Spatial variation in invertebrate communities in New Zealand braided rivers

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ABSTRACT

Large braided rivers are a distinctive feature of the landscape in several regions of New Zealand. The invertebrate communities of braided rivers have been described as taxonomically depauperate, but recent research has suggested otherwise. We conducted a field survey of 11 braided rivers, collecting benthic invertebrates from six reaches dispersed down each river, and sampling up to five habitats per reach. We compared the taxonomic richness of these braided, multi-channel rivers with non-braided, single channel rivers, and found that braided rivers actually support very diverse invertebrate assemblages when all floodplain habitats are included in analyses. We then compared biodiversity patterns within braided rivers. A total of 144 taxa and over 100 000 individuals were collected from the 11 braided rivers. Thirty-four percent of taxa were found in ≤ 3 rivers and comprised < 1% of all individuals, whereas 13% of taxa were found in all rivers and constituted 80% of all individuals. Total taxonomic richness ranged from 99 taxa in the Wairau River to 56 taxa in the Waiapu River. Surprisingly, no consistent longitudinal pattern in taxonomic richness or density was found; however, braided reaches were more diverse than headwater and gorge reaches. At the reach scale, 80% of lateral habitats (i.e. springs and ponds) were more diverse than their associated main channel. These findings show that despite high variation between and within rivers, lateral floodplain habitats are important biodiversity hotspots. Therefore, any assessment of the diversity of braided rivers must incorporate sampling across multiple spatial scales and include the full range of habitats present in the floodplain.

Keywords: braided rivers, floodplain, benthic invertebrates, diversity, New Zealand, habitat heterogeneity, ponds, springs

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1. Introduction

Braided rivers are iconic and definitive features of the landscape in many regions of New Zealand, contributing greatly to scenic and recreational values. However, like many other waterways, they are also regarded as a potential resource to be exploited. Irrigation, impoundment, hydro-electric power generation and aggregate mining are all increasing threats to the physical integrity of New Zealand's streams and rivers (Young et al. 2004). Consequently, the biodiversity of these rivers and streams is under threat.

Braided rivers (defined as rivers flowing in multiple channels across an alluvial gravel floodplain) differ fundamentally from single channel rivers in several respects. The primary factors that influence stream/river morphology are sediment dynamics and hydrology. Rivers braid because large quantities of sediment are regularly rearranged by flood events, preventing the formation of stable banks and riparian vegetation characteristic of single channel rivers. Iconic braided rivers of the South and North Islands, such as the Rakaia and Ngaruroro Rivers, have regular and numerous floods per year that exceed three times the median flow (14.3 and 10.4 events, respectively). In contrast, the single channel Clutha River/ Mata-Au (South Island) and Tarawera River (North Island) have far fewer large floods (0.6 and 0, respectively). As a consequence of these high levels of physical disturbance, braided rivers and their floodplains contain a diverse array of surface and sub-surface aquatic habitats. Many of these habitats have very disparate physical and chemical characteristics, but they are all linked by either surface or subterranean flow. For example, secondary channels, or side braids, split from the main channel, while springs emerge on the floodplain creating wetlands, streams and ponds. Ponds are also formed during scouring flood flows, appearing as ponds during recession. Finally, ground waters beneath the floodplain surface contribute to the three-dimensional habitat mosaic of braided rivers. Most rivers and streams possess a subterranean aquatic habitat (the hyporheic zone) created by water permeating the substrate beneath and adjacent to the stream. However, in a braided river with an extensive floodplain, the vertical and lateral influence of the river can be on a much greater scale, extending metres vertically and possibly kilometres horizontally (e.g. the Flathead River floodplain in Montana, USA; Stanford & Ward 1988). This means that surface flow of the river may represent a relatively minor proportion of the total river ecosystem inhabited by flora and fauna.

Past research has indicated that the main channels of braided rivers in New Zealand are characterised by low invertebrate diversity (Sagar 1986; Scrimgeour & Winterbourn 1989). However, studies by Digby (1999), Gray et al. (2006) and Gray & Harding (2009) have shown that springs and spring creeks on the braided river floodplain can be hotspots of bio-productivity and biodiversity. Benthic invertebrates underpin the food webs that support numerous rare, endemic birds, fish, skinks and geckos, as well as substantial recreational fisheries (Gray & Harding 2007).

Because of the iconic nature of braided river systems and increasing pressures on their integrity, a knowledge and understanding of the spatial patterns of benthic invertebrate diversity within them is of particular importance to conservation managers in New Zealand. In this study, we present the first systematic assessment of benthic invertebrate biodiversity within and across multiple braided river floodplains in both the North and South Islands, as well as a comparison between braided and non-braided systems. This report focuses on several key aspects of spatial diversity. Specifically, an assessment of taxonomic richness, density and assemblage composition of braided rivers was made at the catchment, reach and habitat scales, and an analysis of the rare and spatially restricted taxa was undertaken for 11 New Zealand braided rivers.

2. Methods

2.1 SITE SELECTION

2.1.1 Catchments

Rivers were selected to reflect the number of braided rivers in New Zealand, based on an analysis from Wilson (2001). Canterbury has 56 rivers with braided reaches, comprising 59% of New Zealand's entire braided river floodplain area. In contrast, the West Coast has 41 rivers, but these are smaller and comprise only 17% of the total national floodplain area. Nelson/Marlborough, Southland, Otago, Hawke's Bay and East Cape each have between 5 and 13 rivers with braided reaches, and each region contributes less than 10% to the national total. Initially, six rivers were selected in Canterbury, three on the West Coast of the South Island, two in Hawke's Bay, and one each in East Cape, Southland and Nelson/Marlborough. However, we removed two Canterbury rivers and one West Coast river from the list, due to a sustained period of high flows during spring 2006, leaving 11 rivers in the survey (Fig. 1). Otago rivers were not included in the survey because they were generally braided in their upper reaches only.

