

INTERACTIVE EFFECTS OF BASIN FEATURES AND LAND-USE CHANGE ON MACROINVERTEBRATE COMMUNITIES OF HEADWATER STREAMS IN THE PATAGONIAN ANDES

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ABSTRACT

Composition and structure of macroinvertebrate communities were documented in relation to hydrochemical variables over a 10-month period in four headwater tributaries of the Futaleufú River, northwestern Chubut, Argentina. The streams are located along the strong rainfall gradient that decreases from west to east and they have different basin features. At Blanco and Baggilt streams, riparian vegetation consisted primarily of native *Nothofagus* forest, while in the Nant y Fall and Rifleros, basins with a long legacy of domestic grazing, the introduced *Salix fragilis* was the dominant riparian species. Macroinvertebrate species richness, density, and biomass were similar among rivers; however, biomass of shredders was highest in the *Nothofagus* forested streams and collector-filterers were significantly higher in *Salix fragilis*-bordered rivers. Water temperatures were higher in non-native *Salix* sites than in the native or mixed forested sites. Canonical community analysis indicated community composition was related to geomorphic attributes of the rivers, especially slope, basin height (elevation change), distance to the source, substratum size, and *Salix* coverage. Moreover, seasonally dynamic variables, rainfall and water temperature were good community predictors. Land-use change (conversion from *Nothofagus* to pastures and the *Salix fragilis* invasion in the riverbanks of pasture-dominated catchments) was interactive with natural stream attributes as determinants of macroinvertebrate distribution and abundance. Copyright © 2004 John Wiley & Sons, Ltd.

KEY WORDS: benthic; streams; functional feeding groups; Patagonia; *Salix*; *Nothofagus*

INTRODUCTION

Conversion of native forest into pastures as a consequence of use of land for agriculture has produced wide-scale degradation of aquatic ecosystems in several countries (Collier *et al.*, 2001). Clearing and replacement of native species of riparian vegetation by exotic species are causing concern because riparian functions can be altered (Cummins *et al.*, 1989). In forested streams, riparian vegetation is the main source of organic material processed by aquatic organisms as it is transported downstream (Vannote *et al.*, 1980; Minshall *et al.*, 1985). Studies have shown a variety of long- and short-term abiotic effects of forestry practices, including increased sediment and nutrient inputs (Murphy *et al.*, 1982; Wallace *et al.*, 1997) and discharge (Hartman and Scrivener, 1990), and decreased shading resulting in higher water temperature (Ward and Stanford, 1979). These changes in abiotic characteristics can affect the structure and function of the stream biota including invertebrates and fishes (Ward and Stanford, 1982; Rowe *et al.*, 2002).

The introduction of exotics trees in Argentina's central Andean-Patagonian region dates back to the early twentieth century with the arrival of Welsh immigrants. They distributed *Salix fragilis* L in the Chubut River system with the idea that it would reduce soil erosion from agricultural fields and provide wind breaks for cattle and houses (Enricci *et al.*, 2000). The precolonization situation of the riverbanks is unknown. However, we assume most of the riparian vegetation for rivers in the mountain area was composed of the *Nothofagus* forest that extended near to the parafluvial zone, as occurs presently in areas not invaded by *Salix*. Watercourses mainly retained native species in their rivers corridors in the Precordillera where the forest distribution is sparser, and rivers draining grasslands

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probably had small patches of native riparian forest. Today, the non-native *Salix fragilis* is naturalized in riparian areas and widely distributed from very small streams to large rivers in Patagonia. However, its influence on the functioning of the biota or its effect on the ecology of the rivers in Patagonia have not been documented.

Clearing riparian forests in Australian agricultural areas allowed invasion and dominance by willows as well. These 'willowed' reaches had significantly lower macroinvertebrate species richness, density, and evenness than native evergreen forested reaches (Read and Barmuta, 1999). Lester *et al.* (1994) observed grassland streams in New Zealand, whose riparian zones were forested with *S. fragilis*, supported relatively few invertebrates, and Glova and Sagar (1994) found that *Salmo trutta* abundance increased. Winterbourn (1986) also noted increases in algal and secondary production and sedimentation problems, although these seem to be localized or short-term phenomena.

Macroinvertebrate communities are an important component in Patagonia's stream ecosystem and have a high degree of endemism and remarkable biogeographic differences (Illies, 1969; Ringuet, 1961). The first research studies of macroinvertebrate distribution in rivers of Patagonia were carried out by Wais (1987, 1990). The distribution of macroinvertebrates along altitudinal gradients (Albariño, 1997; Miserendino and Pizzolon, 2000), and some functional and ecological aspects (Wais, 1990; Wais and Bonetto, 1988; Modenutti *et al.*, 1998; Albariño and Balseiro, 1998; Miserendino, 2001a) have been studied in rivers of the area. Moreover, there is some indication that changes in dominant land use at the catchment spatial scale can have significant impact on lotic macroinvertebrate communities (Miserendino and Pizzolon, 1999, 2003).

The goal of this research was to compare macroinvertebrate communities of four headwater streams in the Patagonian Andes that differ in nature and coverage of riparian vegetation and land use. We hypothesized the composition of riparian vegetation (*Nothofagus versus Salix*) and differences in land uses (native forest *versus* pasture) would lead to differences in composition, density, and functional attributes in macroinvertebrate communities. We analysed seasonal changes of biomass and density of macroinvertebrates and functional feeding groups (FFG) and also examined relations to environmental attributes at reach and watershed scales.

METHODS

Study area

The study was done in four low-order tributaries of the Futaleufú River (Chubut, Argentina), which drains into the Pacific Ocean through Chile. The Blanco, Baggilt, Rifleros, and Nant y Fall catchments (Figure 1) are located along the strongly west–east decreasing rain gradient characteristic of the east side of the Andes, especially between 40 and 43° S (Paruelo *et al.*, 1998). These are high gradient streams. Blanco and Baggilt headwaters have small glaciers, and headwater lakes exist in Baggilt and Nant y Fall (Table I). All four catchments are dominated by granitic and dioritic rocks. Extensive outcrops of crystalline bedrock produce dilute waters, a distinctive characteristic of the Andean-Patagonian Cordillera region (Drago and Quirós, 1996).

Mean annual air temperature in the area is 9.7°C, with the mean of the coldest and warmest months being 3.1°C and 15.8°C, respectively (Amico *et al.*, 2001). Mean rainfall during winter (June–August) is four times higher than during summer months (December–February) (Coronato and del Valle, 1988).

Blanco and Baggilt catchments are covered by the native deciduous forest of *Nothofagus pumilio* (Fagaceae) locally called 'lenga', between 800 and 1300 m, and by the native, perennial *Austrocedrus chilensis* (Cupressaceae), which is also common in the high forest in Rifleros. The downstream portions of the Rifleros and Nant y Fall basins are covered by native *N. antarctica* (ñire) forest. Human presence in this area of Patagonia is very recent, starting around 100 years ago with the Welsh colonization. Primary land uses are extensive cattle production and silviculture, and these activities are more intense in Nant y Fall where grazing (number of animal per km²) is four times higher than in the other basins (Estadística de Existencia Ganadera, 1992). Owing to agriculture activities and logging, 23% of the Rifleros Basin and 24% of the Nant y Fall Basin have been converted to pasture. No towns exist in the catchments and human density is well below 1/km².

