there were significant differences ( $P < 0.05$ ) between sub-catchments for abundance of water mites SC, richness as  $E(S_n)$  and diversity ( $H'$ ,  $1/d$  and  $\lambda$ ) (Table 5). The richness was compared as rarefaction rate (Figure 3) and the difference between sub-catchments is significant ( $P < 0.05$ ). The expected richness for the tropical stream (Río Lima) in Guatemala was calculated in 23 species considering a subsample of 170 individuals.

Predictability (P) (Table 4) was high in both sub-catchments (0.62 and 0.56 respectively), due to the high contingency (M):  $M/P > 65\%$ , which is determined by the marked seasonality of precipitation (Table 3).

**TABLE 3.** Frequency matrices based on precipitation data. The classes are logarithmic (base 2) and each number in the matrix is the frequency of event (number of years) with falls a yield in mm in this month.

SC <sub>1</sub>												
Month	J	F	M	A	M	J	J	A	S	O	N	D
Class (i)												
1						1	1	1				
2						1	1	1				
3									1			
4					1		2					
5					1		4	1	2			
6					4	2	2	2	1	1		
7					1	5		4	4	3	3	1
8		1	2	1	3	1		1	2	2	5	3
9	3			8						4	2	5
10	2	7	6	1								1
11	5	2	2									
S=11											Z=120	
SC <sub>2</sub>												
Month	J	F	M	A	M	J	J	A	S	O	N	D
Class (i)												
1					1	1	2	2	1			
2					1		1		1			
3						1						
4				1		1	1	2	2	2	1	
5					4	3	2	3	2		2	
6					3	4	3	3	1	2	5	1
7			1	4			1		3	2	2	1
8	1	3	1	4	1					4		7
9	6	7	7	1								1
10	3		1									
11												
S=11											Z=120	



## Discussion

In contrast to Giberson and Cobb (1995), who compared watersheds with different degrees of flood predictability to assess its influence on the mayfly community, I investigated neighboring sub-catchments with similar indices of rainfall predictability to eliminate this factor as variable. The results showed an interesting similarity in species composition, probably reflecting the close proximity of the sub-catchments and the dispersal potential of water mites using insects as vectors (Bilton *et al.* 2001). The conformance of species-abundance data to a log-normal model could suggest that the water mite taxocoenoses are similar in structure between the two sub-catchments. Combining abundance and richness in several indices ( $\lambda$ ,  $1/d$ ,  $H'$ ), showed similar results (Table 5), but are differently affected by abundance. For diversity measures,  $\lambda$  appears to be the parameter most suitable for demonstrating differences in diversity between sub-catchments, due to its discriminatory capability and moderate sensitivity to sample size. The other indices do not show with certainty that differences exist between sub-catchments, although  $H'$  has the same attributes as  $\lambda$  (Magurran 1989). However, significance by  $H'$  might be calculated as well as by Richness rarefaction index.

Turcotte and Harper (1982) considered spates as the main regulators of macroinvertebrate densities in non-seasonal environments such as Andean tropical rivers. Jacobsen *et al.* (1997) suggested spates regime had a negative impact on diversity of insects in streams closer to the equator. In subtropical Andean rivers, with seasonal precipitation, a combination of drought and flooding events is regulating the benthic community. However the same pattern of precipitation (high P for M) does not show correlation with taxocoenosis diversity and richness parameters. These results suggest that, in spite of the same seasonal rainfall, different patterns of diversity and richness are possible in each sub-catchment (Table 5). This result agrees with observations for mayflies made by Giberson and Cobb (1995) showing that flood distribution does not explain all differences between rivers.

Evidently, there are local factors operating in each sub-catchment that also can be influence the structure of the taxocoenosis. One or more local factors (discharge volume or rock type) affect the flow and morphometry of each sub-catchment in different ways, determining different conditions in the biotope (substrate, particle size or critical shear stresses) that influence the water mite taxocoenosis. Different influences by some factors such as total discharge (Table 2), could influence directly the channel characteristics and the water mite preferences. But the volume of discharge also can produce effects on the habitat availability for potential prey (Giberson & Cobb 1995; Flory & Milner 1999) that indirectly impact the structure of a predator taxocoenosis such as the water mites. In this sense, Williams (1980) suggested that the relationship of a predator to a heterogeneous substratum could also be determined at secondary or tertiary level because the substratum defines the environment for its prey.