The rivers surveyed had mean flows ranging from 44 m^3/s in the Tukituki River to 370 m^3/s in the Waitaki River, while catchment size ranged from 998 km^2 for the Taramakau River to 11 887 km^2 for the Waitaki River (Table 1). Rivers also ranged in terms of the average number of flood events per year that exceeded three times the median flow (FRE3), from 24 in the Landsborough River to 0.6 in the Lower Waitaki River. At the time of sampling, there was also considerable variation in the number of days since an FRE3, ranging from 6 days in the Landsborough and Taramakau Rivers to 85 days in the Tukituki River. Rivers were further characterised according to topographical, hydrological, climatic and land-use categories, which were derived from the River Environment Classification (REC; Snelder et al. 2005) and varied considerably among rivers (Table 1).

Figure 1. The 11 braided river catchments included in the survey.

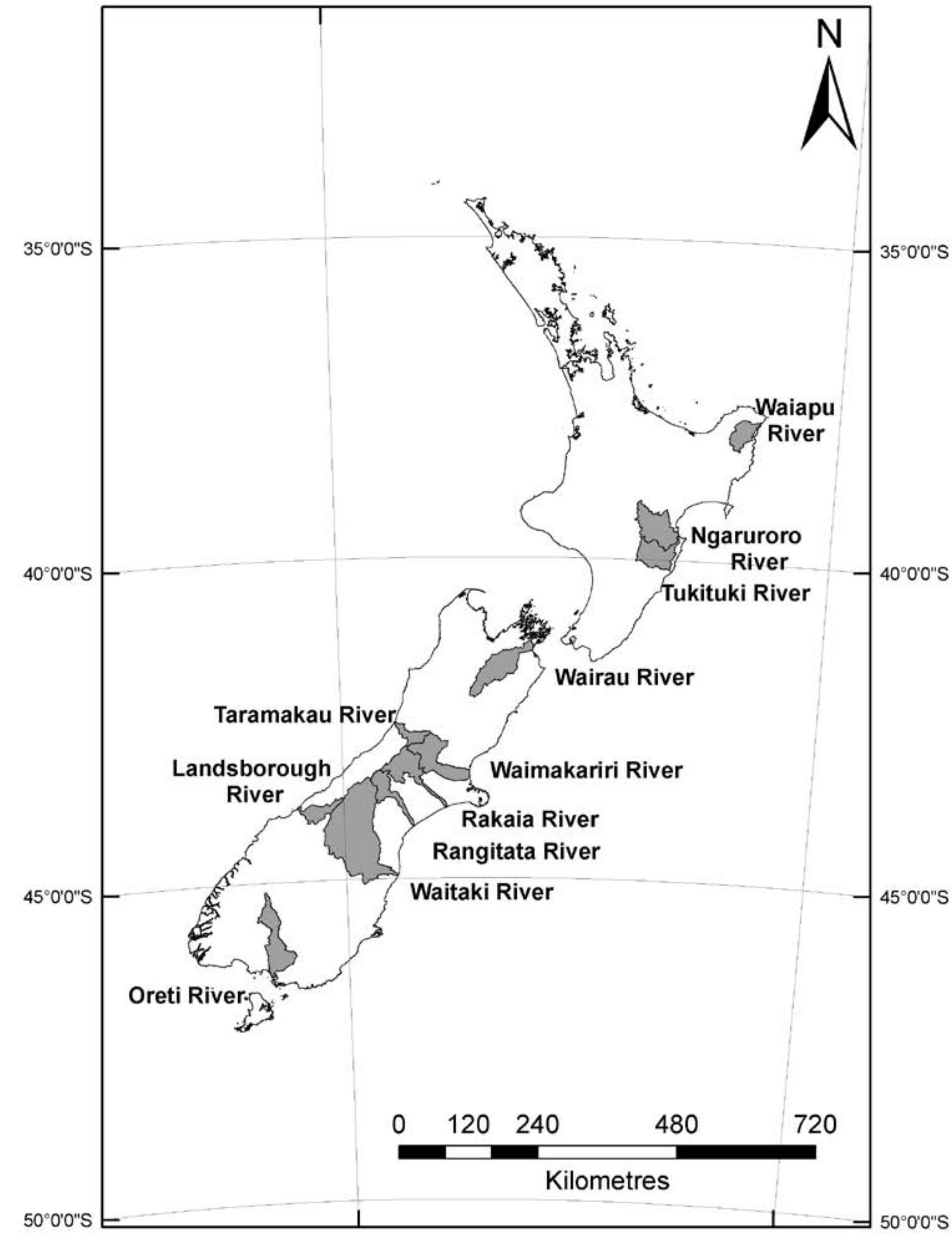


TABLE 1. CATCHMENT CHARACTERISTICS OF THE 11 BRAIDED RIVERS CONSIDERED IN THIS STUDY, AS DERIVED FROM THE RIVER ENVIRONMENT CLASSIFICATION (SNELDER ET AL. 2005).