We selected very similar sampling reaches in size, elevation, and location, but these reaches had marked differences in riparian composition and coverage. Blanco River was located in the less impacted basin and its entire riparian corridor still remains as native *Nothofagus* forest. The Baggilt was an intermediate situation having

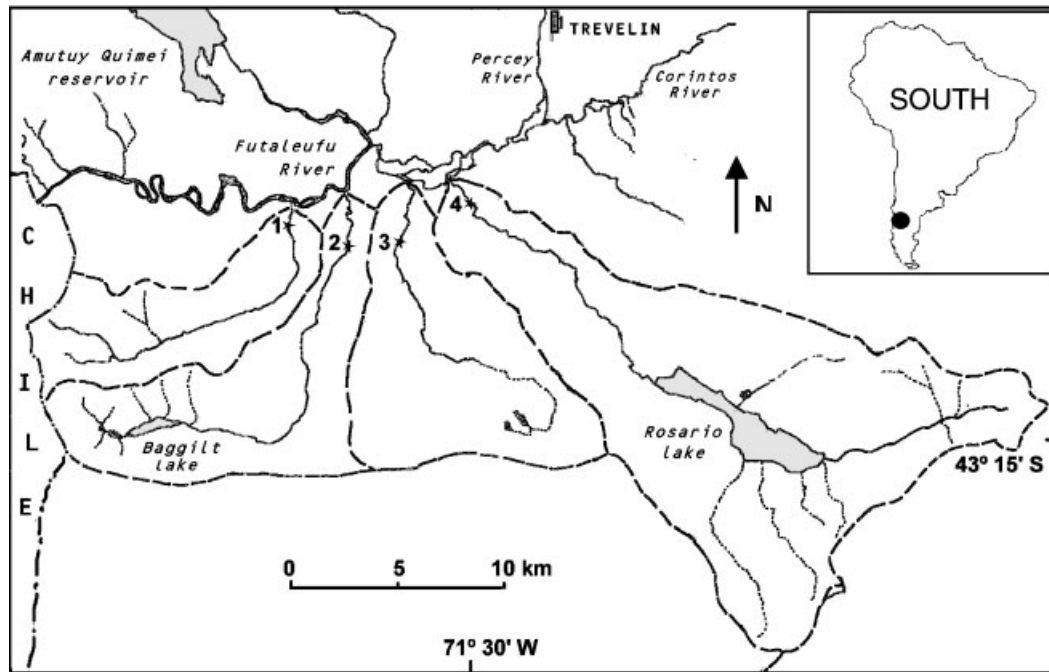


Figure 1. Study area showing drainage basins (dashed lines) and location of sampling sites in four streams of the Futaleufú basin, Argentina: 1, Blanco; 2, Baggilt; 3, Rifleros; 4, Nant y Fall

low coverage of *Salix fragilis*, but still retaining a high percentage of native vegetation. The Rifleros and Nant y Fall reaches were in the opposite situation in which the riparian corridor has been completely invaded by *Salix fragilis* nearly down to the thalweg (Table I). We suspect that at those sites (Rifleros and Nant y Fall), in precolonial time, trees such as *Nothofagus* spp. or native prairie were present. Today, in both cases, *Salix* has invaded.

Physical and chemical characteristics

Monthly mean discharge data were obtained from gauging stations in the Baggilt stream and Nant y Fall River from EVARSA (1994). Substrate composition was estimated as percentage of boulder, cobble, gravel, pebble, and sand using a 1 m² grid (Gordon *et al.*, 1994). Air and water temperatures were measured at each site with a mercury thermometer at the time of sampling. Stream order was assigned from Coronato and del Valle (1988). Annual rainfall precipitation at each basin was estimated using the regression models of Jobbágy *et al.* (1995), and monthly rainfall for the study period was provided by the Forestry Experimental Station (INTA-Esquel Centro Regional Patagonia Sur).

Specific conductance, pH, total alkalinity, and carbonate alkalinity were measured bimonthly ($n = 6$) and total nitrogen and total phosphorus were determined on two occasions. Specific conductance was measured with a Horiba U-7meter and pH with an ORION 720 SA meter, both at 20°C. Total alkalinity and carbonate hardness (eriochrome black) were determined by titration with colorimetric end-point; total nitrogen and total phosphorus were analysed following Golterman *et al.* (1978).

Macroinvertebrate collection

Streams were sampled approximately every five weeks from September 1991 to July 1992. Macrozoobenthos were collected with a Surber net (30 × 30 cm, 250 μm mesh size). Eight samples were taken at each site, and pooled for the analysis. Samples were preserved with 4% formaldehyde solution. A total of 36 macroinvertebrate samples were analysed. At the laboratory, macroinvertebrates were sorted and identified to the lowest possible taxonomic level using regional keys (Domínguez *et al.*, 1994; Angrisano, 1995; Bachmann, 1995; Illies, 1963).

Table I. Physical features, morphometric parameters and historical mean values of hydrological variables in four streams in the Patagonian Andes of the Futaleufú basin, Argentina

Features	Blanco	Baggilt	Riferos	Nant y Fall
Catchment descriptors				
Surface area ^{a,b} (km ²)	55.2	83.4	90.5	218.7
Basin max. height ^c (m)	2271	2271	800	1875
Basin mean height ^d (m)	1372	1351	616	1098
Height of sampling site ^c (m)	450	460	415	310
Slope of main channel ^d (m/km)	58.5	39.8	21.1	19.1
Rainfall ^e (mm/y)	1200	1100	750	600
Discharge ^f (m ³ /s)	na	4.09	na	2.47
Unit-area discharge ^f (l/s/km ²)	na	58.4	na	7.38
Area above the timberline ^a (%)	30.6	16.8	0.0	8.7
Glaciers in headwaters ^a (%)	5.0	1.3	0.0	0.0
Lakes ^a (%)	0.0	1.1	0.2	4.5
Basin vegetation ^a				
Native forest of <i>Austrocedrus chilensis</i> (%)	6.8	6.0	11.1	0.9
Native deciduous forest of <i>Nothofagus pumilio</i> (%)	37.8	33.7	0.0	15.5
Native deciduous forest of <i>Nothofagus antarctica</i> (%)	6.3	28.4	61.2	39.0
Total native forest (%)	50.9	68.1	72.3	55.4
Non riparian wetlands (%)	5.0	3.2	4.5	7.7
Pasture/prairie (%)	8.4	9.5	23.1	23.6
Reach features				
Stream order ^c	2	3	3	3
Distance from source ^c (km)	13	14	16	16
Width (m)	35–15	20–18	12–9.3	12–8
Habitat unit	Riffle	Run	Run	Run/pool
Substratum size	Boulder/cobble	Boulder/cobble	Cobble/pebble	Pebble-sand
Native riparian vegetation <i>Nothofagus</i> spp. (%)	60	20	0	0
Exotic riparian vegetation <i>Salix fragilis</i> (%)	0	40	90	90

na, not available.

^a Upstream of sampling reach, based on a georeferenced Landsat TM image (30 × 30 m resolution).

^b Pizzolon *et al.* (1992).

^c From IGM (Geographical Military Institute) charts.

^d Estimated after Gordon *et al.* (1994), from IGM topographic charts 1:50 000.

^e Estimated from Jobbágy *et al.* (1995).

^f EVARSA (1994).

Organisms were stored in 70% ethyl alcohol with the addition of glycerin. Voucher collections were retained in the Laboratorio de Ecología Acuática of the Universidad Nacional de la Patagonia.

