

Effects of landscape and desertification on the macroinvertebrate assemblages of rivers in Andean Patagonia

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With 8 figures and 5 tables

Abstract: Spatial patterns in macroinvertebrate assemblage structure were examined in rivers from 6 main basins in the mountains and the Patagonian plateau, Argentina. Surber samples were taken during the low water period from 36 sites and environmental variables were also assessed. Five site groups were identified using detrended correspondence analysis (DCA), one in the mountains, one in the piedmont, and three on the plateau (north, central and south). DCA axis 1 separated sites along a physical gradient of water velocity and stream order, whereas axis 2 separated sites according to geographic location, latitude and substratum size. Piedmont sites had greater species richness than the mountains, north plateau and south plateau sites.

Invertebrate density was significantly greater on the north plateau and piedmont than in the mountains and south plateau, whereas diversity (H') was significantly higher in the mountains and on the piedmont. From a landscape perspective, higher categories in biogeographical classifications (phytogeography, biozones) appear to be most useful for predicting macroinvertebrate assemblages in Patagonian rivers. Amounts of benthic organic matter and the density and biomass of functional feeding groups (FFG) were also examined in a subset of 25 rivers. During base discharge, wood, leaves and total benthic organic matter decreased significantly from the mountains to the plains, but no significant relationship was found between quantity of fine particular organic matter and distance from the source. Shredder biomass decreased significantly from the headwaters downstream, and collector biomass increased. Predator biomass was relatively similar at all sites. A strong association was found between FFGs and their food resources. The EPT index and H' decreased as desertification status increased suggesting that land degradation influences macroinvertebrate assemblages. Loss of riparian cover as a consequence of overgrazing and other land use practices has negative effects on aquatic environments in Patagonia.

Key words: functional feeding groups, degradation, invertebrate diversity, invertebrate density, biozones.

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Introduction

Studies of large-scale spatial patterns of invertebrate assemblage structure improve our understanding of how communities respond to physical and biological attributes of the landscape at multiple scales (TATE & HEINY 1995, CARTER et al. 1996). In some studies, stream macroinvertebrate assemblages have been found to respond strongly to broad-scale landscape attributes such as climate, vegetation, soil type and topography (RABENI & DOISY 2000, WAITE et al. 2000), whereas in others a weak correspondence was observed between macroinvertebrate assemblage structure and regional variables (SANDIN & JOHNSON 2000). In the latter cases, many organisms seemed to vary continuously and independently along environmental gradients, and correspondence between faunal groups and landscape units were inconsistent (HAWKINS & VINSON 2000). Nevertheless, HAWKINS et al. (2000) concluded that in general landscape accounted for more biotic variance than would be expected by chance.

Riparian vegetation plays a crucial role in determining the productivity and trophic relationships of stream ecosystems (CUMMINS et al. 1989), and the relative abundance of allochthonous and autochthonous organic matter in running waters can be expected to determine distribution and abundance patterns of invertebrate functional feeding groups (VANNOTE et al. 1980). The first studies to address the question of how functional organization of macroinvertebrate assemblages in rivers differs among biomes were carried out in North America (CUSHING & VANNOTE 1983, MINSHALL et al. 1983). They showed that functional group assemblages could be biome specific, and CORKUM (1991) demonstrated that biome type could have an overriding effect on the spatial distribution of lotic fauna. Additionally, agriculture, forestry and other land use practices are resulting in large-scale changes in the physical, biological and functional attributes of aquatic ecosystems (LAKE et al. 1987, WINTERBOURN 1995, AGUIAR et al. 2002). In Patagonia one of the main environmental problems affecting biomes is the phenomenon of desertification (DEL VALLE et al. 1998), which is defined as land degradation in arid, semiarid and subhumid areas resulting from anthropogenic activities not adapted to the land use in these regions (UNEP 1991). The location, extent and severity of desertification in the Patagonian region have been well documented (SORIANO & MOVIA 1986, PARUELO et al. 1991). However, studies of how land use practices at landscape scales affect benthic community and functional assemblages are scarce in South America (JACOBSEN et al. 1997, OMETO et al. 2000), and especially in Patagonia.

Andean Patagonia incorporates two distinct regions: the mountain chain and the plateau. Several extensive macroinvertebrate surveys have been carried out in streams and rivers mainly in the mountains (WAIS 1987, 1990), and

the distributional patterns of macroinvertebrates along altitudinal gradients have also been examined (ALBARIÑO 1997, MISERENDINO & PIZZOLÓN 2000). Current speed, conductivity, substrate size and abundance of aquatic plants are major variables structuring faunal assemblages (MISERENDINO 2001 a). The distribution of functional feeding groups along streams in Patagonia corresponds well with the predictions of the RCC (River Continuum Concept) with biomass of shredders decreasing and collector biomass increasing downstream from the headwaters (MISERENDINO & PIZZOLÓN 2000). However, the effects of biozones and landscape on FFG distribution in Patagonia are essentially unknown.

The aims of the present research were: (1) to examine the spatial distribution of macroinvertebrates in Patagonian rivers in relationship to environmental features and land use; (2) to describe functional organization of macroinvertebrate communities within a landscape perspective; and (3) to assess the main factors explaining functional feeding group distribution.

Study area

The Patagonian Andes are characterized by mountain chains and several eastern foothill systems that extend for about 2000 km from Neuquén to Tierra del Fuego (Fig. 1). Maximum altitude is over 3600 m a.s.l., the climate is cool-temperate, and rainfall declines dramatically from the mountains to the Atlantic Ocean (PARUELO et al. 1998). Some sites in the mountains receive 3000 mm y⁻¹ precipitation, whereas low temperatures and high drought characterize the steppe, where precipitation can be as low as 100–150 mm y⁻¹. Geomorphologic features and local climate define four biozones: (1) Andean-Humid, (2) Sub-Andean Sub-humid, (3) Extra-Andean oriental and (4) Extra-Andean occidental (DEL VALLE 1995).

The strong west-east rainfall gradient has resulted in two main phytogeographical provinces: the Sub-Antarctic Forest and the Patagonian Steppe. Perennial (*Austrocedrus chilensis*, *Nothofagus dombeyi* and *Maytenus boaria*) and deciduous species (*N. pumilio*, *N. antarctica*) dominate the sub-Antarctic forests, with *N. pumilio* commonly forming a canopy over low-order streams. Some piedmont watercourses located between the mountains and the plateau are flanked mainly by the introduced willow *Salix fragilis*. The limited precipitation on the Patagonian Plateau results in xerophytic vegetation with the herbaceous-shrub-like steppe dominated by *Mulimun spinosum*, *Stipa* spp., *Senecio* spp., *Colletia spinosissima*, *Adesmia* sp., *Fabiana imbricata* and *Poa* sp. (TELL et al. 1997).

In the present study, 36 streams on the eastern side of the Andes between 41° 53' S, 71° 29' W and 50° 25' S, 72° 27' W were sampled (Fig. 1). Sites ranged in altitude from 175 to 1350 m a.s.l. (Table 1). Mountain rivers have a pluvionival regime, with two seasonal peaks in flows. One peak results from heavy winter precipitation (April to July) and the other from melting ice and snow during spring. Steppe rivers are fed by pluvial precipitation from the west.