The expected richness for the streams of both sub-catchments were lower than was found for a tropical stream in Guatemala (Böttger 1980). This result agrees with the comparison of subtropical and tropical water mites taxocoenosis in Australia (Walter and Proctor 1998). However, my results contrast with the general belief that the benthic fauna increases in diversity towards lower latitudes (Stanford & Ward 1983; Covich 1988, Romero & Fernández 2001), discussed recently by Huston (1994), and Vinson & Hawkins (1998).

## Conclusion

The water mite taxocoenosis described in this study might be described as typical for the subtropical Andean Mountain region. It presents a structure characteristic for a stable environment, in agreement

with the stable periodicity in the benthic zone (Romero & Fernández 2001). However I found differences in diversity and richness within sub-catchments, probably attributable to local factors (e.g. volume of local precipitation) or particular characteristics of some streams (e.g. drainage morphology or stability of bed materials).

**TABLE 4.** Predictability indices of precipitation in SC<sub>1</sub> and SC<sub>2</sub> calculated as in Colwell (1974, see text for explanation and calculations).

	SC <sub>1</sub>	SC <sub>2</sub>
Total Predictability	0.62	0.56
Constancy	0.15	0.18
Contingency	0.48	0.38

**TABLE 5.** Diversity and richness measures for the two subcatchments sampled in winter 1991. Significant differences are shown (\*P<0.05).

Index/parameter	SC <sub>1</sub>	SC <sub>2</sub>
Total of individuals	723	244
Shannon-Wiener i. (H')	2.7	3.4*
Berger-Parker i. (d)	0.35	0.33
Reciprocal B.-P. i. (1/d)	2.87	3.05
Log-normal curve p. ( $\lambda$ )	19.8	27.5
Number of species	17	18
Rarefaction i. [E(S <sub>n=170</sub> )]	13	16*

The similarity in the specific composition between the two sub-catchments reflects their close proximity and the high vagility of water mites.

Rainfall is a very important factor in the ecosystems of this region (Villalba *et al.* 1992); however, the precipitation pattern (frequency or high predictability) can not explain differences in the structure of the taxocoenoses, and in this sense for example the greatest difference among sub-catchments is in discharge. This result parallels observations from other latitudes (Rader & Ward 1989; Giberson & Cobb 1995), and we must search for additional reasons contributing to the differences in the organization of the taxocoenoses between the two sub-catchments.

Richness of the water mite taxocoenosis of tropical streams appear higher than at lower latitudes, which does not agree with the more accepted concept in river ecology theory.

### Acknowledgements

The author belongs to the staff of the Argentine National Council of Scientific Research (CONICET) which permanent support is greatly acknowledged.

I thank J. Jackson, E. Domínguez, R. Gerecke, H. Smit and B. Rosso de Ferradás for suggestions and constructive criticism and two anonymous referees for valuable comments on the manuscript.