CATCHMENT	REGION	CATCHMENT AREA (km^2)	RIVER ORDER[a]	MEAN FLOW (m^3/s)	FRE3 EXCEDENCE[b]	DAYS SINCE FRE3[c]	SOURCE OF FLOW[d]	CLIMATE[e]	CATCHMENT VEGETATION[f]
Waiapu	East Cape	1574	6	82	7.1	16	Hill	Cold and extremely wet	Pastoral
Ngaruroro	Hawke's Bay	2009	6	46	10.4	57	Hill	Cold and wet	Pastoral
Tukituki	Hawke's Bay	2495	6	44	10.0	85	Low elevation	Cold and dry	Pastoral
Wairau	Nelson/ Marlborough	3574	7	99	11.5	63	Hill	Cold and wet	Indigenous forest
Taramakau	West Coast	998	6	150	22.6	6	Hill	Cold and extremely wet	Indigenous forest
Waimakariri	Canterbury	3541	7	128	15.3	10	Mountain	Cold and wet	Scrub/tussock
Rakaia	Canterbury	2830	7	175	14.3	75	Glacial mountain	Cold and extremely wet	Bare ground
Rangitata	Canterbury	1809	6	109	10.9	15	Glacial mountain	Cold and extremely wet	Bare ground
Landsborough	West Coast	1341	6	277	24.0	6	Glacial mountain	Cold and extremely wet	Indigenous forest
Waitaki (Upper)[g]	Canterbury				9.4	80	Glacial mountain	Cold and extremely wet	Bare ground
Waitaki (Lower)	Canterbury	11 887	7	370	0.6	1000+	Lake	Cold and wet	Scrub/tussock
Oreti	Southland	3513	7	62	13.4	15	Low elevation	Cold and dry	Pastoral

[a] River order (Strahler) is a classification used to define stream size based on a hierarchy of its tributaries. When two first-order streams come together they form a second-order stream, when two second-order streams come together they form a third-order stream, etc. Streams range from headwaters (Strahler order 1) to the Amazon River (12).

[b] The FRE3 value represents the number of flood events that exceed three times the median flow of a river.

[c] Days since FRE3 flood event were sometimes variable, so the median value for the reaches was taken.

[d] Source of flow is predominantly defined by topography of the river catchment.

[e] Rivers are assigned to one of six spatially averaged climatic zones based on temperature and precipitation.

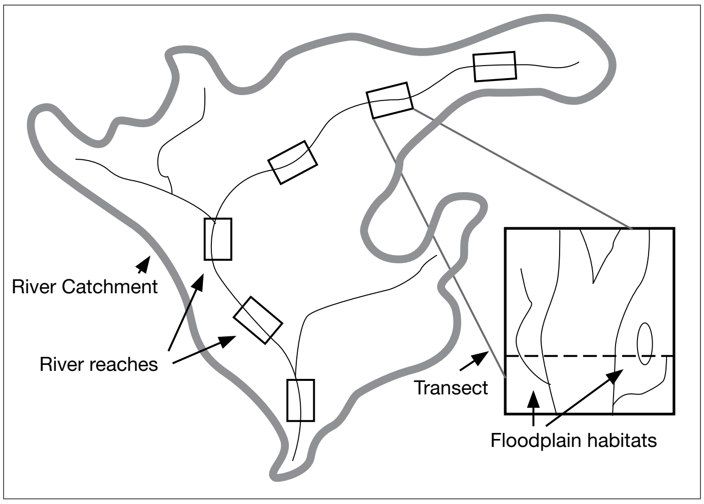
[f] Catchment vegetation assigns rivers to one of seven categories representing the predominant land-cover of the catchment.

[g] Catchment area and maximum river order apply to the entire Waitaki River catchment and cannot meaningfully be calculated for the truncated upper river. Data presented apply to the entire river system.

2.1.2 Reaches

Six reaches, each approximately 1 km long, were selected at intervals along each river (Fig. 2). The uppermost reach was in the steeper headwaters above the point where a distinct floodplain first appeared on a 1:50 000 topographical map. In this reach, each river was generally 3rd to 4th order (Strahler 1954). The lowest reach was close to the river mouth, but above tidal, estuarine and brackish water influences. Intermediate reaches were spaced approximately evenly between the top and bottom sites, and their selection was influenced by accessibility. Where possible, a gorge reach was included on each river.

Figure 2. Diagram of study design within each braided river catchment.



Each reach was classified subjectively according to geomorphological type (Table 2). This classification incorporated three broad-scale factors:

1. **Lateral sediment inputs**—These are generated by tributaries with high sediment loads and occur primarily in mountainous areas; where rivers flow through lowland hill country or across alluvial plains, lateral inputs are generally infrequent. Lateral sediment inputs and structures such as alluvial fans influence the topography of the river bed and have been associated with the occurrence of groundwater upwelling and spring creeks (Gray 2005).
2. **Natural floodplain confinement**—Rivers flowing through valleys are confined by mountain sides or steep alluvial terraces incised by the river. Valley confinement has been linked to floodplain geomorphology (Stanford & Ward 1993). Natural confinement can also occur at gorges and may create distinct discontinuities in the braided river continuum (Stanford & Ward 2001). 'Unconfined' rivers flow unconstrained across broad alluvial plains.
3. **Anthropogenic floodplain confinement (channelisation and impoundment)**—Many rivers in New Zealand have been channelised in their lower reaches to restrict lateral migration of the river channel (termed 'impacted').

Steep, incised headwaters were also included in order to represent the full range of geomorphological types present in braided rivers. Morphological types were identified by a combination of GIS, digital mapping and ground truthing. Examples of reach types are shown in Appendix 1.

TABLE 2. GEOMORPHOLOGICAL REACH CLASSIFICATION.

The reach classification uses the lateral input of sediments, and both natural and anthropogenic (impacted) floodplain confinement to categorise river reaches. The classification also included gorge reaches, which exhibited no floodplain and bedrock constriction, and headwaters, which were upstream of any discernable floodplain.