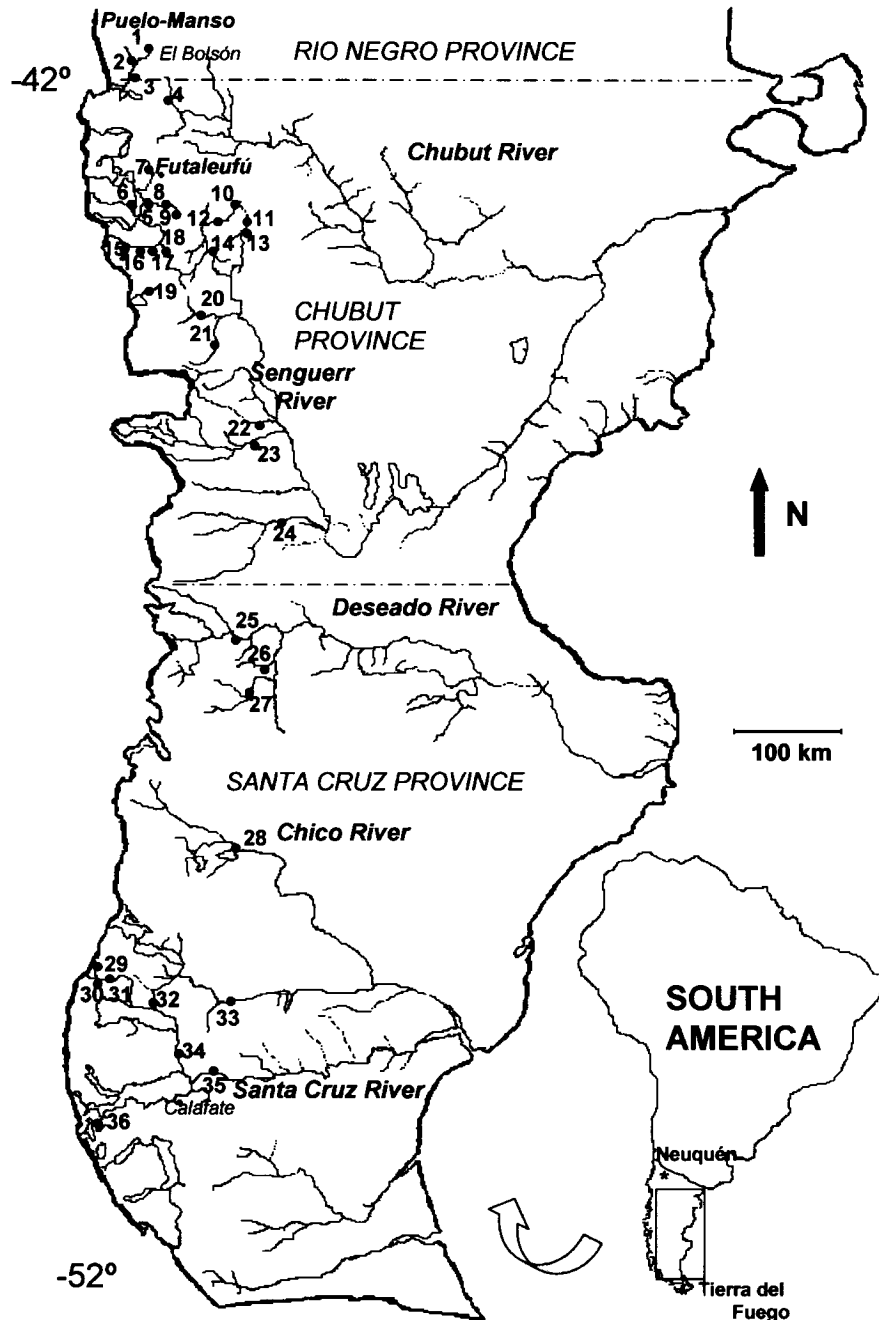


Fig. 1. Study area showing the locations of the 36 stream and river sites within the Patagonian ecoregion, Argentina. Names of the rivers are in Table 1.

The Puelo-Manso, Futaleufú-Yelcho and Corcovado-Palena basins drain into the Pacific Ocean, whereas the Chubut, Senguerr, Deseado, and Santa Cruz basins drain to the Atlantic Ocean across the sub-Andean steppe. A 2000-km² area of great glaciers and continental ice is present in the southwest of the Santa Cruz province, an area that is part of Los Glaciares National Park. Other river basins sampled drain through the plateau into the Atlantic Ocean.

Materials and methods

Field methods

Sampling was carried out on a 1000 km long transect from El Bolsón to Calafate in April 1996 (Fig. 1). All sites were located on permanent streams and were sampled during base flow. Other samples taken in the same way and season from the Esquel-Percy river system and the Puelo-Manso basin were also included in the study (March 1991 sites: 10 to 14, March 1995: sites 2–3) to increase the altitudinal and latitudinal extent of the survey. In each selected reach, habitat types were differentiated visually (run/riffles/pools) and 10 Surber samples (30 × 30 cm, mesh size 250 µm) were taken from all of them where possible in accordance with their abundance. However, in the large Santa Cruz and Las Leonas rivers sampling was confined to the sides of the river where water depth was <45 cm. Surber samples were pooled and fixed with 4% formaldehyde. In the laboratory, samples were elutriated and sieved (pore size 250–1000 µm). Detritus in samples from 25 of the 36 rivers (Table 1) was divided into fine (250–1000 µm) and coarse (>1000 µm) fractions (FPOM and CPOM, respectively), and CPOM was divided further into wood, leaves and other materials (grass, roots, buds) (VOELZ & WARD 1990). Since all detritus was collected from the streambed the term benthic organic matter (BOM) is used for total detritus (i.e., FPOM plus CPOM). All detrital fractions were dried (60 °C for 24 h) and weighed.

Macroinvertebrates were picked from samples, visually, and stored in 70% ethyl alcohol before being identified to the lowest possible taxonomic level using regional keys (DOMÍNGUEZ et al. 1994, LOPRETTO & TELL 1995). Plecoptera, Ephemeroptera and Trichoptera were identified to genus or species level and Diptera to genus or operational taxonomic units (such as Orthocladiinae sp. 1) when necessary. Functional feeding groups were assigned by gut analyses (10 individuals/taxon/site), knowledge of feeding modes, and using available references (MERRITT & CUMMINS 1978, DOMÍNGUEZ et al. 1994). Functional group biomass was estimated by measuring body length of all individuals in a taxon to the nearest 0.5 mm and using the regression models of MISERENDINO (2001 b). Results were expressed as milligrams dry mass per m².

Stream order was determined according to STRAHLER (1957). Altitude, latitude, longitude, and distance from the source were taken from maps (1:50,000, 1:100,000 and 1:250,000) and available references (CORONATO & DEL VALLE 1988). Substratum composition was assessed by estimating the percentage of cover of each fraction (boulder, cobble, gravel, pebble and sand) in a grid (1 m²) (GORDON et al. 1994). In large rivers with a maximum depth of >45 cm only the dominant substratum in the littoral zone was recorded.

Average depth was calculated at each site from five measurements on a profile across the channel with a calibrated stick. Since sampling was carried out in a low water period, surface current speed was obtained by timing a bobber (average of 3 runs) as it moved over a distance of 10 metres (GORDON et al. 1994). Percentage cover of macrophytes, filamentous algae and aquatic mosses in the sampling area was assessed, visually. The main riparian plant species were recorded. Water samples were collected in plastic bottles (1500 cc) and kept at 4 °C prior to the measurement of conductivity using a HORIBA U-7 meter.

The extent and severity of desertification in the catchment of each river was evaluated using a digital map of desertification status in the Patagonian region (DEL VALLE et al. 1998). The main criteria used to determine classes of desertification on the map were degradation of vegetative cover (overgrazing, woodcutting) and soil (water erosion, wind erosion, soil crusting, salinization). To assign land degradation levels within each basin of interest, the dominant degradation status was determined by counting the numbers of pixels (1000×1000 m blocks) representing different states of desertification using a geographical information system (GIS) (ERDAS Imagine®, Inc. 8.5). Only pixels in the stream catchment above the sampling point were assessed. When a basin included different degrees of desertification, the dominant status (more than 50 % of the area) was assigned, but when two categories were equally represented, an intermediate value was assigned.

Data analysis

Environmental variables and macroinvertebrate abundance data were $\log(x+1)$ transformed prior to statistical analysis to normalize and stabilize variances. Detrended correspondence analysis (DECORANA) was used to identify gradients in community structure, and was carried out using the PC-ORD multivariate statistical package (version 3.0, 1997, McCUNE & MEFFORD). A total of 83 taxa with abundances greater than 0.5 % of the total abundance of invertebrates at a site were used for the analysis. DECORANA clusters sites with similar taxonomic composition close together and produces site scores that can be related to environmental variables. Pearson product-moment correlations with Bonferroni-adjusted probabilities were used to detect significant environmental covariables. To identify environmental predictors, a set of independent variables was used in multiple regression analysis (forward stepwise method) with DCA axes 1 and 2 (SPSS package, Standard version, SPSS inc. 1989–1999). Macroinvertebrate density, species richness, EPT richness (number of Ephemeroptera, Plecoptera, Trichoptera taxa), SHANNON-WIENER diversity ($H' = -\sum p_i \ln p_i$) and density of FFGs were calculated to define groups identified by DECORANA. One-way ANOVAs were used to compare measured community attributes among the defined site groups, followed by a Least Significant Differences (LSD) test when appropriate.

Regression analysis was used to examine relationships between the mass of benthic organic matter fractions and the biomass of functional feeding groups, and distance from the stream source (km). Dependent variables were $\log(x+1)$ transformed and the quadratic term was included in regressions to test for possible curvilinearity in invertebrate response.