Macroinvertebrate abundance was obtained by counting all individuals in the sample and expressing results as number per square metre. Biomass was assessed by measuring body length of all individuals of all taxa to the nearest 0.5 mm, using the regression models of Miserendino (2001b). Results were expressed as milligrams of dry mass per square metre. Species richness (total taxa in the sample) and EPT taxa (EPT = Σ of Ephemeroptera, Plecoptera, Trichoptera taxa) were also determined. Functional feeding groups (FFGs) were assigned by gut content analysis and using available references (Merritt and Cummins 1978; Domínguez *et al.*, 1994; Albariño and Balseiro 1998; Díaz Villanueva and Albariño 1999).

Data analysis

Community attributes of the streams were compared using a two-way ANOVA without replication model (Sokal and Rohlf, 1995), with rivers as fixed effect in the treatments. This model assumes that the interaction between months and rivers is not present. Previous inspection of the data indicated that interaction was unlikely to be present. Variables were transformed by $\log(x + 1)$ to improve normality prior to running ANOVA, and homogeneity of

variances was tested using Bartlett's test. Significant differences between means were assessed with the T-method, in post hoc comparisons (Sokal and Rohlf, 1995).

Canonical correspondence analysis (CCA) was performed using PCORD statistical package (version 3.0; McCune and Mefford, 1997) to assess the relationships between macroinvertebrate assemblage and environmental variables. We included the basin and reach descriptors and land-use-related variables in the analysis. CCA is a direct gradient analysis that assumes a unimodal model for the relationships between the response of each species to environmental gradients, and that ordination axes are linear combinations of the environmental variables (ter Braak, 1986). Variables and species density were transformed as $\log(x + 1)$, prior to analysis. Also, variables that covaried with other measured variables (Pearson correlation coefficient $r > 0.65$; $P < 0.01$) were removed prior to CCA. Thus, elevation of the site, basin maximum height, stream order, and *Nothofagus* coverage were not used in the final ordination. Rare taxa (<1% at a sampling site) were not included in the CCA. The environmental variables considered in the final ordination were: basin area, basin height, slope, distance from the source, width, substratum size, *Salix* coverage, rain, and water temperature. Discharge and the chemical variables were not used in the multivariate analyses because complete data were not available for all sites or dates. A Monte Carlo permutation test (999 permutations) was used to verify the significance of the model.

RESULTS

Physical and chemical factors

The substrate was mainly boulders and cobbles at Blanco and Baggilt, whereas substrate size was smaller at Rifleros and Nant y Fall (Table I). Historical flow records of Baggilt Stream (17 years) showed a bimodal hydrograph with two peaks, one in June during the rainy season and the other in November due to snowmelt. In contrast, historical records at Nant y Fall River (39 years) showed a very small snowmelt peak close to the winter rainfall peak, because this catchment has no glacier runoff and has a very short snowmelt period. Moreover, the year of study was not normal because no winter peak occurred and rainfall in December was twice as high as the long-term trend (Figure 2).

Rifleros was warmer than the other sites (Figure 3). Conductivity, pH, alkalinity, and total hardness increased from west to east inversely with the rainfall gradient (Table II). Chemical data provided a clear distinction among rivers, with conductivity and total alkalinity significantly higher at Rifleros and Nant y Fall than Blanco and Baggilt (ANOVA $F_{k20} = 62.2$, $P < 0.001$; $F_{TA} = 28.96$, $P < 0.001$). Conductivity recorded at the Nant y Fall River was five times higher and alkalinity was 2.7 times higher than in the Blanco and Baggilt. Total phosphorus was similar in all four streams, but total nitrogen was 50% higher in the Nant y Fall River. Coefficient of variation for the chemical variables (Table II) was low in Baggilt, and especially in Nant y Fall, both basins having lakes at their headwaters.

Species richness, density, and biomass of macroinvertebrates

Altogether, 72 taxa of macroinvertebrates, mainly insects, were identified: Plecoptera (15 species), Ephemeroptera (7), Trichoptera (16) and Diptera (23, 11 were chironomids); the amphipod *Hyaella cuvispina*, Lumbriculidae sp., and the gasteropod *Chilina patagonica* were more abundant at Rifleros and Nant y Fall (Table III).

Differences in mean species richness, abundance, and biomass were not significant among rivers (ANOVA, $P_{\text{richness}} = 0.14$; $P_{\text{density}} = 0.42$ and $P_{\text{biomass}} = 0.13$; Table IV). Total density in autumn/winter months in Rifleros and Nant y Fall, was greater (60% and 20% respectively) than in spring/summer months. Conversely, the highest density in the Baggilt and Blanco rivers was in September, being 40% and 30%, respectively, of the annual abundance (Figure 4). Biomass patterns were similar to the density pattern. Total species richness did not differ significantly over the year, but *Simulium* sp. (Simuliidae) and *Smicridea annulicornis* (Hydropsychidae) were responsible for the high densities and biomass in Los Rifleros and *Meridialaris laminata* (Leptophlebiidae) in Baggilt (Figure 5).

There were significant differences in macroinvertebrate group abundance between rivers (ANOVA test, $P < 0.001$) (Table IV). Nant y Fall had significantly lower density of Plecoptera than the rest of the streams,

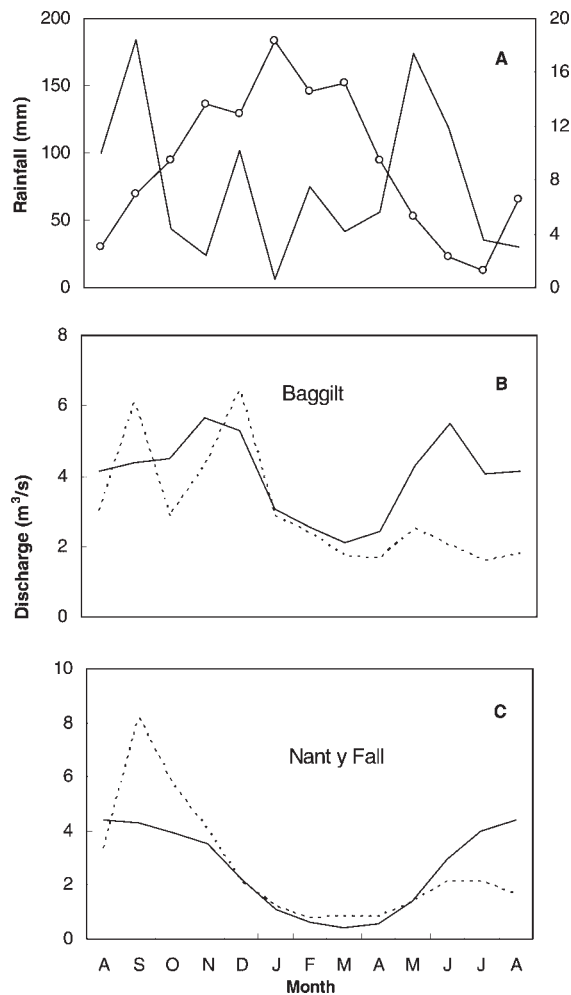


Figure 2. (A) Monthly rain (line without symbols) and mean surface air temperature (line with circles) in the Futaleufú basin, Argentina. Discharge values (m^3/s) at Baggilt (B) and Nant y Fall (C) rivers. Continuous lines are historical records (average of 17 and 39 years, for Baggilt and Nant y Fall, respectively), and dashed lines are records made during the study (1991–1992)