MORPHOTYPE	LATERAL INPUTS	NATURAL CONFINEMENT	ANTHROPOGENIC CONFINEMENT
High lateral, confined	High	Yes	No
Low lateral, confined	Low	Yes	No
Low lateral, unconfined	Low	No	No
Impacted	Low	No	Yes

2.1.3 Habitats

At each reach, a single transect was walked across the entire floodplain (Fig. 2). Each of the following five habitat types were sampled (when present): the main channel, a side braid or secondary channel (with upstream and downstream connection to the main channel), a spring creek, spring source (at least 50 m downstream from the spring source), and a floodplain pond. All sites were sampled on separate tributaries, i.e. spring creeks and spring sources were independent streams.

Biological samples were collected during base flow conditions between December 2006 and April 2007, and consisted of three Surber samples (0.11 m^2, mesh size 250 µm) and a single extensive kick-net sample (mesh size 250 µm) (Stark et al. 2001). Kick netting was performed for 5 minutes over an approximately 3-m^2 area within each habitat. Quantitative pond samples were taken using a modified Surber sampler (0.11 m^2, mesh size 250 µm), which was fully enclosed so that invertebrates could be washed into the net by hand.

Samples were preserved in 70% ethanol in the field, washed onto 250-µm sieves and sorted in the laboratory under 40× magnification. Identifications were made to the lowest taxonomic level possible, except for Oligochaeta, which were not differentiated below order, and Chironomidae, which were not separated below tribe. Identifications were made using the keys of Winterbourn (1973), Chapman & Lewis (1976), Cowley (1978), McLellan (1991, 1998), Winterbourn et al. (2000), Scarsbrook et al. (2003), Smith (2001) and a description by Percival (1945).

2.2 ANALYSIS

Species accumulation curves were used to estimate efficacy of sampling effort. A species accumulation curve plots the number of observed species against some measure of sampling effort (usually number of samples or individuals). Theoretically, the curve will reach an asymptote when no further increase in sampling effort returns new species. Species accumulation curves were calculated for each river (Fig. 3). Note that only quantitative data were used to calculate species accumulation curves. Total taxonomic richness also included semi-quantitative kick-net data, so the richness values in Fig. 3 do not match those presented in subsequent figures.

Saturation analysis was used to estimate the proportion of the total taxonomic richness that had been collected by sampling. Total taxonomic richness was estimated by functional extrapolation of the species accumulation curve using the Michaelis Menten means (MMMeans) total richness estimator. The actual number of taxa collected was then expressed as a percentage of the estimated total. Taxa accumulation curves were plotted and saturation analysis was performed using EstimateS (Colwell 2005).

To compare invertebrate richness in braided and single channel rivers, we extracted invertebrate richness data for a single year from the National Rivers Water Quality Monitoring Network (NRWQN) (Smith et al. 1989) and converted it to presence/absence data. Prior to analysis, the NRWQN dataset was adjusted to a level of taxonomic resolution that was equivalent to this survey.

To investigate the relationship between invertebrate distributions and physical environmental factors, biological and physical covariance was analysed using a direct gradient, multivariate technique. Redundancy Analysis (RDA) was chosen, as prior analysis of the dataset showed that the species distributions were linear (Leps & Smilauer 2003). A total of 144 taxa (Appendix 2) and 15 physical variables describing the 12 rivers (Upper and Lower Waitaki were considered separately[1]) were included. Nominal variables describing source of flow, climate and catchment vegetation were extracted from the REC and binary coded. After an initial unconstrained analysis (Table 3A), manual forward selection and Monte-Carlo permutations were used to select variables that best ($P < 0.01$) explained species assemblage variation. The final constrained ordination model contained three variables: 'Longitude', which was a continuous variable, and 'climate' and 'source of flow', each of which were represented by a single 'dummy' variable from each category (Table 3B). The binary nature of these variables meant that only one 'dummy' variable could be included in the reduced model, even though other alternative variables may have also been relevant. Ordination of whole river invertebrate assemblages and catchment-scale physical variables was performed in CANOCO (version 4.02, Microcomputer Power, Ithica, New York).