Since data on benthic organic matter were available for only 25 sites, only those 25 were used to perform a canonical correspondence analysis (CCA) (TER BRAAK 1986), in order to explore functional group responses to environmental variables. The 1st and 2nd axes of a CCA represent the most important environmental gradients along which species are distributed. The direction of each environmental vector indicates the maximum rate of change for that particular environmental variable and its length indicates its relative importance in explaining the ordination.

Results

Environmental features of rivers and streams

Stream orders ranged from 2 to 6 and wet width from 1.5 to 200 m. Substratum type was highly diverse, ranging from fine sand to boulders and bedrock. Since sampling was carried out in the low-water period, flow was absent from some plateau rivers. Mountain streams with high channel slopes had water velocities of more than 2.5 m s⁻¹. Water conductivity ranged from 20 to 545 $\mu\text{S cm}^{-1}$ (at 20 °C). Maximum conductivity values were observed in Willimanco stream, which has a ionic spectrum of the calcium-sulfate type rather than the calcium-bicarbonate type predominant in the northwest area. In general, plateau rivers had higher conductivity than mountain streams (Table 1). Watercourses located in the *Nothofagus* forest showed greater riparian coverage than piedmont or plateau rivers, which were predominantly in grassland.

Maximum biomass of wood was recorded at Rañinto (20.08 DM g m⁻²) and Cascada (17.71 DM g m⁻²), whereas the highest biomass of “leaves” was found in Mitre (7.6 DM g m⁻²) and Baguilt (3.96 DM g m⁻²). All these sites were located in deciduous forest. Samples from sites on the plateau did not contain wood or tree leaves, but included other materials especially grasses, seeds and buds. FPOM was most abundant in medium sized rivers like the Quemqueutreu (2.7 DM g m⁻²) and Desaguadero (3.12 DM g m⁻²), both of which had riparian forest cover including *Nothofagus* spp. and *Salix fragilis*. Desertification was most severe in the Pinturas, Ecker, Chalia and Leonas sub-basins where 5 sites were situated. It was moderate-severe in Chubut, Senguerr, Deseado and Santa Cruz basins containing 10 sites, but 6 sites showed no desertification effects, or only slight effects (14 sites) (Table 1).

Several environmental variables were inter-correlated, including the geographical descriptors biozone and phytogeographical region, and the river features depth and wet width. Water temperature was correlated with latitude. Moreover, desertification status was strongly correlated with location (latitude), landscape classification (biozone, phytogeographical region), and distance from the source (Table 2). Conductivity and substratum size were negatively correlated, and aquatic plant coverage increased with conductivity.

Table 1. Physical, chemical and biological variables measured in 36 Patagonian streams. Biozones: Andean humid (1); Sub-Andean Sub-humid (2); Extra-Andean occidental (3) and oriental (4). Phytogeographical regions: *Nothofagus* forest (1), Patagonian steppe (2) (subandine sector) and (3) central sector. Desertification status: (0) non affected, (0.5–1) light, (>1–2) moderate, (>2–3) moderate to severe and (>3) severe to very severe.

Site	Stream	Latitude (S)	Longitude (W)	Biozone	Phyt. Region	Desertification status	Elevation m a.s.l.	Stream order	Distance from the source (km)	Wet Width (m)	Depth (cm)	Velocity (m s ⁻¹)	Water Temperature (°C)	Conductivity (µS cm ⁻¹)	Substrate index	Wood (DM g m ⁻²)	Leaves (DM g m ⁻²)	Other (DM g m ⁻²)	FPOM (DM g m ⁻²)	BOM (DM g m ⁻²)	Aquatic plants (% cover)
1	Río Quemqueutreu	41°53'	71°29'	2	1	0	450	4	40	30	35	1.50	16	40	8.5	3.77	0.49	12.8	2.74	19.8	0
2	Río Azul	42°05'	71°33'	1	1	0	258	4	32.5	45	40	0.56	16	50	8.5	7.10	0.48	5.71	0.64	13.3	0
3	Río Golondrinas	42°05'	71°35'	2	1	0.5	280	2	11.75	12	20	0.30	14	50	4	1.07	0.27	4.11	0.96	6.42	50
4	Río Chubut	42°10'	71°1'	3	2	3	700	4	79	60	40	0.28	17	68.1	6.5	0.48	0.05	1.24	0.00	1.77	50
5	A La Cascada	42°45'	71°36'	1	1	0	550	2	6	7	27	1.11	14	34.4	8.5	17.7	3.80	4.59	0.56	26.7	0
6	Río Desaguadero	42°45'	71°37'	1	1	0	500	2	13	23	37	1.21	16	48.9	6.5	3.11	2.60	5.52	3.13	14.4	0
7	Río Centinela	42°45'	71°38'	1	1	0	600	3	9	7	26	1.53	10	41.2	8.5	12.62	2.52	2.76	0.82	18.7	0
8	Río Fontana	42°54'	71°36'	1	1	0.5	650	2	7	7	24	1.05	10	30.6	7	-	-	-	-	-	0
9	Río Rañinto	42°54'	71°36'	1	1	0.5	650	1	7	15	31	1.11	9	38.2	8	20.08	1.34	2.01	0.24	23.7	0
10	A la Hoya	42°45'	71°14'	2	1	1	1350	1	2	2.3	15	0.67	4	28	9	-	-	-	-	-	0
11	A Lag. Willimanco	42°54'	71°17'	2	1	1	650	3	9	2	10	0.50	14	545	4	-	-	-	-	-	80
12	A Esquel	42°54'	71°19'	2	1	1	600	4	25.3	6	10	0.60	14	184	6.5	-	-	-	-	-	25
13	A Valle Chico	42°54'	71°18'	2	1	1	560	4	28.5	3	10	0.60	11	265	4	-	-	-	-	-	0
14	Río Percy	43°00'	71°28'	2	1	1	400	5	40	27	39	0.33	13	83	7	-	-	-	-	-	25
15	Río Blanco	43°10'	71°35'	1	1	0	425	2	13	15	20	0.57	12	36	8.5	-	-	-	-	-	0
16	Río Baguait	43°10'	71°33'	1	1	0	400	4	14	18	35	0.81	12	34.6	8.5	0.91	3.96	2.02	0.21	7.11	0
17	A Los Rifleros	43°10'	71°31'	2	1	1	425	1	16	9.3	7.8	0.56	12	92	6	-	-	-	-	-	25
18	Río Nant y Fall	43°10'	71°31'	2	1	1	400	3	16	8	28	0.41	14	95	5.5	0.09	0.14	1.42	0.11	1.76	25

Table 1. Continued.