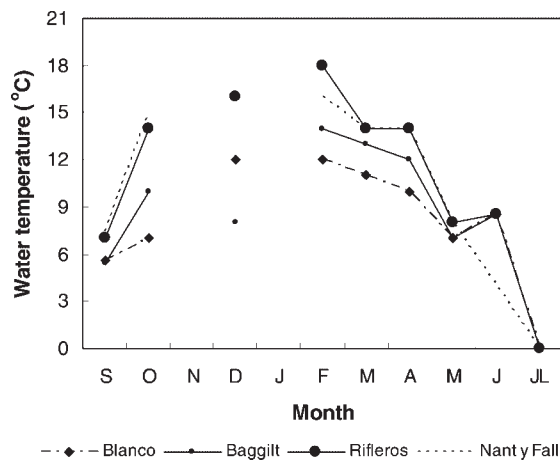


Figure 3. Water temperature records at the Blanco, Baggilt, Rifleros and Nant y Fall rivers during the study period (1991–1992)

Table II. Mean values and variation coefficient percentage of the chemical variables in rivers of the Futaleufú Basin, Argentina, during 1991–1992

River	Conductivity ($\mu\text{S}/\text{cm}$)	pH	Total alkalinity (meq/l)	Carbonate alkalinity (Ca CO ₃)	TN (mg/m ³)	TP (mg/m ³)
Blanco	16.8 (52)	7.1 (7)	0.50 (28)	19.8 (21)	69.7	26.3
Baggilt	21.6 (18)	7.2 (6)	0.51 (16)	21.4 (7)	64.0	21.5
Rifleros	62.8 (32)	7.7 (3)	1.06 (17)	41.5 (19)	63.5	16.8
Nant y Fall	90.9 (5)	7.7 (3)	1.38 (10)	53.3 (2)	164.5	13.0

TN, total nitrogen; TP, total phosphorus.

Sampling size: $n = 2$ for TN and TP, $n = 6$ for remaining variables.

Table III. Mean annual densities of invertebrate taxa in four streams of the Futaleufú basin ($n = 9$)

Taxa	FFG	CO	Blanco	Baggilt	Rifleros	Nant y Fall
Plecoptera						
Austroperlidae						
<i>Klapopteryx kuscheli</i> Illies	S	<i>Kk</i>	13.6	8.5	0	0
Perlidae						
<i>Pictetoperla gayi</i> Pictet	P	<i>Pg</i>	0	10.1	0	0
<i>Kempnyela genualis</i> Navás	P	<i>Kg</i>	0	1.2	0	0.9
Gripopterygidae						
<i>Notoperla achiplatae</i> Enderlein	Sc	<i>Na</i>	7.4	0	0	0
<i>Notoperlopsis femina</i> Illies	Sc	<i>Nf</i>	0	0	48	9.4
<i>Antarctoperla michaelseni</i> Klapálek	S	<i>Am</i>	0.7	36	3.9	0.8
<i>Antarctoperla</i> sp.	S	<i>A</i>	0.1	30.6	9.4	3.1
<i>Limnoperla jaffueli</i> Navás	Sc	<i>Lj</i>	6.9	0.2	3.7	0
<i>Aubertoperla illiesi</i> Illies	Sc	<i>Ai</i>	8.3	14.6	3.7	0
<i>Potamoperla myrmidon</i> Illies	Sc	<i>Pm</i>	0	0	0.1	0
<i>Senzilloides panguipulli</i> Navás	S	<i>Sp</i>	189.8	11.2	0	1.1
<i>Pelurgoperla personata</i> Illies	CG	<i>Pp</i>	0	0.5	0	0.1
<i>Rhitroperla rossi</i> Froehlich	S	<i>Rr</i>	0.1	0	0	0
<i>Udamocercia arumifera</i> Enderlein	Sc	<i>Ua</i>	0	0.4	0	0
<i>Chilenoperla puerilis</i> Illies	S	<i>Chip</i>	0.4	0.5	0	0
Ephemeroptera						
Ameletopsidae						
<i>Chiloporter eatoni</i> Lestage	P	<i>Ce</i>	0.6	0.6	0	0
Baetidae						
<i>Baetis</i> sp.	CG	<i>B</i>	10.9	4	30	5.6
Leptophlebiidae						
<i>Meridialaris laminata</i> Ulmer	CG	<i>Ml</i>	0	227.9	159.8	22.4
<i>Meridialaris chiloeensis</i> Demoulin	CG	<i>Mc</i>	179.9	55.4	15.4	96.4
<i>Meridialaris diguilina</i> Ulmer	CG	<i>Md</i>	0	0	0	110.3
<i>Penaphlebia chilensis</i> Eaton	CG	<i>Pen</i>	0	7.13	3.89	7.78
<i>Nousia delicata</i> Navás	CG	<i>Nod</i>	0	0	46.33	0
Trichoptera						
Leptoceridae						
<i>Brachysetodes major</i> Schmid	S	<i>Bm</i>	5.6	26	107.6	65.2
<i>Nectopsyche unispina?</i> Flint	P	<i>Nu</i>	0	0.1	0.4	0
Sericostomatidae						
<i>Parasericostoma ovale</i> Schmid	S	<i>Po</i>	0.1	0.2	91.1	21.4
<i>Myotrichia murina</i> Schmid	S	<i>My</i>	0.1	0	0	0
Hydrobiosidae						
<i>Cailloma</i> sp.	P	<i>Cai</i>	0.7	0.1	0.2	0
<i>Neotopsyche</i> sp.	P	<i>Neo</i>	0	0.2	2.3	3.8