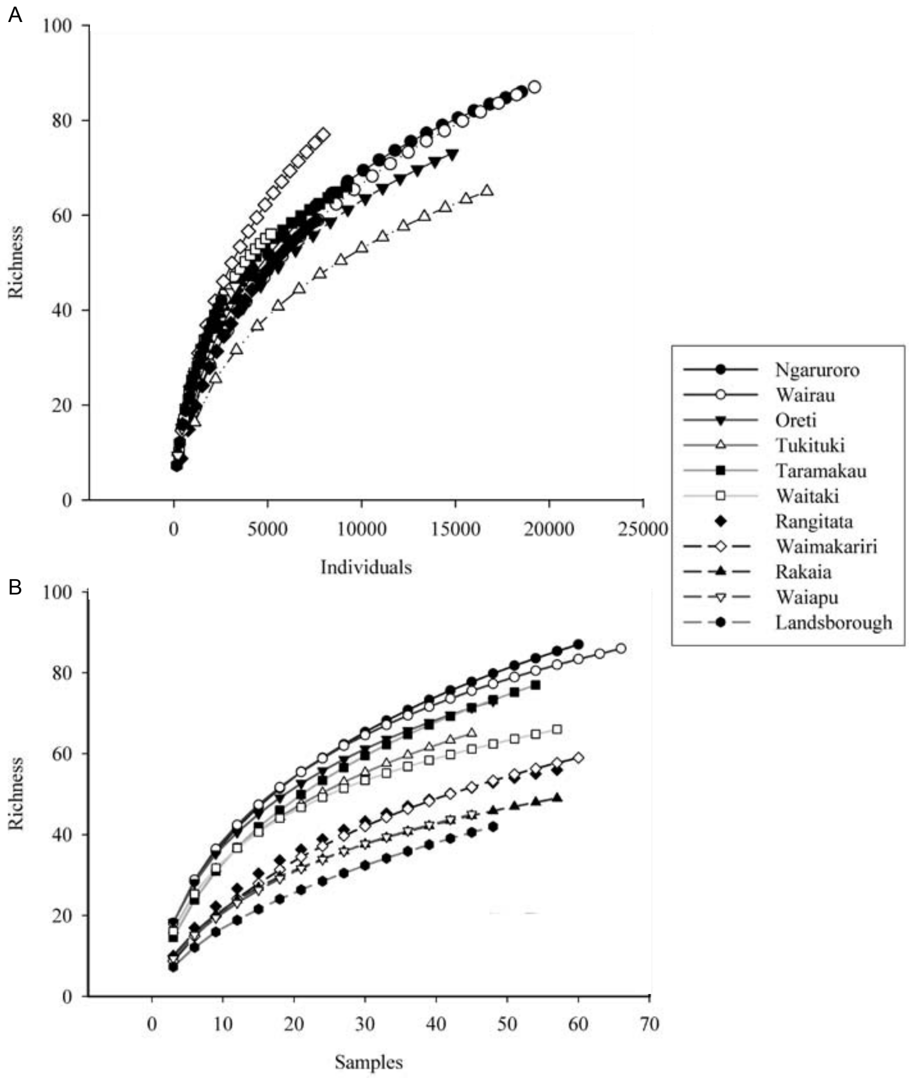


Figure 3. Taxa accumulation curves for each of the 11 rivers included in this survey, scaled according to the number of A. individuals and B. samples collected for all quantitative samples taken. Calculated in EstimateS (Colwell 2005).

[1] For the characterisation of river environments (section 2.1.1) and analysis of river invertebrate assemblage relationships to catchment-scale environmental factors (section 3.2.2), the Waitaki River was divided into upper and lower catchments above and below the Waitaki Dam. Impoundment creates a major discontinuity in a river continuum such that both invertebrate communities and the physical environment are quite distinct. This point is illustrated by comparison of the variables listed in Table 1 and by the separation of the upper and lower river in Fig. 6 later in the report. However, for the sake of brevity, the upper and lower reaches were combined for all subsequent analyses of invertebrate communities.

TABLE 3. EIGENVALUES, CUMULATIVE PERCENTAGE VARIANCE OF SPECIES–ENVIRONMENT RELATIONS (% SP/ENV) AND CORRELATION COEFFICIENTS FOR PHYSICAL VARIABLES.

A. All 15 physical variables included in an unconstrained Redundancy Analysis (RDA); and B. three physical variables remaining after manual forward selection and Monte-Carlo testing of variable significance in a constrained RDA. Significant correlation results are in bold (critical value correlation coefficient (d.f. = 11, $P < 0.01$) = 0.684).

A

		FACTOR 1	FACTOR 2	FACTOR 3
	Eigenvalues	**0.165**	**0.132**	**0.114**
	% sp/env	**17.9**	**32.2**	**44.5**
	Longitude	0.1368	**0.8613**	0.0925
	Latitude	0.1125	**0.8325**	–0.0355
	Mean flow	–0.5214	–0.3049	–0.1395
	Hill	0.5945	0.4463	0.4068
Source of flow	Glacial mountain	–0.6454	–0.2213	0.3061
	Mountain	–0.1636	–0.4581	–0.0882
	Low elevation	0.3045	0.1261	–0.4023
	Lake	–0.1602	–0.0957	–0.5852
	Cold and extremely wet	–0.5616	0.0859	**0.6958**
Climate	Cold and wet	0.3549	–0.1908	–0.4199
	Cold and dry	0.3045	0.1261	–0.4023
	Indigenous forest	0.3521	–0.1496	0.5343
Catchment	Pastoral	0.3308	**0.6915**	–0.3146
vegetation	Scrub and tussock	–0.2402	–0.4107	–0.4994
	Bare ground	–0.5055	–0.2497	0.2381

B

		AXIS 1	AXIS 2
	Eigenvalues	**0.15**	**0.121**
	% sp/env	**40.9**	**74**
	Longitude	–0.0294	**0.9437**
	Hill	0.4745	**0.7472**
	Cold and extremely wet	**–0.684**	0.0569

3. Results

3.1 COMPARISON OF DIVERSITY BETWEEN BRAIDED AND SINGLE CHANNEL RIVERS

The most striking difference between braided and single channel river types was the high taxonomic richness found in braided rivers when all floodplain habitats were included in the comparison (Fig. 4). This 'holistic' braided river taxonomic richness far exceeded the numbers of taxa found in the main channels of the same rivers (our survey) and of the main channels of both braided and single channel rivers from the NRWQN. However, this comparison needs to be viewed with caution because of differing levels of sampling intensity between river types (more samples were taken to survey all habitats in a reach than just to survey a main channel). When only main channel values were compared, significantly more taxa were found in the main channels of single channel rivers (NRWQN) than in the main channels of our braided rivers.