Site	Stream	Latitude (S)	Longitude (W)	Biozone	Phyt. Region	Desertification status	Elevation m a.s.l.	Stream order	Distance from the source (km)	Wet Width (m)	Depth (cm)	Velocity (m s ⁻¹)	Water Temperature (°C)	Conductivity (µS cm ⁻¹)	Substrate index	Wood (DM g m ⁻²)	Leaves (DM g m ⁻²)	Other (DM g m ⁻²)	FPOM (DM g m ⁻²)	BOM (DM g m ⁻²)	Aquatic plants (% cover)
19	Río Frío	43°17'	71°30'	1	1	0.5	570	3	24	13	18.5	0.40	14	88	6	11.30	0.35	2.63	2.93	17.2	50
20	Río Tecka	43°29'	70°5'	3	2	2.5	660	4	55	3	24.8	0.66	8	173	5	0.32	<0.05	<0.05	3.77	4.09	60
21	A Cherke	44°03'	70°45'	3	2	2	730	4	57.8	10	35	0	8	130	5.5	<0.05	<0.05	9.95	0.74	10.8	0
22	Río Verde	45°07'	70°45'	3	2	3	690	1–2	75.8	7	28.7	0	9	169	6	<0.05	<0.05	1.63	1.54	3.17	25
23	Río Senguerr	45°03'	70°51'	3	2	2	690	4	46.3	80	33	1.30	10	25.4	6.5	1.25	<0.05	3.84	0.60	5.70	0
24	Río Mayo	45°40'	70°17'	3	3	3	470	5	140	20	16.25	0.51	10	236	5.5	-	-	-	-	-	60
25	Río Félix Gde	46°35'	70°55'	3	3	3	200	3	99.7	18	18.4	0.44	7	77	5	-	-	-	-	-	0
26	Río Pinturas	47°05'	70°42'	3	3	4	600	2	80	1.5	9.3	0.22	10	309	5.5	<0.05	<0.05	4.57	<0.05	4.57	25
27	Río Ecker	47°10'	70°52'	4	3	3.5	600	3	70	21	21.6	0.33	7	102	5	-	-	-	-	<0.05	50
28	Río Chico	48°25'	70°37'	4	3	3	450	4–5	79	60	93	0.75	5	74	6.5	<0.05	<0.05	1.48	0.65	2.13	0
29	Río Diablo	49°17'	72°55'	1	1	1	750	2	5	10	32	0.29	7	20	7.5	0.17	0.06	1.88	1.26	3.37	25
30	A° del Puesto	49°18'	72°54'	1	1	1	750	2	10	6	25	1.66	4	28.6	8.5	15.71	1.93	2.31	0.77	20.7	0
31	Río de las Vueltas	49°18'	72°54'	1	1	2.5	750	4–5	43	30	35	1.87	7	34.8	8.5	2.29	0.32	1.25	<0.05	3.86	0
32	Río Cangrejo	49°33'	72°17'	2	3	3	250	2–3	41.3	14	19.25	0.43	10	37	8	0.40	<0.05	0.13	0.20	0.74	25
33	Río Chalia	49°35'	71°30'	4	3	3.5	250	2–3	76.1	14	14	0.30	8	87	4	<0.05	<0.05	0.33	0.08	0.41	25
34	Río Las Leonas	50°10'	72°	4	3	4	250	5–6	23.1	100	40	0.69	8	44.6	5	<0.05	<0.05	4.34	2.70	7.84	0
35	Río Santa Cruz	50°15'	71°54'	4	3	3.5	175	6	8.19	200	40	2.50	8	39	5	-	-	-	-	<0.05	0
36	Río Mitré	50°25'	72°27'	1	1	1	250	2–3	28.5	30	34.6	1.36	9	57.6	8	2.32	7.61	2.35	0.24	12.52	0

Table 2. Pearson product-moment correlation matrix for environmental variables measured on 36 Patagonian rivers during base flow. Bonferroni adjustments were made to establish the critical correlation coefficient ($r_{0.0005(2,34)} = 0.55$) for determining significance at $P < 0.05$.

	Latitude	Biozone	Phytog. region	Desertification	Elevation	Stream order	Distance from source	Wet width	Depth	Current velocity	Water temperature	Conductivity	Substratum size
Latitude													
Biozone	0.38	1											
Phytog. Region	0.54	0.82*	1										
Desertification status	0.66*	0.85*	0.84*	1									
Elevation	-0.30	-0.23	-0.27	-0.18	1								
Stream order	0.11	0.36	0.29	0.29	-0.21	1							
Distance from source	0.23	0.58*	0.61*	0.63*	-0.21	0.44	1						
Wet width	0.33	0.30	0.38	0.25	-0.49	0.46	0.23	1					
Depth	0.19	0.06	0.11	0.02	-0.14	0.39	0.05	0.70*	1				
Current velocity	0.08	-0.30	-0.15	-0.28	-0.15	0.07	-0.38	0.23	0.10	1			
Water temperature	-0.58*	-0.27	-0.28	-0.39	-0.24	0.15	0.06	0.08	-0.08	-0.01	1		
Conductivity	-0.14	0.37	0.13	0.30	0.05	0.19	0.48	-0.42	-0.44	-0.51	0.20	1	
Substratum size	-0.10	-0.63*	-0.39	-0.48	0.26	-0.20	-0.34	0.09	0.35	0.32	-0.07	-0.66*	1
Aquatic veg. coverage	-0.10	0.25	0.12	0.25	0.11	0.09	0.29	-0.27	-0.38	-0.25	0.23	0.59*	-0.51

Invertebrate assemblage structure and environmental relationships

The relative magnitude of eigenvalues in a DCA analysis indicates the relative importance of the axes. Both axes 1 and 2 had high values: 0.55 and 0.38, respectively, and on them, five groups of sites were separated, one in the mountains, one in the piedmont and three on the plateau (north, central and south) (Fig. 2). Regressions of DCA axes 1 and 2 with environmental variables indicated several significant relationships (Table 3). The main environmental gradient associated with axis 1 was related to water velocity and stream order, whereas axis 2 was associated most strongly with latitude.

Invertebrate density ranged from 7 to 12,249 ind m^{-2} with the mean value for all sites being 1325 ind m^{-2} . The total number of invertebrate taxa was greatest in the piedmont, and the North and South Plateau sites had the lowest number of taxa (Table 4). Mean species richness per site was 13 for the mountains (range = 10–17), 20 for the piedmont (range = 13–28), 13 for North Plateau (range = 7–20), 17 for Central Plateau (range = 4–26) and 12 for South Plateau (range = 5–20). The EPT index was highest for the piedmont sites, whereas diversity (H') was highest in the mountain and piedmont rivers (Fig. 3).

Significant differences in density, mean taxon richness and EPT taxa richness were found among groups (ANOVA, $p < 0.05$). Invertebrate density was

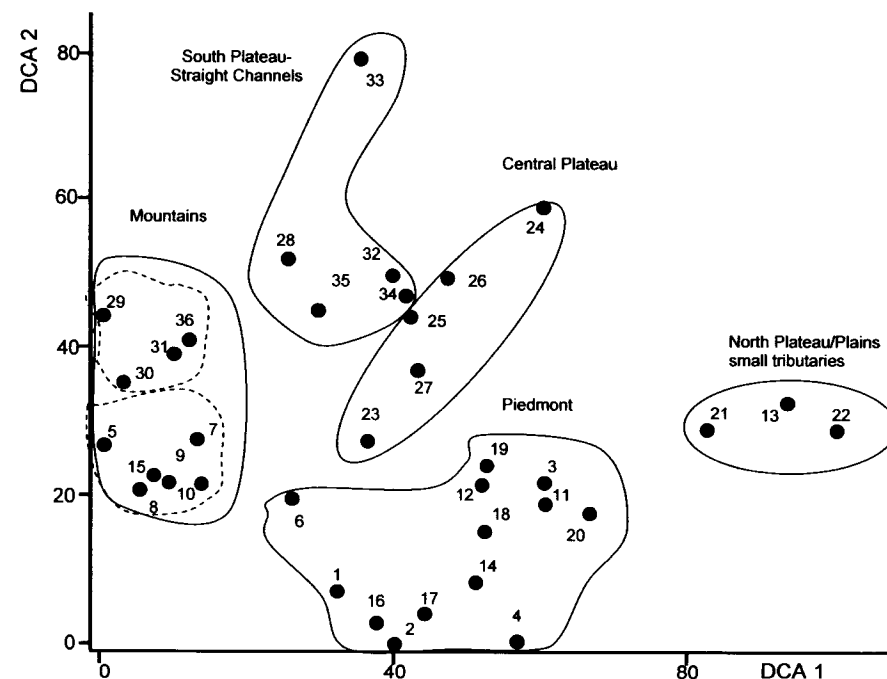


Fig. 2. Detrended correspondence analysis (DCA) ordination plot of site scores on the first two axes and identification of 5 site groups.

Table 3. Results of forward stepwise multiple regression on axis 1 and 2 scores for detrended correspondence analysis (DCA) on macroinvertebrate abundance data and a set of independent environmental variables measured in 36 Patagonian rivers. B = regression coefficient.

	B	t Statistic	P-value
DCA 1			
Regression model		$R^2 = 0.59$ $F_{(6,29)} = 9.42$	$p < 0.0001$, $n = 36$
Intercept	3313	2.80	0.009
Current velocity	-0.64	-5.39	<0.001
Stream order	0.42	3.21	0.003
DCA 2			
Regression model		$R^2 = 0.70$ $F_{(3,32)} = 28.9$	$p < 0.00001$, $n = 36$
Intercept	-3565	-7.66	0.0001
Latitude	0.83	8.51	0.0001
Substratum size	-0.22	-2.42	0.02

significantly greater on the North Plateau and piedmont than in mountain and South Plateau rivers (LSD test; $p < 0.05$). However, sites on three rivers (Verde, Valle Chico and Mayo) on the central and north plateaus were domi-

Table 4. Taxa found in five groups of Patagonian rivers identified by DCA. Values show mean abundances of taxa (ind m⁻²) for each DCA group. FFG: functional feeding groups; S: shredder, CG: collector-gatherers; CF: collector-filterer, Sc: scraper and P: predator.