Continues

Table III. Continued

Taxa	FFG	CO	Blanco	Baggilt	Rifleros	Nant y Fall
<i>Rheochorema</i> sp.	P	<i>Rhe</i>	0.1	0.1	2	2.7
Hydropsychidae						
<i>Smicridea annulicornis</i> Blanchard	CF	<i>Sa</i>	0.2	34.5	328.4	6.2
<i>Smicridea</i> sp.	CF	<i>Smi</i>	0	0	1.6	0
Glossomatidae						
<i>Mastigoptila</i> sp.	Sc	<i>Gl</i>	0	0	3.1	0.1
Limnephilidae						
Limnephilidae sp.	S	<i>Lim</i>	0	0.2	0	0.7
<i>Magellomya</i> sp.	S	<i>Mag</i>	0	0	0	0.2
<i>Austrocosmoecus</i> sp.	S	<i>Aus</i>	1.2	0	0	0
Hydroptilidae						
<i>Oxyethira</i> sp.	Sc	<i>Oxi</i>	1.7	0	0.7	1.3
<i>Neotrichia</i> sp.	Sc	<i>Ne</i>	0	0	21.6	0.1
Philorheithridae	S	<i>Phi</i>	0.11	0	0	0
Diptera						
Chironomidae						
<i>Paratrichocladius</i> sp.1	CG	<i>P</i>	22.1	161.4	94	45.6
<i>Paratrichocladius</i> sp.2	CG	<i>P1</i>	4.7	70	20.4	5.9
Orthoclaadiinae sp. 1	CG	<i>Ort 1</i>	2.3	0	5.0	0
Orthoclaadiinae sp. 2	CG	<i>Ort 2</i>	0	34.7	3	5.1
Orthoclaadiinae sp. 3	CG	<i>Ort 3</i>	4.7	2.5	0	0
Orthoclaadiinae sp. 4	CG	<i>Ort 4</i>	0	25.5	0	0
Orthoclaadiinae sp. 5	CG	<i>Ort 5</i>	16.4	0.1	3.2	0
Orthoclaadiinae sp. 6	CG	<i>Ort 6</i>	0	0.9	0	2.2
<i>Pentaneura</i> sp.1	CG	<i>Pe</i>	0	0	0	1.6
<i>Pentaneura</i> sp.2	CG	<i>Pe 2</i>	0	0.4	10.9	8.7
<i>Ablabesmya</i> sp.	CG	<i>Abl</i>	0	0	0	0.3
Simuliidae						
<i>Simulium</i> sp.	CF	<i>Sim</i>	32.8	16.2	175.1	16.4
<i>Gigantodax</i> sp.	CF	<i>Gig</i>	0.3	0	0	0
<i>Cnesia</i> sp.	CF	<i>Cne</i>	11.8	1.6	18.3	16
Tipulidae						
<i>Hexatoma</i> sp.	P	<i>Hex</i>	0.2	0	16.2	0
<i>Limnophila</i> sp.	P	<i>Limn</i>	0	0	0.1	0.1
<i>Molophilus</i> sp.	S	<i>Mol</i>	0.1	0.1	0.1	0.1
Athericidae						
<i>Dasyoma</i> sp.	P	<i>Das</i>	26.7	10.4	10.8	1.2
Empididae	P	<i>Emp</i>	0.6	9.9	25.3	1.4
Muscidae						
<i>Lispoides</i> sp.	P	<i>Lis</i>	0	0	1.2	0
Ceratopogonidae	P	<i>Cer</i>	0.1	0	0.6	0.1
Tabanidae	P	<i>Tab</i>	0	0.5	0.1	0
Blephariceridae						
<i>Edwardsina</i> sp.	Sc	<i>E</i>	11.4	0	0	0
Coleoptera						
Elmidae						
Elmidae sp.	Sc	<i>Elm</i>	0.1	28.1	23.3	17.4
<i>Austrelmis</i> sp.	Sc	<i>Elm2</i>	0.3	0	0.3	1.1
Dytistidae						
<i>Lancetes</i> sp.	P	<i>Lan</i>	0.0	0.1	0	0
Hydrophilidae						
<i>Tropisternus setiger</i> Solier	P	<i>Tro</i>	0	0	5.2	0
Megaloptera						
Sialidae	P	<i>Sial</i>	0	0	0	0.1
Crustacea						
Amphipoda						

Continues

Table III. Continued

Taxa	FFG	CO	Blanco	Baggilt	Rifleros	Nant y Fall
<i>Hyalella curvispina</i> Shoemaker	CG	<i>Hc</i>	0	0	1.2	19.4
Acari	P	<i>O</i>	0	0.4	0	0
Oligochaeta						
Lumbriculidae sp.	CG	<i>Lum</i>	0.4	7	22.4	39.8
Hirudinea						
Glossiphoniidae sp.	P	<i>Glos</i>	0	0	0	2.7
Turbellaria						
Dugesiiidae						
Girardia sp.	P	<i>Gi</i>	0.1	0	0	3.7
Gasteropoda						
Chiliniidae						
<i>Chilina patagonica</i> Sowerby	Sc	<i>Chp</i>	0	0	7.8	5.3

Functional feeding groups (FFGs) assigned: S, shredder; P, predator; Sc, scraper; CG, collector-gatherer and CF, collector-filterer. CO, Code used for ordination.

Table IV. Annual mean total density, biomass, species richness, EPT taxa, and macroinvertebrate groups density ($n = 9$) in four streams of the Futaleufú basin, Argentina. Standard deviation in parentheses. Results of the two-way ANOVA without replication test among rivers are in the right-hand column

	Blanco	Baggilt	Rifleros	Nant y Fall	F	P
Density (ind/m ²)	564 (331)	841 (895)	1275 (1038)	555 (229)	0.98	ns
Biomass (mg/m ²)	607 (439)	777 (606)	1543 (1438)	902 (578)	2.07	ns
Species richness	13.2 (2.48)	16.62 (3.46)	17.6 (6.32)	16.88 (2.85)	1.97	ns
EPT taxa	7.3 ^a	10.1 ^b	8.5 ^{ab}	8.4 ^{ab}	3.82	0.02
Plecoptera	227.3 ^a	114.3 ^a	66.0 ^a	15.4 ^b	19.1	0.001
Ephemeroptera	191.3	295.0	242.4	242.6	0.8	ns
Trichoptera	9.8 ^a	61.8 ^{ac}	506.4 ^b	102.1 ^{bc}	17.74	0.001
Diptera	134.2	334.0	402.1	104.8	0.56	ns
Coleoptera	0.4 ^a	28.3 ^b	29.1 ^b	18.8 ^b	17.2	0.001
Annelida	0.4 ^a	7.4 ^b	21.2 ^{bc}	42.4 ^c	25.2	0.001

Different superscript letters in a row show significant differences ($P < 0.01$) indicated by T-method after a significant ANOVA.

whereas Trichoptera density was higher in Rifleros than in Blanco and Baggilt. Coleoptera density was significantly lower at Blanco than the rest of the sites. Annelida density was significantly higher in Nant y Fall than in Blanco and Baggilt.

Assemblage structure and temporal patterns

Senzilloides panguipulli was the most abundant Plecoptera species in Blanco Stream (Table III), and decreased in density from October to March (Figure 5). *Antarctoperla michaelsoni* and *Anctartoperla* sp. were the most abundant stoneflies in Baggilt Stream (Table III); both species peaked in winter (Figure 5). *Meridialaris chiloeensis* (Leptophlebiidae) was the dominant Ephemeroptera in Blanco and peaked in June and July, while *M. laminata*, the dominant Ephemeroptera in the Baggilt, peaked during September (Table III, Figure 5).

Trichoptera, Ephemeroptera, and Diptera together represented more than 80% of the total invertebrate abundance in the Rifleros and Nant y Fall. In the Rifleros Stream, the trichopterans; *Smicridea annulicornis*, *Brachisetodes major*, and *Parasericostoma ovale*, were the most conspicuous species (Table III); however, *S. annulicornis* was three times more abundant than the other species in March (Figure 5). Ephemeroptera in Nant y Fall had two peaks, one due to *M. diguilina* in December and the other one due to *M. chiloeensis* in May and June.

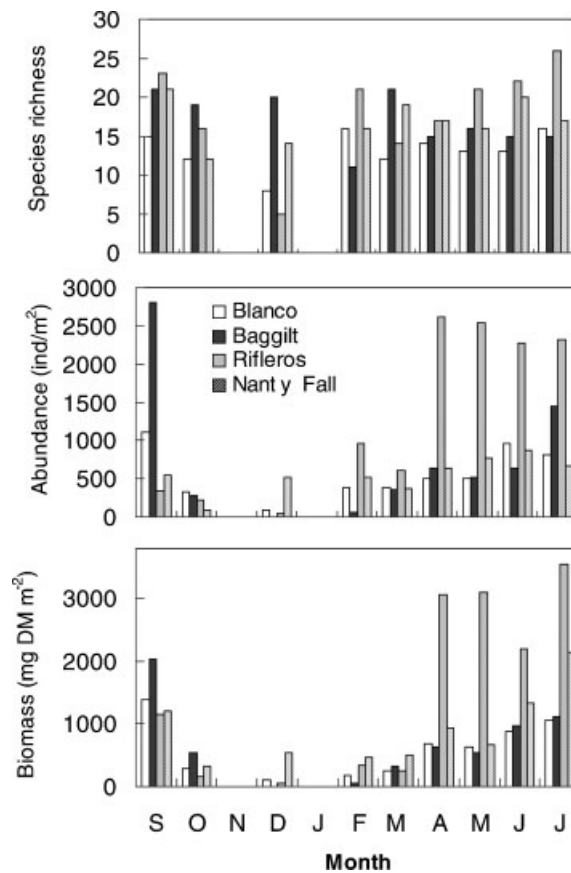


Figure 4. Mean monthly variation in species richness, abundance and biomass of the total taxa in four rivers of the Futaleufú basin, Argentina

In Los Rifleros Stream, *M. laminata* and *Nousia delicata* were the dominant Ephemeroptera (Table III); the former increased from May to July (Figure 5).