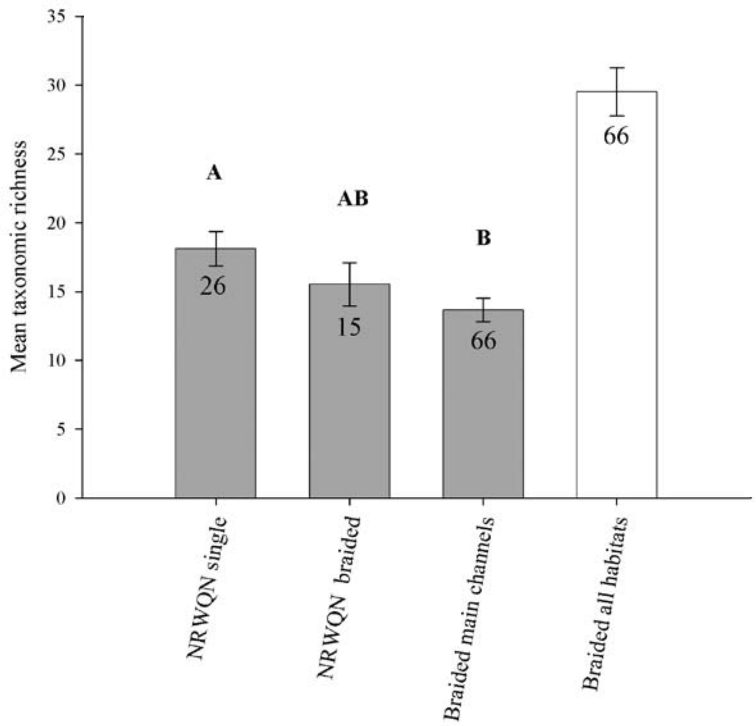


Figure 4. Taxonomic richness of single channel and braided rivers. Shaded bars represent invertebrate richness calculated from the main channels of single channel rivers (National Rivers Water Quality Network (NRWQN) data) and braided rivers (data from NRWQN and this survey). The open bar is taxonomic richness calculated across all habitats found within each reach of the braided rivers included in this survey. The number of sites is labelled below each error bar (SEM). When the three main channel habitat datasets were analysed separately, a significant difference in taxonomic richness was found between single channel NRWQN and main channel habitats in our survey (ANOVA: $F=4.174$, d.f. $=2, 104$, $P=0.018$, Bonferroni = 0.015). Significant differences are denoted by the letters above each column.

3.2 TAXONOMIC RICHNESS, DENSITY AND ASSEMBLAGE DIVERSITY ACROSS SPATIAL SCALES

3.2.1 Sampling efficacy

Although accumulation curves do not reach an asymptote, they are comparable in shape and provide useful information, particularly when considered in relation to numbers of individuals collected (Fig. 3). Marked differences in taxonomic richness were found depending on the numbers of individuals collected. For example, only 3264 individuals (and 56 taxa) were collected from 15 samples in the Waiapu River, whereas 18 520 individuals (and 99 taxa) were found in 22 samples from the Wairau River. Variation in the number of individuals and samples collected reflected both the density of invertebrates within different rivers and the number of habitat types located within each river.

3.2.2 Catchment scale

A total of 144 taxa were collected from the 11 river systems. Taxonomic richness ranged from 56 taxa in the Waiapu River to 99 taxa in the Wairau River, representing 38% and 68% of the entire taxa pool, respectively (Fig. 5A). The five rivers with the highest taxonomic richness were in five separate geographic regions. Saturation analysis indicated that the range of sampling efficacy was 70–86% across all rivers (Appendix 3). All ordinal groups were represented in each river system, with the exception of Plecoptera, which were absent from the Waiapu River. In most rivers, invertebrate taxonomic richness was dominated by trichopterans, except for the Landsborough and Waiapu Rivers, which contained a greater number of dipteran taxa. Generally, the proportions of ordinal groups remained constant despite variation in overall richness among rivers.

Total numbers of invertebrates collected ranged from approximately 19 500 individuals in the Wairau and Ngaruroro Rivers, to fewer than 3500 individuals in the Landsborough and Waiapu Rivers (Fig. 5B). In terms of relative abundance, all rivers were dominated by Diptera, except for the Ngaruroro, Rakaia and Waitaki Rivers, which contained proportionately more Ephemeroptera. The Waitaki River stood out as containing an unusually high proportion of Crustacea, largely due to the high numbers of *Paracalliope fluvitalis* found in the impounded lower reaches. This amphipod is normally associated with stable, weedy streams, but in this case was found in high densities in the main channel of the Waitaki River.

Redundancy Analysis between benthic assemblages and catchment-scale variables within each river revealed distinct differences in habitat assemblages corresponding to gradients in longitude, climate and source of flow (Fig. 5, Table 3). The first three axes of the initial unconstrained ordination explained 41% of the variation in 'species' data and 44.5% of the 'species'–environment relations. However, correlations between the axes and individual environmental variables were generally weak. There were no significant correlations with axis 1, although the 'glacial mountain' category appeared to be important. Axis 2 was significantly correlated with longitude, latitude and 'pastoral land cover', whilst axis 3 correlated with the REC climatic category 'cold and extremely wet'

(Table 3A). The reduced, constrained model produced by manual forward selection incorporated three variables. Although the first two axes explained only 27% of the variation in 'species' data, the 'species'–environment relationship was much stronger (74% in total), and there were strong individual correlations between 'species' gradients (axes 1 and 2) and longitude, source of flow and climate (Table 3B). The ordination plot groups similar sites closer together, in accordance with both their biological and physical characteristics. Hence, rivers were separated according to geographical location, climate and source of flow (Fig. 6).