Taxonomic group	Taxa	FFG	Moun.	Pied.	Plateau		
					North	Centr	South
Platyhelminthes	<i>Cura</i> sp.	P	0.3	0	0	0	0
	<i>Girardia</i> sp.	P	5.6	5.1	0	0	0
Annelida	Lumbriculidae sp.	CG	0.6	14.6	2.0	2.7	0
	<i>Limnodrilus variegatus</i> MÜLLER	CG	0	6.9	0	0	0
	<i>Limnodrilus udekemianus</i> CLAPAREDE	CG	0	0	2.0	0	0
	<i>Nais communis</i> PIGUET	CG	0	0	170.3	1776.0	0
	Glossiphoniidae sp.	P	0	9.9	163.0	1.0	0
Mollusca	<i>Chilina patagonica</i> SOWERBY	SC	0	119.8	21.0	3.8	0.3
	<i>Littoridina (Parchapei)</i> sp.	SC	0	0.7	0.3	0.3	0
	<i>Gundlachia concentrica</i> D'ORBIGNY	SC	0	10.2	0	0	0
	<i>Diplodon chilensis</i> D'ORBIGNY	CF	0	0.1	0	0	0
Arthropoda							
Crustacea	<i>Hyalella curvispina</i> SHOEMAKER	CF	0.1	109.2	497.7	73.3	8.8
	<i>Aegla neuquensis</i> SCHMITT	P	0	2.8	1.0	0.2	0
Arachnida	Oribatida sp.	SC	0	3.4	0	0	0
Insecta							
Plecoptera	<i>Klapopteryx kuscheli</i> ILLIES	SH	19.1	4.33	0	0	0
	<i>Pictoperla gayi</i> PICTET	P	0	1.40	0	0	0
	<i>Kempnyela genualis</i> NAVÁS	P	0	1.3	0	0	0
	<i>Notoperla archiplatae</i> ENDERLEIN	SC-P	18.8	0.1	0	0	0
	<i>Notoperlopsis femina</i> ILLIES	SC	0.1	53.7	0.3	33.2	0.3
	<i>Antarctoperla michaelsoni</i> K LAPÁLEK	SH	0	39.9	0	10.7	0.8
	<i>Antarctoperla</i> sp.	SH	0.1	17.9	0	0	3.5
	<i>Limnoperla jaffueli</i> NAVÁS	SC	8.9	17.5	0	0.2	0
	<i>Aubertoperla kuscheli</i> ILLIES	SC	0.9	1.5	0	0	0
	<i>Potamoperla myrmidon</i> MABILLE	SC	0	3.4	0	18.3	6.5
	<i>Senzilloides panguipulli</i> NAVÁS	SH	16.8	0.3	0	0	0.3
	<i>Pelurgoperla personata</i> ILLIES	CG	0.1	0.4	0	0	0
	<i>Chilenoperla puerilis</i> ILLIES	SH	12.9	0.2	0	0.2	1.3
	<i>Udamocercia arumifera</i> AUBERT	SC	0.3	1.3	0	0.5	0
Ephemeroptera	<i>Chilopteryx eatoni</i> LESTAGE	P	0.8	0.8	0	0	0
	<i>Metamonius</i> sp.	SC	1.7	0	0	0	0
	<i>Baetis</i> sp. 1	CG	5.3	26.3	0.3	6.8	0
	<i>Baetis</i> sp. 2	CG	6.5	20.6	0	15.8	0
	<i>Baetis</i> sp. 3	CG	23.3	11.5	0	7.7	8.8
	<i>Baetis</i> sp. 4	CG	11.8	1.1	0	39.2	2.8
	<i>Baetis</i> sp. 5	CG	0	0	0	7.3	13.5
	<i>Caenis</i> sp.	CG	0	0.1	1.0	0	0
	<i>Meridialaris laminata</i> ULMER	CG	0	227.3	0	2.3	0
	<i>Meridialaris chiloensis</i> DEMOULIN	CG	98.7	11.1	0	47.7	9.8
	<i>Meridialaris diguilina</i> ULMER	CG	0.1	49.7	0	0	0
	<i>Rhigotopus andinensis</i> PESCADOR & PETERS	CG	0	0.4	1.0	0	0
	<i>Penaphlebia chilensis</i> EATON	CG	0	26.3	0	0	0
	<i>Nousia bella</i> PESCADOR & PETERS	CG	0	19.3	15.0	8.0	0
	<i>Nousia minor</i> DEMOULIN	CG	0	24.7	0	0.2	0
Trichoptera	<i>Brachysetodes major</i> SCHMID	S	0	6.7	0	0.3	0
	<i>Hudsonema flammii</i> NAVÁS	S	0	1.3	0	0	0
	<i>Nectopsyche</i> sp.	S	0.1	0.5	0	0	0
	<i>Parasericostoma ovale</i> SCHMID	S	0	174.7	0.3	0	0
	<i>Myotrichia murina</i> SCHMID	S	0	0.8	0	0	0

Table 4. Continued.

Taxonomic group	Taxa	FFG	Moun.	Pied.	Plateau		
					North	Centr	South
	<i>Cailloma</i> sp.	P	1.4	0.7	0	1.2	7.0
	<i>Neoatopsyche chilensis</i> SCHMID	P	0.1	3.1	0	0.5	0.5
	<i>Australochorema rectispinum</i> SCHMID	P	0	1.1	0	0	0
	<i>Rheochorema</i> sp.	P	0.8	1.8	0	0	1.3
	<i>Rheochorema lobuliferum</i> FLINT	P	0.2	0	0	0.4	0
	<i>Smicridea annulicornis</i> BLANCHARD	CF	0.1	95.1	0	14.5	0.3
	<i>Mastigoptila</i> sp.	SC	0	0	0	0.2	0.3
	<i>Mastigoptila longicornuta</i> SCHMID	SC	0	0.1	0	0	0
	<i>Limnephilidae</i> sp.	S	0	1.3	0	0	0
	<i>Austrocosmoecus</i> sp.	S	0.2	0	0	0	0
	<i>Monocosmoecus</i> sp. 1	S	0.3	0	0	0.3	0
	<i>Monocosmoecus</i> sp. 2	S	0	0.3	0	0	0
	<i>Monocosmoecus</i> sp. 3	S	0	1.1	0	0	0
	<i>Hydroptila</i> sp.	S	0	0	0	0.2	0
	<i>Oxyethira</i> sp.	S	0.1	10.1	6.3	0.2	1.0
	<i>Ochotrichia (Metrichia)</i> sp.	S	0	0.5	0	10.2	0
	<i>Neotrichia</i> sp.	S	0	2.9	0	0.7	0
Coleoptera	Elmidae sp.	SC	0.6	98.4	3.0	595.2	71.5
	<i>Austrelmis</i> sp.	SC	0	8.0	0	265.3	23.0
	<i>Lancetes</i> sp.	P	0	0.7	1.0	1.3	0.3
	<i>Andogyrus ellipticus</i> BRULLÉ	P	0	0.2	0	1.5	0
	<i>Tropisternus setiger</i> SOLIER	P	0	1.2	0	0	0
Diptera	<i>Paratrachocladus</i> sp. 1	CG	0.2	34.8	67.7	0	0
	<i>Paratrachocladus</i> sp. 2	CG	20.5	33.5	400	257.7	2.3
	Orthoclaadiinae sp. 1	CG	0	9.2	0	0.8	24.3
	Orthoclaadiinae sp. 2	CG	0	0.7	0	0	5.5
	Orthoclaadiinae sp. 3	CG	1.1	9.2	0	0	0
	Orthoclaadiinae sp. 4	CG	0	0	0	0	0.5
	Orthoclaadiinae sp. 5	CG	1.0	2.5	0	0	0
	Orthoclaadiinae sp. 6	CG	0	1.3	0	0	0
	<i>Chironomus</i> sp.	CG	0	0	636.3	0	0
	<i>Rheotanytarsus</i> sp.	CG	0	0.1	0	1.0	0
	<i>Pentaneurini</i> sp.	CG	0	0.1	0	41	0.5
	<i>Pentaneura</i> sp.	CG	0.4	4.9	0	0	0
	<i>Ablabesmya</i> sp.	CG	0	6.6	6	0	0
	<i>Simulium</i> sp.	CF	4.3	6.0	0	68.5	0
	<i>Gigantodax</i> sp.	CF	2.9	6.7	0	1.3	0
	<i>Cnesia</i> sp.	CF	0.1	0	0	0	1.8
	<i>Hexatoma (Eriocera)</i> sp.	P	0.2	10.1	0	9.8	1.5
	<i>Limnophila</i> sp. 1	P	1.8	0.2	0.3	0	0
	<i>Limnophila</i> sp. 2	P	0	0	0	0.8	1.5
	<i>Molophilus</i> sp.	P	0	0.1	0	0	0
	<i>Dasyoma</i> sp.	P	10.6	5.1	0	2.8	0
	Empididae	P	1.7	0.7	0	0.8	0.5
	Tanyderidae	P	1.0	0	0	0	0
	<i>Lispidos</i> sp.	P	0	0.3	1.7	4.7	6.5
	Syrphidae	P	0	0.1	0.7	0	0
	Ceratopogonidae	P	0	0.1	4.0	0.5	0
	Tabanidae	P	0	0	0	1.3	0
	<i>Edwardsina (Edwardsina)</i> sp.	SC	3.5	0	0	0	0
	Psychodidae	P	0.1	0	0	0.2	0
Anisoptera	<i>Aeshna</i> sp. 1	P	0	0.1	0.3	0	0
	Total species richness		47	82	25	61	31