Functional feeding groups

Shredders reached 50% of the total biomass and 40% of the total density in the *Nothofagus* forested site (Blanco Stream) (Figure 6). Density of collector-gatherers was more than 50% of the total density in Baggilt and Nant y Fall, while collector-filterers were significantly higher in density and biomass in Los Rifleros than the rest of the sites (ANOVA; $F_{\text{density}} = 10.8$; $F_{\text{biomass}} = 17.4$; $P < 0.001$) (Figure 6). At most rivers, shredders increased from April to July coinciding with the litterfall period. An increase of collector-filterers was observed in autumn in both Rifleros and Baggilt by the presence of *Smicridea annulicornis* (Hydropsychidae) (Figure 7). In Baggilt River, predators contributed with high biomass throughout the study reflecting the presence of large larvae of *Kempnyella genualis*, *Pictetoperla gayi* (Perlidae), and the *Chiloporter eatoni* (Ameletopsidae). Scrapers increased from March to April, but did not contribute much biomass.

Macroinvertebrate community and environmental relationships

The CCA ordination showed a strong relationship between macroinvertebrate species distribution and measured environmental variables. The environmental variables selected in the analysis are represented in the biplot by arrows, which point in the direction of maximum change in the value of the associated variable (Figure 8). The species–environmental correlations were 0.84, 0.85 and 0.80 for the first, second, and third axis respectively (Table V), suggesting a close relationship between the environmental variables selected. The Monte Carlo test of significance of canonical axes (to judge the significance of that relation) produced significant values for all

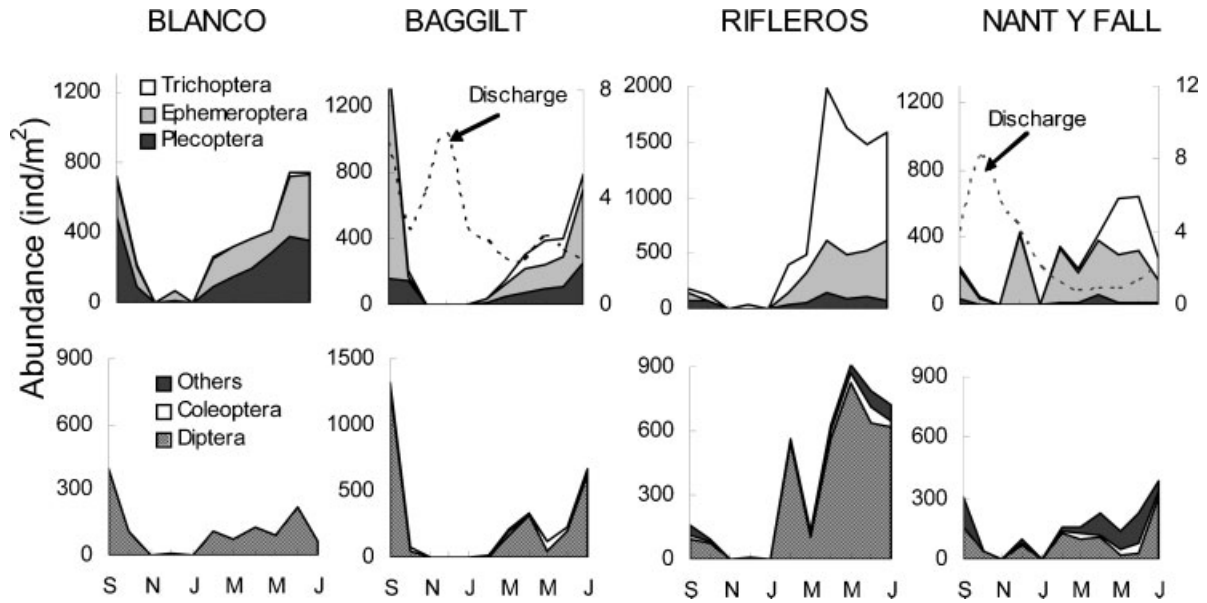


Figure 5. Monthly changes in abundance (mean number per month based on eight pooled Surber samples) of common taxa in Blanco, Baggilt, Rifleros and Nant y Fall rivers. Discharge (m^3/s) is showing in Baggilt and Nant y Fall (right-hand scale)

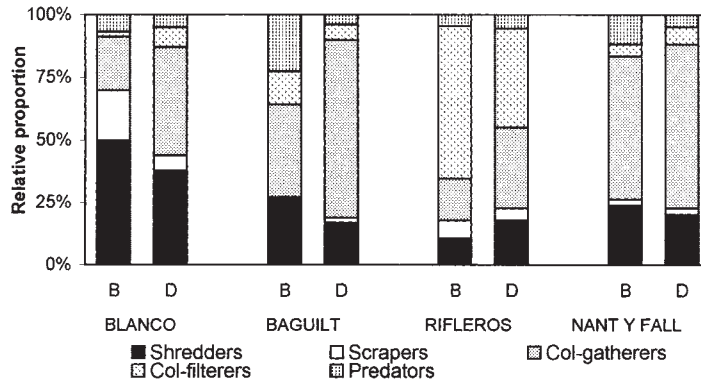


Figure 6. Comparison between the relative percentage of biomass (B) and density (D) of feeding groups of macroinvertebrates (FFG) in the Blanco, Baggilt, Rifleros and Nant y Fall rivers

the axes (Table V). The strongest explanatory factors were physical variables, but only 20.3% of variation in the species data was accounted for by the environmental variables measured (Table V). The main environmental gradient (axis 1) was determined by geomorphic features of the basin and the streams—slope, basin height, distance from the source, and substratum size—but also by the percentage of coverage of *Salix fragilis*. The biplot displayed in Figure 8A highlights the existence of a geomorphic gradient along CCA axis 1. Thus, sites mainly on the Blanco River, with greatest slope and substratum size and no *Salix fragilis*, are clustered in the right quadrants. All samples from Rifleros are positioned in both upper and lower left quadrants, Rifleros basin had the lowest slope and this site had also the greatest distance from the headwater. The third axis showed an environmental gradient associated mainly with factors that changed seasonally, as shown by strong correlations with rain and water temperature. Sampling dates during the period of major discharge (June–July–September–October) and lower temperatures are positioned in the two upper quadrants in at least three of the studied rivers (Figure 8A). Samples taken in the summer during the low water period (December–February–March) are positioned in the two lower quadrants. Figure 8B illustrates the position of the invertebrate assemblages along the same gradients. *Edwardsina*