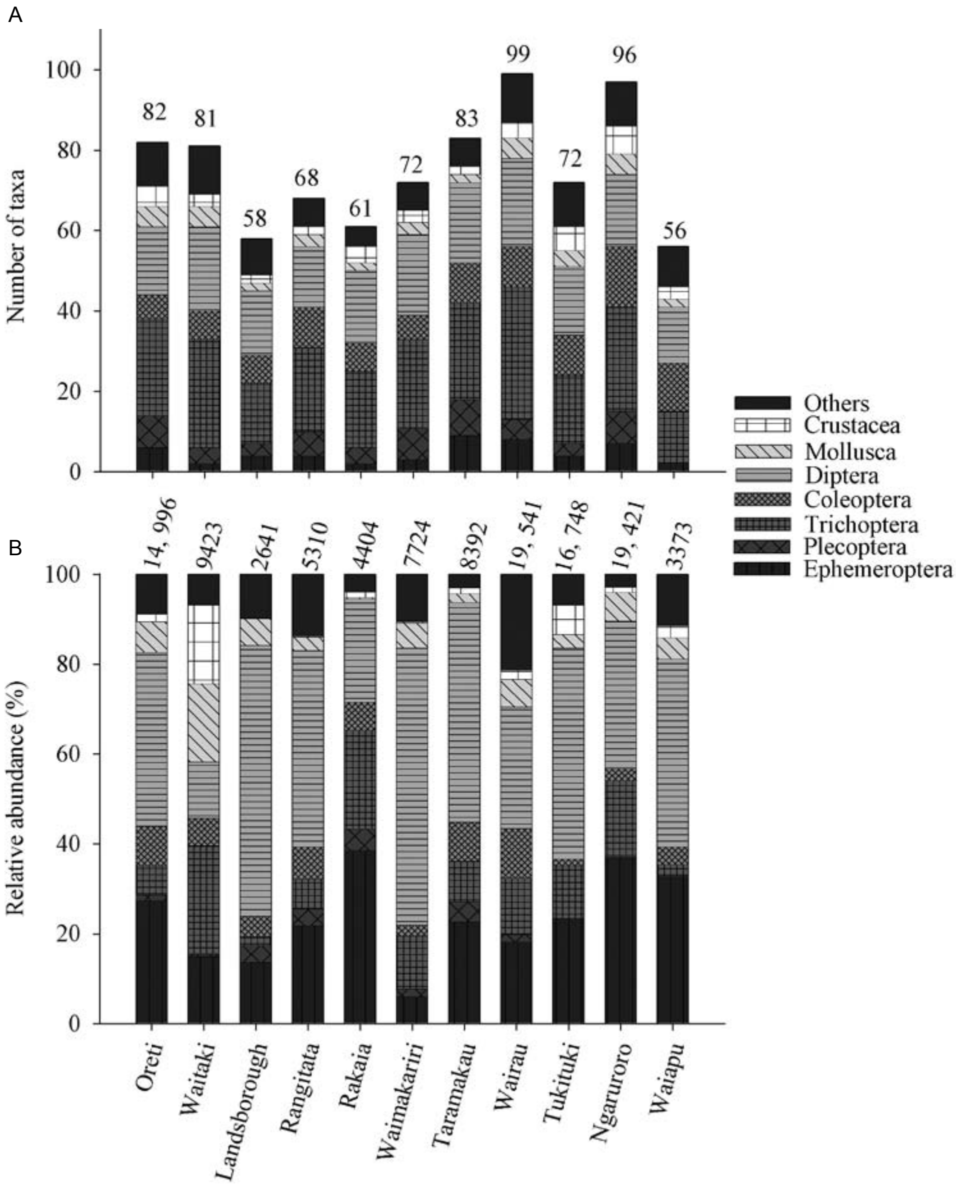


Figure 5. A. The total taxonomic richness and ordinal (or higher) groups, and B. relative abundance of taxa within ordinal (or higher) groups for 11 braided rivers sampled between December 2006 and April 2007. The total number of individuals collected in each river is also shown.