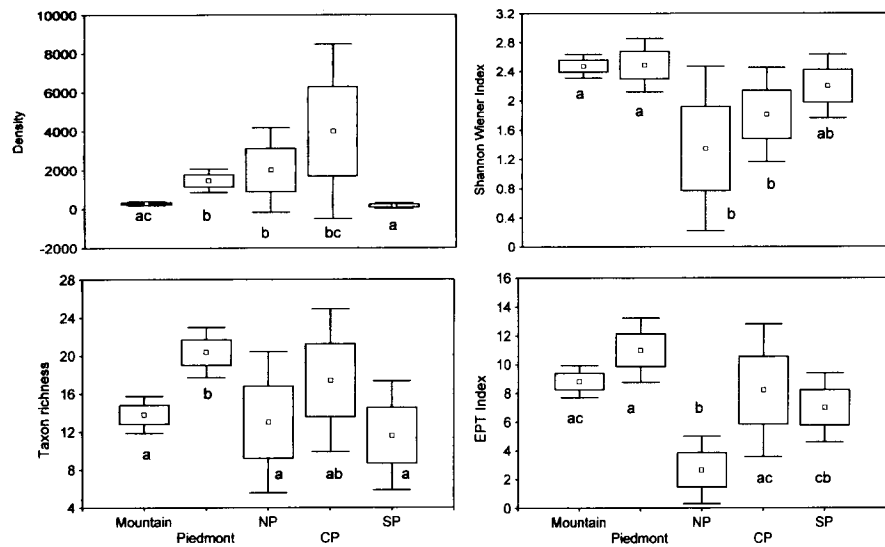


Fig. 3. Mean total density (ind m⁻²), taxon richness, Shannon-Wiener index and EPT index identified by detrended correspondence analysis. Central box is the mean, large box is \pm SE, end of whisker is \pm 1.96 SE. n is 10, 13, 3, 5 and 5 for Mountain, Piedmont, North, Central and South Plateau, respectively. Regions denoted with the same letter are not significantly different (post hoc LSD test after a significant ANOVA $p < 0.05$).

nated by single taxa (i.e., *Chironomus* sp. or *Nais communis*, respectively). Consequently, rivers on the central plateau had lower diversity values than piedmont and mountain rivers. The piedmont sites also had greater species richness than the mountains, north plateau and south plateau sites (LSD test, $p < 0.05$). Sites on the north plateau had the fewest EPT taxa. South plateau sites also had significantly fewer EPT taxa than piedmont sites (LSD test, $p < 0.05$) (Fig. 3).

A total of 100 taxa were collected from 36 sites in the river survey (Table 4). Only five taxa occurred in all five site groups: *Hyaella curvispina*, *Notoperlopsis femina*, *Oxyethira* sp., *Neotrichia* sp., and *Paratrichocladius* sp. 2. Some taxa were more abundant in the mountains than at piedmont sites: *Senzilloides panguipulli*, *Klapopteryx kuscheli* and *Notoperla archiplatae* (Plecoptera) and *Edwardsina* sp. (Diptera). In the piedmont rivers, *Pictoperla gayi*, *Kempnyella genualis*, *Notoperlopsis femina*, *Antarctoperla michaelsoni* (Plecoptera), *Meridialaris laminata* (Leptophlebiidae), *Parasericostoma ovale* and *Smicridea annulicornis* (Trichoptera) were the most common insects. On the plateau, *Nais communis*, *Hyaella curvispina*, *Paratrichocladius* sp. 2 and Elmidae were the most abundant invertebrates. Platyhelminthes, and the mol-

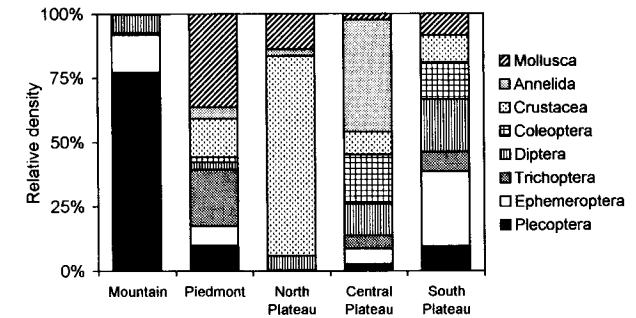


Fig. 4. Relative abundance of major macroinvertebrate taxa in the 5 groups identified by detrended correspondence analysis.

Table 5. Environmental variables having a significant correlation (Pearson r) with invertebrate community indices ($n = 36$ for all variables except organic fractions $n = 25$, * $p < 0.05$, ** $p < 0.005$); ns: non significant.

	Taxon richness	EPT	H'
Distance from the source	ns	ns	-0.33*
Latitude	-0.41*	ns	ns
Conductivity	ns	ns	-0.50**
Substratum size	ns	ns	0.34
Aquatic plant coverage	0.43**	ns	ns
FPOM	0.40*	0.40*	0.44**
BOM	ns	0.37*	0.38*
Desertification status	ns	-0.38*	-0.41*

luses *Gundachlia concentrica* and *Diplodon chilensis*, were absent from rivers on the plateau but were common in mountain and piedmont rivers. Moreover, the chironomids *Chironomus* sp. and *Pentaneurini* sp., and the glossosomatid caddisfly *Mastigoptila* sp. peaked in abundance or were recorded, exclusively in some plateau rivers.

Plecoptera and Ephemeroptera declined in relative abundance from the mountains to the piedmont, whereas relative abundance of Trichoptera was greatest in piedmont rivers (Fig. 4). Coleoptera represented >20% of individuals on the central and south plateaus. Crustacea and Mollusca were rare at the mountain sites (<1%), but Crustacea comprised >60% of the invertebrates on the North Plateau, and Annelida made up >40% on the Central Plateau.

Total species richness and EPT taxon richness decreased with latitude and increased with both aquatic plant coverage and abundance of FPOM. Diversity (H') also increased where FPOM was abundant but decreased as conductivity

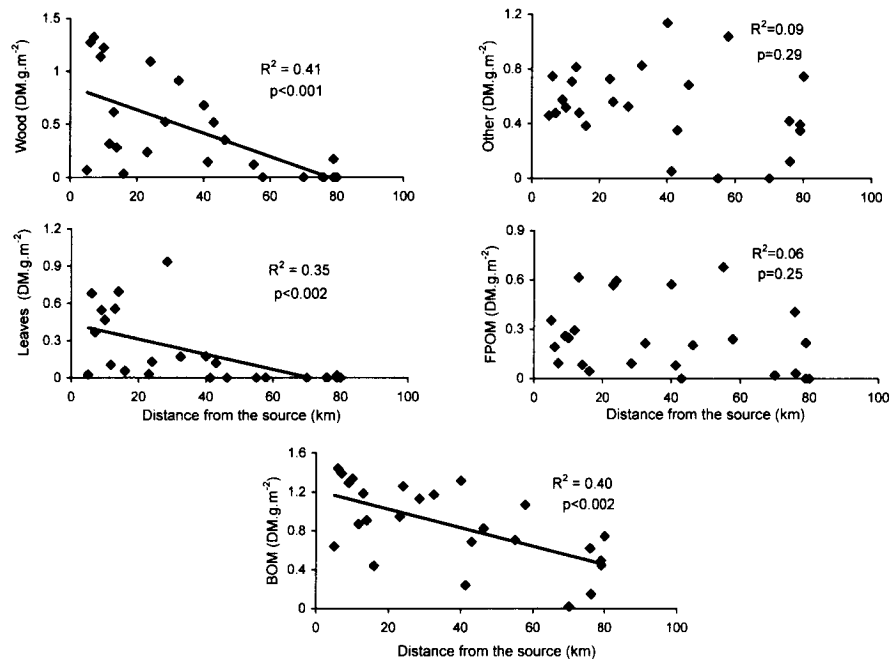


Fig. 5. Organic matter distribution (DM g m^{-2}) plotted against distance from the river source in a subset of 25 rivers in Patagonia. Significant regressions are for $\log(x+1)$ transformed data of the dependent variable.

increased. Both indices were negatively correlated with degree of land degradation (Table 5).