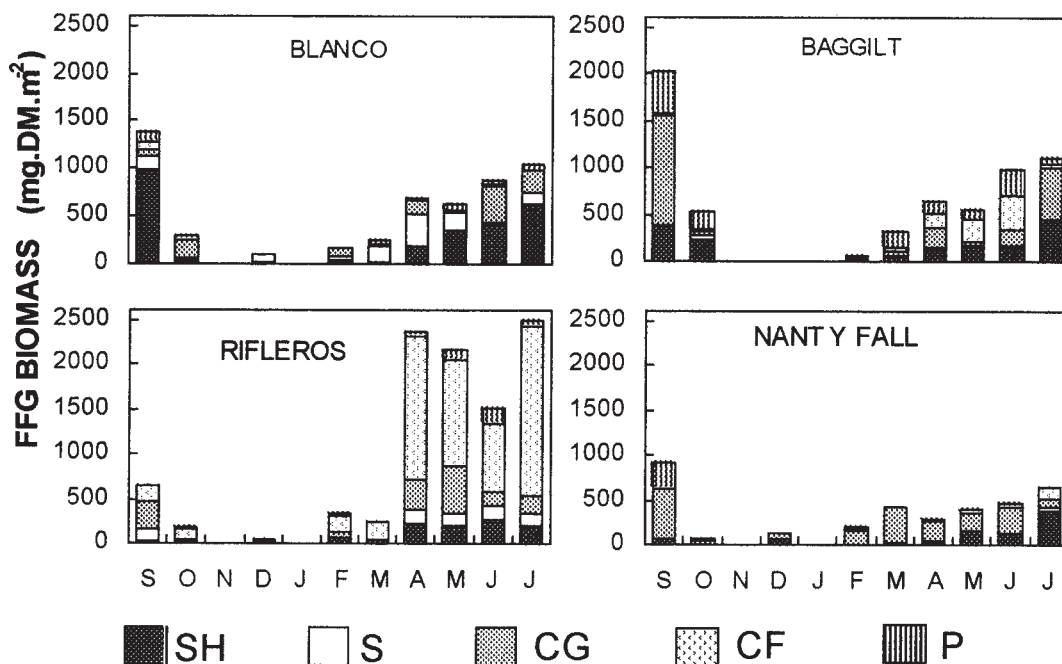


Figure 7. Seasonal changes in functional community organization of macroinvertebrates in the Blanco, Baggilt, Rifleros and Nant y Fall rivers. Data are based on biomass. SH, Shredders; S, scrapers; CG, collectors-gatherers; CF, collectors-filterers; P, predators

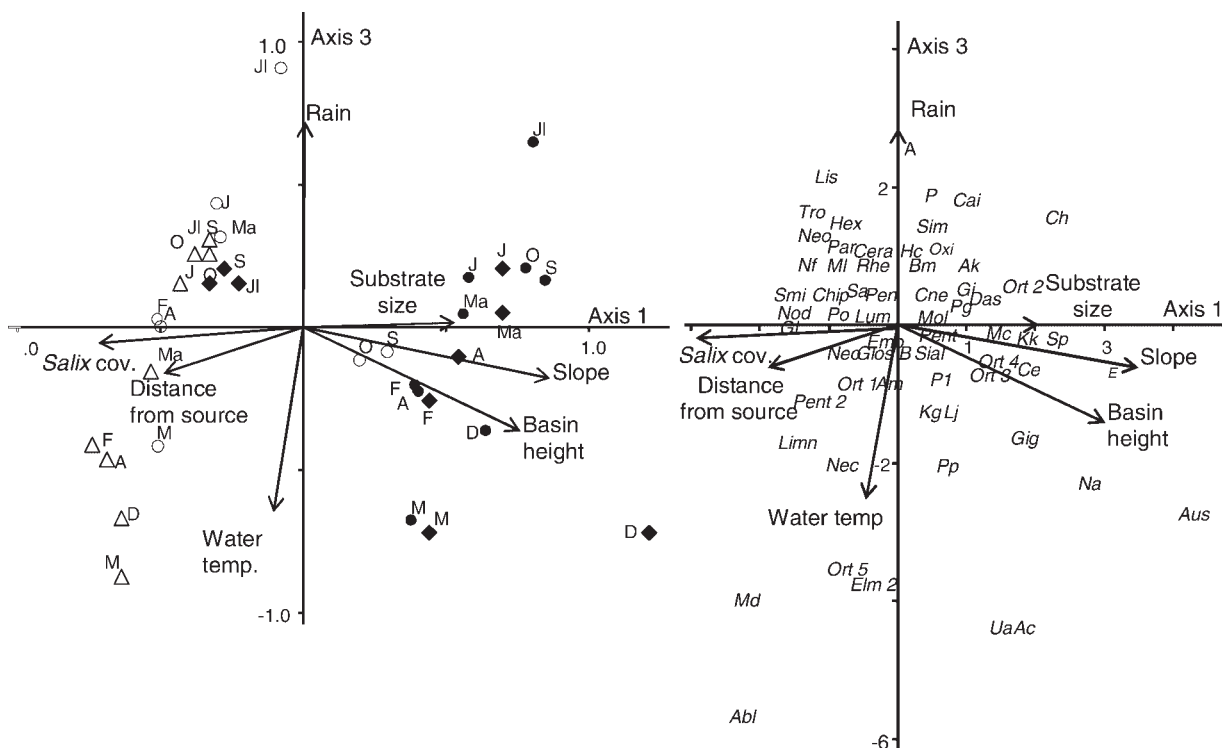


Figure 8. Canonical correspondence analysis ordination plot for (A) sites and environmental variables and (B) species. Codes for sites: black circles, Blanco; open circles, Baggilt; triangles, Rifleros; diamonds, Nant y Fall. Months: S, September; O, October; N, November; F, February; M, March; A, April; Ma, May; J, June; Jl, July. Codes for species in Table III

Table V. Weighted intraset correlation of environmental variables with the axes of canonical correspondence analysis (CCA) for macroinvertebrate taxa in four streams of the Futaleufú basin, Argentina

Variable	Axis 1	Axis 2	Axis 3
Basin area	-0.03	0.74	0.20
Basin height	0.66	-0.09	-0.18
Slope	0.66	-0.05	-0.11
Water temperature	-0.08	0.00	-0.68
Substratum size	0.40	0.02	0.01
Rain	0.01	0.08	0.75
Width	0.38	-0.73	0.13
<i>Salix</i> coverage	-0.55	0.48	0.05
Distance from source	-0.37	0.79	-0.16
Eigenvalues	0.28	0.17	0.15
Species-environment correlation	0.84	0.85	0.80
Cumulative percentage variance of species data	9.6	15.2	20.3
<i>P</i> values for Monte Carlo permutation test	0.01	0.04	0.01

sp. (Diptera), *Notoperla archiplatae* (Plecoptera), and *Austrocosmoecus* sp. (Trichoptera) were exclusively recorded in the Blanco River, whereas *Senzilloides panguipulli* and *Klapopteryx kuscheli* were recorded in both Blanco and Baggilt. Mostly, species common in fast-flowing water are positioned to the right on axis 1. *Notoperlopsis femina* (Plecoptera), *Smicridea anulicornis* (Trichoptera), and *Nousia delicata* (Ephemeroptera) are placed on the opposite end; these species are more common in run habitats, with lower slope. Moreover, species that peaked at Rifleros and Nant y Fall in September and October are positioned in the upper left quadrant. Species that peaked in late summer during the low water period, such as Elmidae sp2, *Meridialaris diguilina*, and Orthocladiinae sp5 (Chironomidae), are positioned in the lower left quadrant, whereas species that were more abundant in the high water period such as *Antarctoperla* sp., *Lispoides*, *Paratrachocladius* sp., and *Cailloma* sp. are positioned in the two upper quadrants.