## References

- Atmar, W. (2001) A profoundly repeated pattern. *ESA Bulletin*, 82, 208-211.
- Balseiro, E.G. (1992) The role of pelagic water mites in the control of Cladoceran population in a temperate lake of the Southern Andes. *Journal of Plankton Research*, 14, 1267-1277.
- Bilton, D.T., Freeland, J.R. & Okamura, B. (2001) Dispersal in Freshwater Invertebrates. *Annual Review of Ecology and Systematics*, 32, 159-181.
- Böttger, K. (1980) Qualitative und quantitative Benthonstudien an Bergbächen in Guatemala (Zentralamerika), unter besonderer Berücksichtigung der Hydrachnellae (Acari). *Archiv für Hydrobiologie*, 88, 96-119.
- Colwell, R.K. (1974) Predictability, constancy, and contingency of periodic phenomena. *Ecology*, 55, 1148-1153.
- Covich, A.P. (1988) Geographical and historical comparisons of neotropical streams: biotic diversity and detrital processing in highly variable habitats. *Journal of North American Benthological Society*, 7, 361-386.
- Di Sabatino A., Gerecke R., & Martin, P. (2000) The biology and ecology of lotic water mites (Hydrachnidia). *Freshwater Biology*, 44, 47-62.
- Di Sabatino, A., Martin P., Gerecke, R. & Cicolani, B. (2002) Hydrachnidia (Water Mites). In: Rundle, S.D., Robertson, A.L. & Schmid-Araya, J.M. (eds.) *Freshwater Meiofauna: Biology and Ecology*. Backhuys Pub, Leiden, The Netherlands, pp.105-133.
- Ferradás, B.R., Kaisin, J. & Bosnia, A.S. (1987) Seasonal variation of density and biomass of Hydracarina (Acari) in a North-Patagonian reservoir (Neuquén, Argentina). *Studies on Neotropical Fauna and Environment*, 22, 113-127.
- Fisher, S.G. (1997) Creativity, idea generation, and the functional morphology of streams. *Journal of North American Benthological Society*, 16, 305-318.
- Flory, E.A. & Milner, A.M. (1999) Influence of riparian vegetation on invertebrate assemblages in a recently formed stream in Glacier Bay National Park, Alaska. *Journal of North American Benthological Society*, 18, 261-273.
- Frisell, C.A., Liss, W.J., Warren, C.E. & Hurley, M.D. (1986) A Hierarchical Framework for Stream Habitat Classification: Viewing Streams in a Watershed Context. *Environmental Management*, 10, 199-214.
- Giberson, D.J. & Cobb, D.G. (1995) Do floods always disturb mayfly communities? In: Corkum, L.D. & Ciborowski, J.J. (eds.) *Current directions in Research on Ephemeroptera*. Canadian Scholars Press, Toronto, pp. 237-252.
- Hurlbert, S.H. (1971) The nonconcept of species diversity: A critique and alternative parameters. *Ecology*, 52, 577-586.
- Huston, M.A. (1994) *Biological Diversity*. Cambridge University Press, 681 pp.
- Jacobsen, D., Schultz, R. & Encalada, A. (1997) Structure and diversity of stream invertebrate assemblages: the influence of temperature with altitude and latitude. *Freshwater Biology*, 38, 247-261.
- Ludwig, J.A. & Reynolds, J.F. (1988) *Statistical Ecology*. John Wiley & Sons, New York, 337 pp.
- Magurran, A.E. (1989) *Diversidad ecológica y su medición*. Ediciones Vedral, Barcelona, 200 pp.
- Matveev, V.F., Martinez, C.S. & Frutos, M. (1989) Predation-prey relationships in subtropical zooplankton: water mite against cladocerans in an Argentina lake. *Oecologia*, 79, 489-495.
- Proctor, H. & Pritchard, G. (1989) Neglected predators: water mites (Acari: Parasitengona: Hydrachnellae) in freshwater communities. *Journal of North American Benthological Society*, 8, 100-111.
- Rader, R.B. & Ward, J.V. (1989) The influence of environmental predictability/disturbance characteristic on a guild of mountain stream insects. *Oikos*, 54, 107-116.
- Resh, V.H., Brown, A.V., Covich, A.P., Gurtz, M.E., Li, H.W., Minshall, G.W., Reice, S.R., Sheldon, A.L., Wallace, J.B. & Wissmar, R.C. (1988) The role of disturbance in stream ecology. *Journal of North American Benthological Society*, 7, 433-455.
- Romero, F. & Fernández, H.R. (2001) Abundance and Diversity of a Mayfly Taxocene in a South American Subtropical Mountain Stream. In: Dominguez, E. (ed.) *Trends in Research in Ephemeroptera and Plecoptera*. Kluwer Academic/Plenum Pub., London, pp. 173-178.
- Stanford, J.A. & Ward, J.V. (1983) Insect species diversity as a function of environmental variability and disturbance in stream systems. In: Barnes, J.R. & Minshall, G.W. (eds.) *Stream Ecology: Application and Testing of General Ecology Theory*. Plenum Press, New York, pp. 265-278.
- Turcotte, P. & Harper, P.P. (1982) The macro-invertebrate fauna of a small Andean stream. *Freshwater Biology*, 12, 411-419.
- Villalba, R., Holmes, R.L. & Boninsegna, J.A. (1992) Spatial patterns of climate and tree growth variations in

- subtropical northwestern Argentina. *Journal of Biogeography*, 19, 631-649.
- Vinson, M.R. & Hawkins, C.P. (1998) Biodiversity of stream insects: Variation at Local, Basin and Regional Scales. *Annual Review of Entomology*, 43, 271-293.
- Walter, D.E. & Proctor, H.C. (1998) Predatory Mites in Tropical Australia: Local Species Richness and Complementarity. *Biotropica*, 30, 72-81.
- Williams, D.D. (1980) Some relationships between stream benthos and substrate heterogeneity. *Limnology & Oceanography*, 25, 166-172.

*Accepted: 20 June 2003*