Benthic organic matter and functional organization

The amount of wood found in streams decreased significantly from the deciduous *Nothofagus* forest to grassland, as shown by the regression of wood mass against distance from the source ($r^2 = 0.40$, $p < 0.001$, Fig. 5). Similarly, both leaves and total benthic organic matter declined in abundance from the mountains to the plateau ($r^2 = 0.35$, $p < 0.002$; and $r^2 = 0.40$, $p < 0.002$, respectively). The detrital fraction “other” was relatively constant across biomes, reflecting the diverse nature of allochthonous materials (roots, grass, fruits) in grasslands. In contrast, FPOM showed no significant change in abundance across the regions (ANOVA, $P = 0.25$).

Significant regression models with distance from the source were obtained for collectors and shredders ($r^2 = 0.26$ and 0.20 , respectively), with shredders decreasing, and collectors increasing, significantly from the forest to the grassland. A stronger relationship ($r^2 = 0.27$) was obtained for shredders, when the

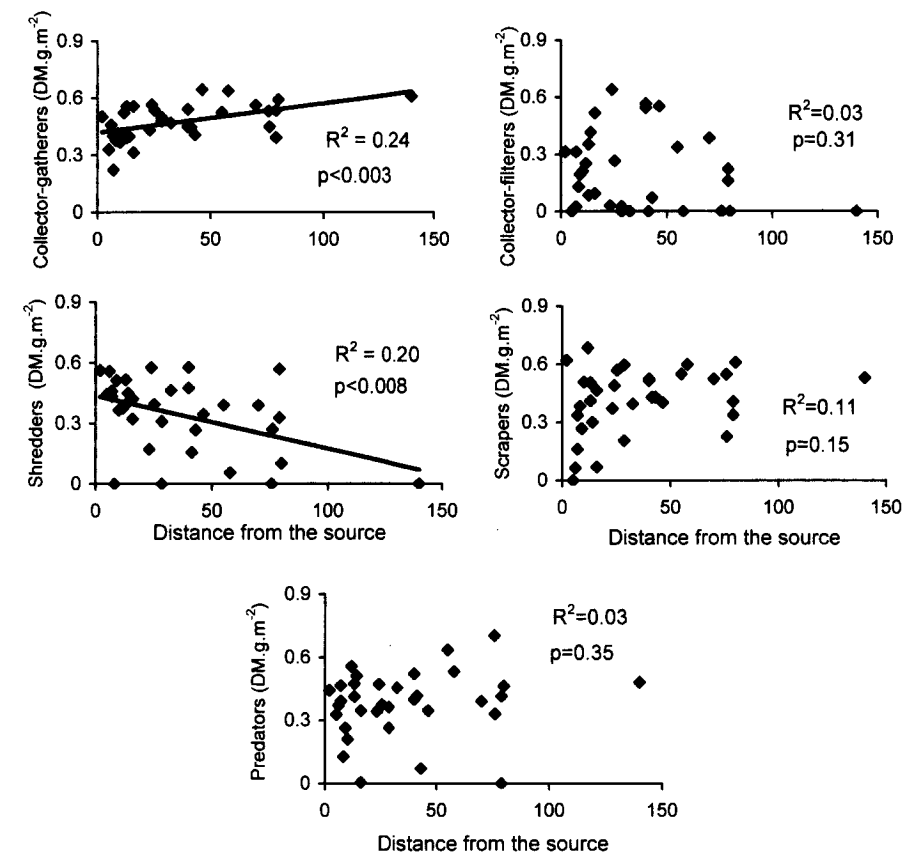


Fig. 6. Relationships between biomass (DM g m^{-2}) and distance from the river source for invertebrate functional feeding groups in 36 rivers of Patagonia. Significant regressions are for $\log(x+1)$ transformed data of the dependent variable.

Mayo river outlier was omitted from the model. No significant relationships were found for filterers, scrapers and predators (Fig. 6).

The relative proportion of FFGs per DCA site group is shown in Fig. 7. Biomass patterns showed more obvious trends than density patterns for shredders and collectors. Mountain and piedmont sites had a higher proportion of shredders than plateau sites, whereas a higher relative abundance and biomass of collectors was observed at the plateau sites. Relative biomass of predators was particularly high on the north plateau where large crayfish (*Aegla neuquensis*) were present in samples. The relative biomass of scrapers decreased from the mountains to the plateau. The high scraper biomass at mountain sites can be explained by the presence of large larvae of *Notoperla archiplatae* (Plecoptera), whereas small gastropods (*Chilina patagonica*) were the main scrapers at piedmont sites.

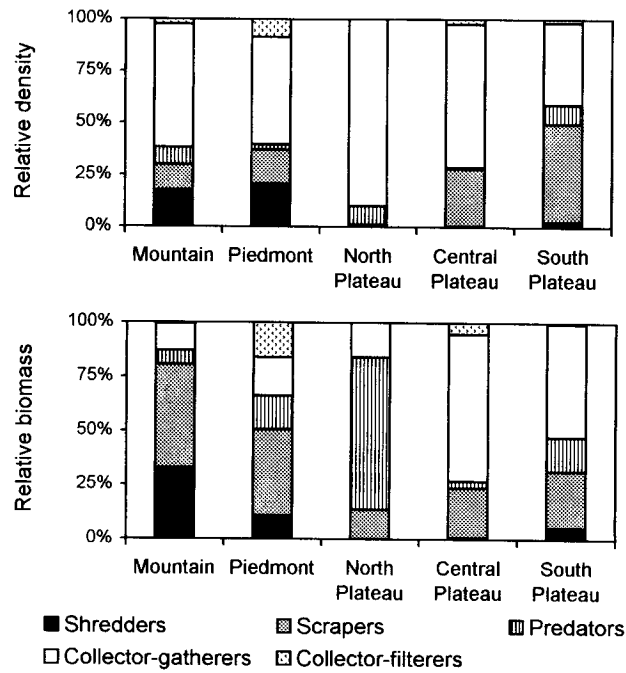


Fig. 7. Relative abundance (top) and biomass (bottom) of functional feeding groups for the 5 site groups defined by detrended correspondence analysis ($n=36$).

The CCA ordination based on FFG biomass (eigenvalues $CCA1 = 0.10$, $CCA2 = 0.04$) showed clear correspondences with the environmental variables selected. The first two axes explained 56% of the variance in FFG data, and correlations between species and environmental variables were 0.904 and 0.756 for CCA1 and CCA2, respectively. Shredder biomass increased as the amount of leaves and wood increased, and also with increasing substratum size and current velocity (Fig. 8). Filterer biomass increased as FPOM became more abundant, while scraper biomass increased downstream in more open rivers.