DISCUSSION

Assemblage structure

Insect assemblage composition was dominated by Diptera (26 taxa), Trichoptera (17 taxa), and Plecoptera (13 taxa), which is similar to that reported in previous studies in mountain streams in the Patagonian Andes (Wais, 1987, 1990; Wais and Bonetto, 1988). Moreover, the macroinvertebrate community was dominated by Leptophlebiidae, Gripopterygidae, and Chironomidae at most sites, and taxa indicative of poor water quality or organic enrichment were absent. The main differences among rivers were in assemblage composition, relative dominance of Plecoptera, Coleoptera, Annelida, and FFG abundance, and biomass.

Macroinvertebrates and land use

Water chemistry was different in the native forested streams than in more developed basins: conductivity and total alkalinity were significantly higher in Rifleros and Nant y Fall than in Blanco and Baggilt. This probably reflected the precipitation gradient, as weathering rates are dependent on water residence time (time of contact with rocks) (cf. Stumm and Morgan, 1981). Plecoptera abundance was significantly lower in the non-native forested reach (Nant y Fall) than in the rest of the reaches. These results are consistent with findings of Hall *et al.* (2001), that Plecoptera are more abundant in streams draining native forest in New Zealand in comparison to those draining agricultural areas. Moreover, Nant y Fall had a significantly higher density of Lumbriculidae sp. than Blanco and Baggilt. This group, mainly inhabitants of fine sediments, could give some indication of an increase in the sedimentation rate in the basins more influenced by agriculture and higher densities of animal stock.

The gastropod, *Chilina patagonica*, was only recorded in Rifleros and Nant y Fall. Collier *et al.* (2000) observed in rivers in agricultural areas that some mollusc species seem to benefit from an increase in rates of primary

productivity due to elevated levels of nutrients and light. Consistently strong relationships among *C. patagonica* and water conductivity have been reported in streams in the area (Miserendino and Pizzolón, 2000). However, *C. patagonica* is absent in organic-enriched reaches, which suggests moderate tolerance to perturbations.

Our work suggests that catchment land use or riparian vegetation were not major factors affecting taxonomic richness, total density, or biomass of macroinvertebrates. These results were in agreement with Collier (1995) who found similar results in stony streams across forested and agricultural areas in New Zealand. However, he found the proportion of native forest cover in the riparian zone appeared as a good predictor of richness in the EPT group. In our study, the mixed forest site showed significantly higher EPT richness than the native forested site, but there were not significant differences among native and *Salix* forested sites. It is likely that the existent riparian vegetation is still carrying out the ecological riparian functions and food supply (litter) is available.

Functional feeding groups, exotics and land use

It has been suggested that willows may support a less diverse aquatic invertebrate fauna than native vegetation in Australian environments (Pidgeon and Cairns, 1981), but in contrast, European 'willowed' rivers had greater species richness than rivers bordered with native eucalypt (Abelho and Graça, 1996). We did not find significant differences in species richness at the *Nothofagus* native and *Salix* forested sites. However, the relative biomass and abundance of shredders was higher in the *Nothofagus* forested area (Blanco) than in the sites with *Salix* forest, and there was a significantly higher density and biomass of filterers and collectors-gatherers in the non-native forested areas.

Because land use and *Salix* distribution overlapped at our study sites, it is difficult to distinguish which changes in the FFGs were in response to agriculture and which were related to the presence of the exotic tree. For example, in Los Rifleros Stream, collector-filterers (Hydropsychidae and Simuliidae) notably increased during the autumn and winter seasons. This is consistent with Read and Barmuta's (1999) findings, where they observed filterers were significantly higher at 'willowed' reaches in autumn, whereas fine and coarse organic matter was higher than in the native forested reaches. However, the increase in collector-filterers at Rifleros Stream could be in response to an increase in the seston, probably coming from lixiviation in the rainy season from an extensively grazed basin. Filter-feeder biomass trends have been related to high organic content of the seston (Valett and Stanford, 1987; Lugthart and Wallace, 1992). Collector-gatherers were also dominant in the non-native forested site Nant y Fall. This basin had the highest livestock count, mainly sheep. Coverage degradation and soil erosion as a result of sheep grazing have been well documented in Patagonia (del Valle *et al.*, 1998), and as a consequence, exposed slopes become more vulnerable to erosion by rainfall and surface runoff (Harding *et al.*, 2000).

Most differences, among native-forested and non-native-forested reaches, seem to be in composition of several groups, for example, the shredders. Shredder assemblages in sites dominated by native forest were *K. kuschelli*, *S. panguipulli*, *P. ovale*, and *B. major*; whereas, at *Salix* bordered sites, more common and abundant shredders were *P. ovale* and *B. major*, which would reflect the dependence of the riparian species composition (*Nothofagus* versus *Salix fragilis*). Linklater and Winterbourn (1993) found assemblages of detritivores were similar in small streams dominated by different forest trees. However, Shulze and Walker (1997) found distinctive invertebrate assemblages, associated with leaf packs of *Eucalyptus camadulensis* and *Salix babylonica* after eight weeks of incubations, indicating that colonizers at willows could be generalists and those at redgum more specialized. Also, Read and Barmuta (1999) observed that the most striking differences between willowed and native reaches were in terms of similarity of macroinvertebrate fauna. Another difference between Patagonian *Nothofagus* and other *Nothofagus* species is that foliar abscission in *Nothofagus pumilio* and *N. antarctica* occurs mostly in autumn in a short period of time, rather than having the main litter fall peak in summer (e.g. *N. solandri* and *N. fusca* in New Zealand). Litterfall in *Salix fragilis* also occurs in autumn. Thus, there were no differences in the timing of leaf abscission in the native and exotics considered in this study. Significant amounts of leaves and organic material were observed in autumn in all the stream channels and shredders accordingly peaked at all sites.

Macroinvertebrates and environmental relationships

Ordination techniques have been used successfully to interpret macroinvertebrate community structure and detect influence of farming activities as well as urban development on invertebrate assemblages (Aguar *et al.*, 2002; Harrison and Harris, 2002). The percentage of native forest seems to be a good predictor of macroinvertebrate

variation in streams in agricultural areas in subtropical environments (Thorpe and Lloyd, 1999). However, because many aspects of stream invertebrate habitat are altered by development, it usually is difficult to link effects to specific factors and multiple stressors are often involved. Consistent with this scenario, in our study, the main physical gradients explaining composition and distribution of macroinvertebrates were those defined by slope, basin height, width, substratum size, distance from the source, and also *Salix* coverage. Rifleros streams with lower slope, draining a low-height basin, appear separated from the other sites in the ordination biplot and had a specific species assemblage. In the opposite situation, Blanco River, with higher slope and basin height, had no *Salix* in the riparian vegetation. Geomorphic features possibly were acting as *Salix* constraints, since the exotic was more abundant in sites with greater distance from the source and lower slope. We observed that water temperature range was lower in the native forested basins in comparison to the more developed basins (Figure 3). Likewise, Quinn (2000) reported that a decrease in stream shading and an increase in water temperature were consistently associated with the gradient from native forest to pasture sites in New Zealand streams.

Although we were not able to clearly separate natural from land-use effects, this study provides a first look at natural and cultural controls on benthos in Patagonian streams. While the streams are naturally different, our analysis strongly suggests that land use, specifically conversion of native forest to pasture and associated invasion of willows, is an emerging issue in Patagonia that requires more robust studies, perhaps involving experiments that control temperature and particulate organic matter quantity and quality.

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