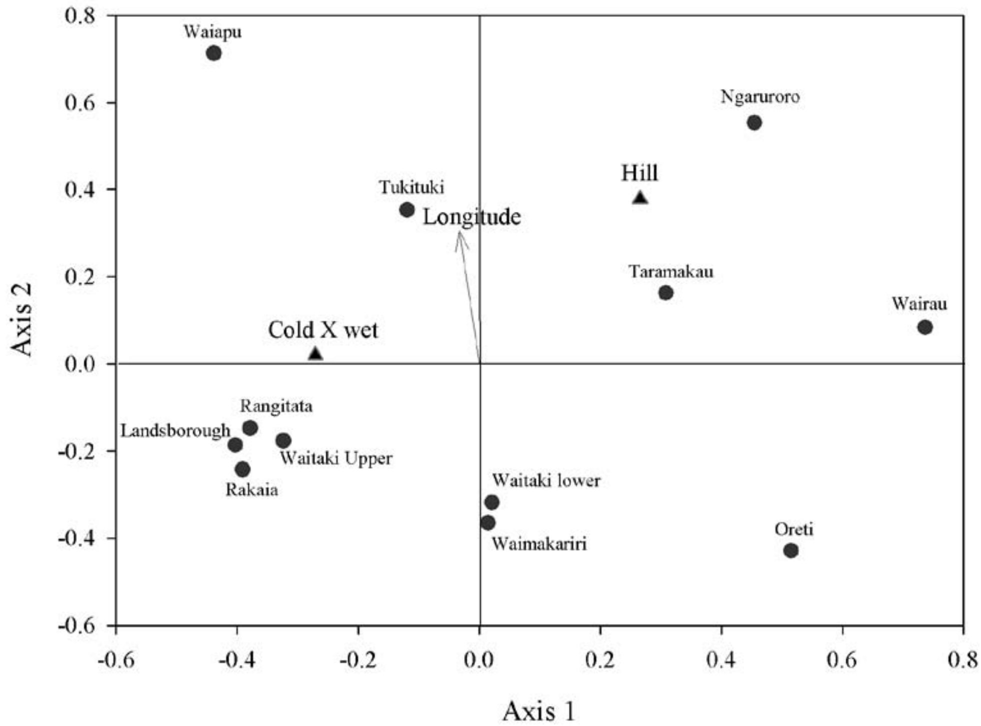


Figure 6. Redundancy Analysis ordination biplot of presence/absence data for braided river invertebrate taxa and three physical variables representing geographical position, climate and topography. Manual forward selection and Monte-Carlo testing (999 permutations) of physical variables were used to produce the reduced model. The continuous variable longitude is depicted by an arrow (correlation strength is represented by arrow length), whereas the nominal variables 'hill' and 'cold and extremely wet' are depicted by centroids (▲). Nominal variables are described in Table 1.

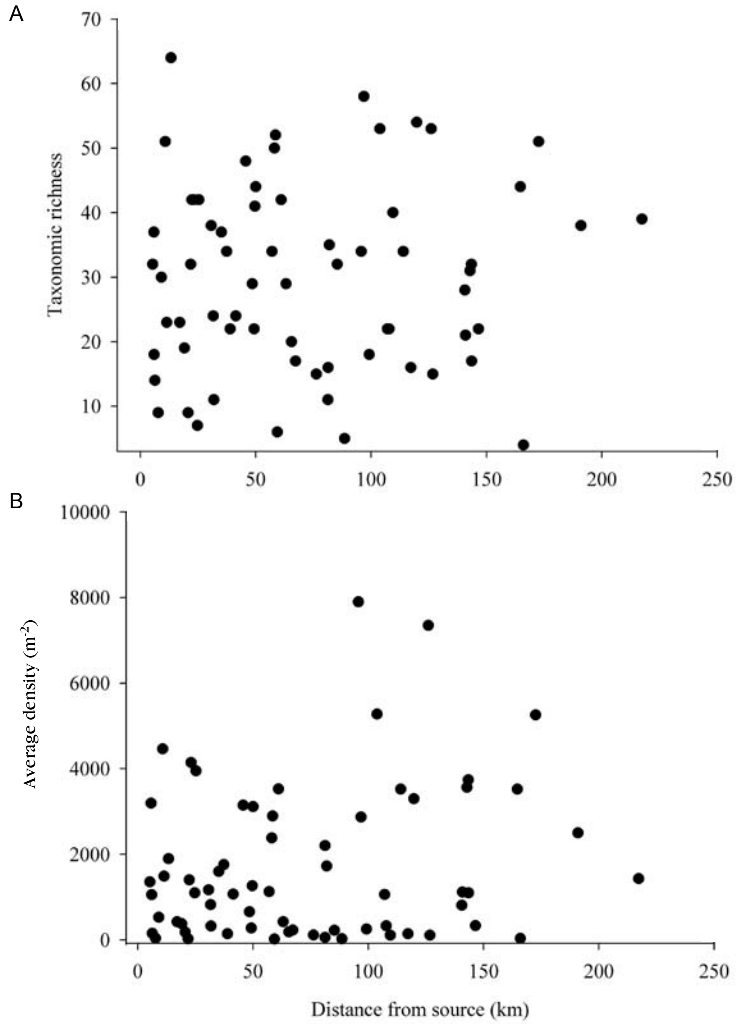
3.2.3 Longitudinal and reach morphological type

Rivers ranged in length from approximately 223 km for the Waitaki River to 61 km for the Waiapu River, and the altitude of headwater sites ranged from 1113 m a.s.l. in the Wairau River to 466 m a.s.l. in the Tukituki River. No consistent relationship was found between taxonomic richness and distance from the source of braided rivers, and richness was highly variable along the entire lengths of all rivers (Fig. 7A). Similarly, there was no significant relationship between distance from source and density of benthic invertebrates (Fig. 7B), although we did observe species-specific distributions (see later).

There were marked differences in taxonomic richness among the six reach types, despite high within-reach variation (Fig. 8A). Braided reaches generally had higher taxonomic richness than headwaters and gorge reaches; however, there were no differences between the three main braided reach types—high lateral confined, low lateral confined and impacted—all of which showed high levels of variation in taxonomic richness. Saturation analysis showed that across all morphological types between 65% and 95% of taxa had been collected (Appendix 3). There was no significant difference between reach morphological types in average density of invertebrates (Fig. 8B).

Invertebrate assemblages in all reach types included the same ordinal groups (Fig. 9), and were dominated by Trichoptera and Diptera. Few groups were absent from any reach type, with the exception of Odonata, which were restricted to braided reaches, and Mollusca, which were not found in the headwaters of any river. Only one crustacean, *Paracalliope*, was found in a gorge reach (Waitaki River, main channel), and the only crustacean found in a headwater reach was *Paraleptamphopus* spp. (Waiapu River, main channel). Coleopteran taxa were also rare in headwater reaches, although Elmidae and Hydraenidae were present in the headwater reaches of five and four rivers, respectively.

Figure 7. Relationship between A. Taxonomic richness, and B. average density and distance from the source in 66 reaches in the 11 rivers sampled between December 2006 and April 2007. Average density was calculated using all samples collected within the reach. Distance was not correlated with richness ($r = 0.06$, $P > 0.05$) or density ($r = 0.197$, $P > 0.05$).



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