Discussion

Macroinvertebrate communities and landscapes

Analysis of geographic trends in the distribution of species can provide insights into the factors most strongly limiting the distribution of taxa (HAWKINS et al. 1997). Many studies at the landscape level report strong gradients in biotic structure associated with elevation or latitude (MARCHANT et al. 1985, TATE & HEINY 1995, JACOBSEN et al. 1997) as well as the physical and chem-

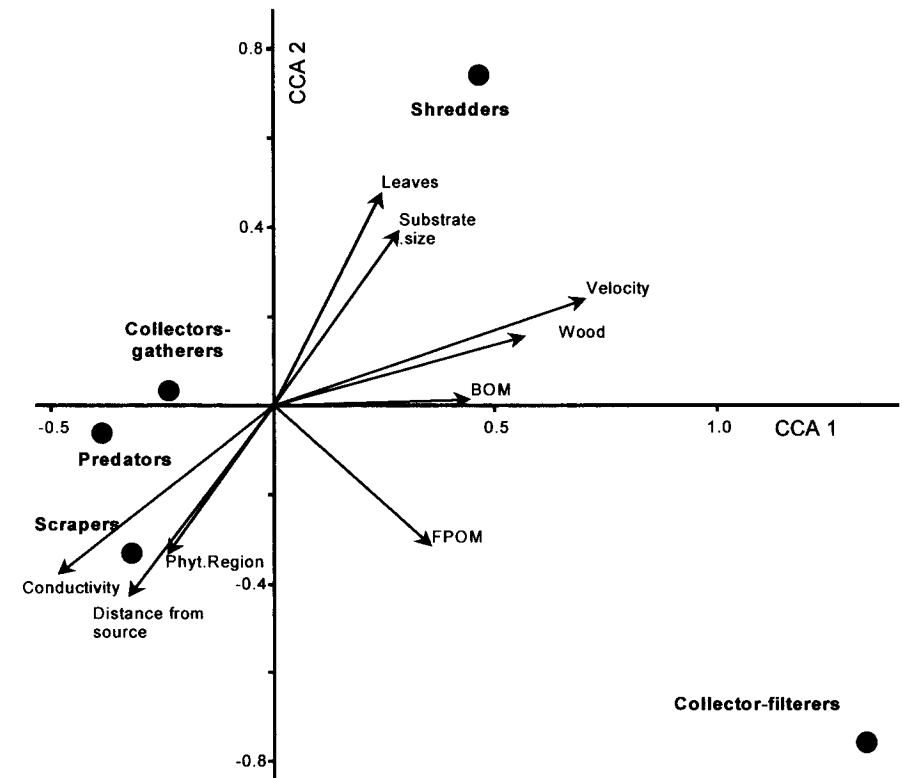


Fig. 8. Canonical correspondence analysis showing the relationships between functional feeding groups of benthic invertebrates, sources of food, and physical chemical variables, in a subset of 25 rivers.

ical features of rivers (WRIGHT et al. 1984, KAY et al. 1999). In the present study of Patagonian streams, macroinvertebrate distribution was affected by geographical, physical and chemical factors. Strong relationships were evident among invertebrate assemblages and biophysical attributes of the surrounding landscape, as well as with latitude. Vegetation and soils in the area are strongly linked to climate, which in consequence determines the broad distribution of phytogeographical regions and biozones in Patagonia (DEL VALLE et al. 1998). In my ordination, the macroinvertebrate assemblages of rivers were grouped according to phytogeographical (*Nothofagus* forest, Patagonian steppe) and biozonal (Andean humid, Sub-Andean sub-humid and extra-Andean) features. Thus, landscape classification on a large scale was useful for predicting macroinvertebrate assemblages because within phytogeographical regions, landscape heterogeneity is relatively low. However, it should be noted that some Patagonian landscape subcategories were poorly sampled (e.g., the Ex-

trandina Oriental: Low Central and Southern mountains), or not considered in the present study (Biozone: Patagonic Monte, Magallanic Steppe).

Although sites were grouped according to their location in the mountains, piedmont and plateau, altitude was not selected as a predictor in the regression analysis. Nevertheless, current velocity, stream order and substratum size, variables that changed along altitudinal gradients, were associated with invertebrate assemblages, and several taxa including *Klapopteryx kuscheli*, *Notoperla archiplatae* and *Senzilloides panguipulli* were found exclusively in the mountains. Similarly, some insects including *Baetis* sp. 5, *Pentaneurini* sp., *Pentaneura* sp., and *Ochotrichia* sp. were only recorded on the plains or were most abundant there. In the mountains the Plecoptera, Ephemeroptera and Diptera dominated, whereas on the piedmont Trichoptera, Annelida and Mollusca were more abundant. On the plateau the most abundant orders were Diptera (mainly Chironomidae), Coleoptera, Oligochaeta and Crustacea. These findings agree with those of WAIS (1984, 1990), and PAGGI & RODRIGUES CAPITULO (in press) for river faunas at lower latitudes in Patagonia.

Except on the South Plateau, the density of invertebrates increased from the mountain to the plateau, consistent with altitudinal abundance patterns recorded by MISERENDINO & PIZZOLÓN (2000). Moreover, more species were collected in the piedmont rivers (82 taxa), than in the mountains (47 taxa). TATE & HEINY (1995) reported greater numbers of taxa in rivers of the mountains than the plains in Colorado, and WARD (1986) found that species richness increased with increasing stream size in the same area. However, CARTER et al. (1996) found maximum richness in lower elevation tributaries in transitional zones between mountains and valleys, in south central Washington. Similarly, I found the highest species richness in medium-sized rivers in the area of transition between the mountains and the plateau. These results are consistent with those of STATZNER & HIGLER (1986) who observed maximum richness of invertebrates where major changes in stream slope created areas of high in-stream hydraulic variability.

Macroinvertebrates and land use

The composition of macroinvertebrate assemblages was explained best by latitude and variables associated with river size. However, there were also significant correlations between desertification status and the diversity of macroinvertebrates (H') and the EPT index, both of which decreased as desertification increased. Similar relationships between macroinvertebrate diversity in rivers and the percentage of non-forested land in North American mountains were reported by SPONSELLER et al. (2001). In Patagonia, overgrazing and agricultural practices have increased the desertification process greatly, and there are vast areas affected, including some natural forests (DEL VALLE et al. 1995). Over-

grazing causes water and wind erosion, salt excess, soil crusting and compaction (DEL VALLE et al. 1998).

Macroinvertebrate diversity and EPT richness in rivers decreased with increasing desertification but only species richness decreased with latitude (Table 5). Sites on rivers located in forested areas with a low degree of desertification had communities with higher diversity than those in areas with moderate or severe desertification. Furthermore, some sites on rivers draining grassland were dominated by species associated with sedimentation (*Chironomus* sp., *Nais communis*). These sites showed strong loss of riparian cover and signs of erosion and compaction of the soil. However, other sites within grassland basins had severe desertification and intermediate diversity values. These sites had strips or patches of native riparian shrubs that appeared to mitigate the effects of basin desertification by buffering nutrient inputs, supplying allochthonous organic matter, enhancing instream habitats, and providing habitat for the terrestrial adult stages of insects with stream-dwelling larvae (WIBERG-LARSEN et al. 2000). Similarly, the presence of native riparian forest can minimize the effects of pastoral agriculture on macroinvertebrate assemblages as found by STOREY & COWLEY (1997) and HALL et al. (2001) in New Zealand. The loss of riparian cover can also affect invertebrate assemblage structure by modifying the temperature regime (SPONSELLER et al. 2001), but this could not be evaluated in the present study since my sampling was confined to autumn.

Functional organization within a landscape perspective

Headwater streams in temperate forests are largely dependent on inputs of allochthonous organic matter from the surrounding terrestrial environment as a basis for secondary production (VANNOTE et al. 1980). I found a strong association between different FFGs and their food resources linked to large-scale variables in the CCA analysis. Thus, shredder biomass was high in *Nothofagus* forest where sources of coarse organic matter were high, biomass of filterers increased where FPOM was most abundant, and scrapers were commonest on the Patagonian steppe where abundant periphyton was observed.

There have been no previous studies on the amount of BOM in Patagonian rivers with which my results can be compared, but the quantities in the forest rivers were similar to those reported for some forested, upland rivers in the Northern Hemisphere in summer (IVERSEN et al. 1982, SOLLINS et al. 1985). The leaf and woody debris fractions were important at most sites in the mountains, even where there was little or no canopy. In the piedmont rivers, leaf fragments of *Salix fragilis* were the dominant organic materials, whereas on the plateau, the main sources of BOM were grasses and shrubs. Consequently, BOM values were lower on the plateau than in the mountains or at the pied-

mont sites. This pattern is consistent with that reported by SCARSBROOK et al. (2001), who found lower litter inputs to streams at pasture than forested sites in New Zealand.

Lotic ecosystems form an integral part of the surrounding landscape with which they are highly interactive (WARD 1989). Therefore, to comprehend the dynamics of rivers we must apply a broad landscape-based, spatio-temporal perspective. The Patagonian region exhibits great biophysical complexity (OESTERHELD et al. 1998), and the macroinvertebrate assemblages of running waters reflect this landscape complexity. My results indicate that land cover and its degradation affect the macroinvertebrate assemblages of rivers and streams in Patagonia, but that the retention of native trees in riparian areas can help maintain or enhance aquatic biodiversity. Because desertification and habitat degradation are increasing rapidly in Patagonia, the identification and protection of areas with high biological value is an urgent requirement (DU PISANI et al. 1995).

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