



# Spatial variation in invertebrate communities in New Zealand braided rivers

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Duncan Gray and Jon S. Harding

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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  $\leq 3$  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<sup>3</sup>/s in the Tukituki River to 370 m<sup>3</sup>/s in the Waitaki River, while catchment size ranged from 998 km<sup>2</sup> for the Taramakau River to 11 887 km<sup>2</sup> 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.

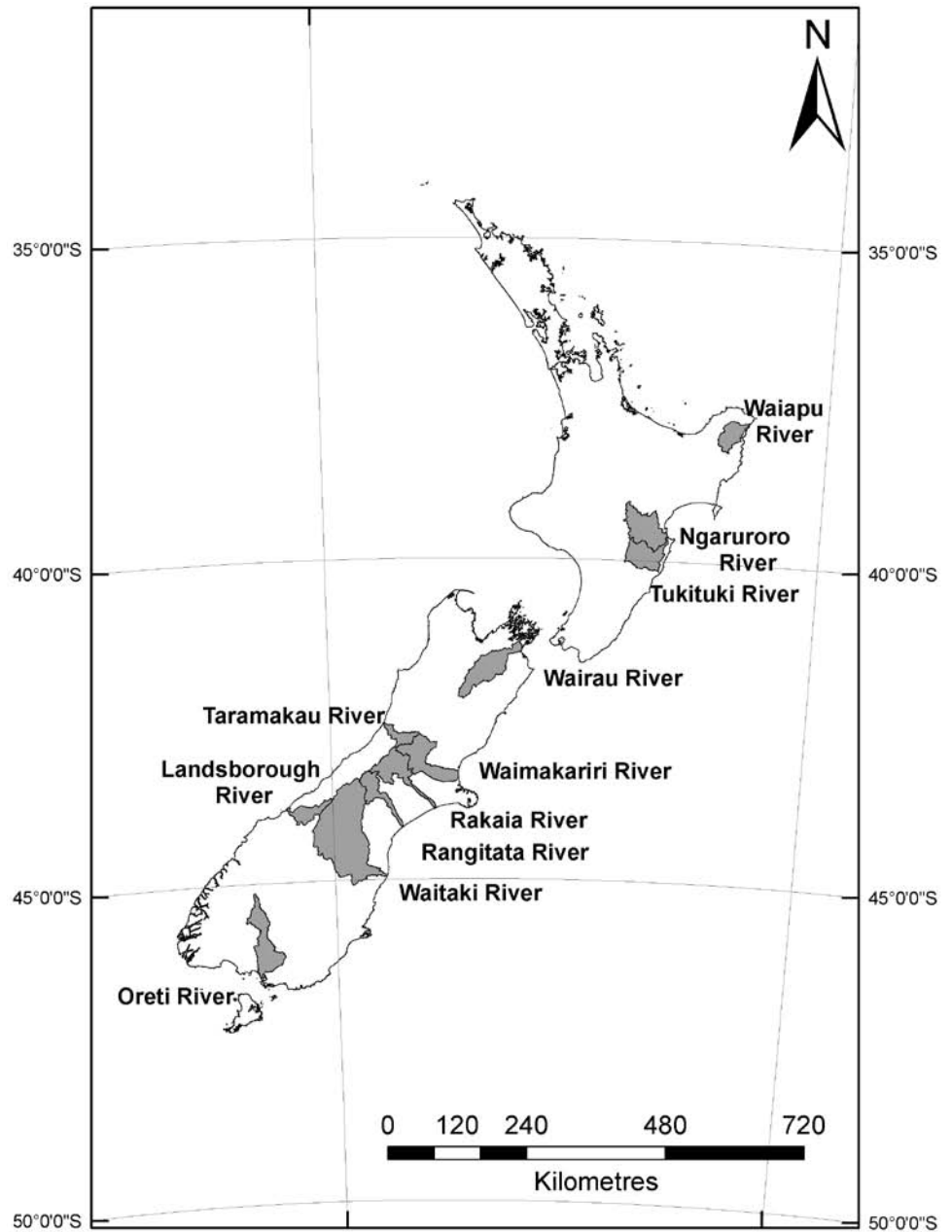


TABLE 1. CATCHMENT CHARACTERISTICS OF THE 11 BRAIDED RIVERS CONSIDERED IN THIS STUDY, AS DERIVED FROM THE RIVER ENVIRONMENT CLASSIFICATION (SNELDER ET AL. 2005).

CATCHMENT REGION		CATCHMENT AREA (km <sup>2</sup> )	RIVER ORDER <sup>a</sup>	MEAN FLOW (m <sup>3</sup> /s)	FRE3 EXCED- ENCE <sup>b</sup>	DAYS SINCE FRE3 <sup>c</sup>	SOURCE OF FLOW <sup>d</sup>	CLIMATE <sup>e</sup>	CATCHMENT VEGETATION <sup>f</sup>
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) <sup>g</sup>	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

<sup>a</sup> 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).

<sup>b</sup> The FRE3 value represents the number of flood events that exceed three times the median flow of a river.

<sup>c</sup> Days since FRE3 flood event were sometimes variable, so the median value for the reaches was taken.

<sup>d</sup> Source of flow is predominantly defined by topography of the river catchment.

<sup>e</sup> Rivers are assigned to one of six spatially averaged climatic zones based on temperature and precipitation.

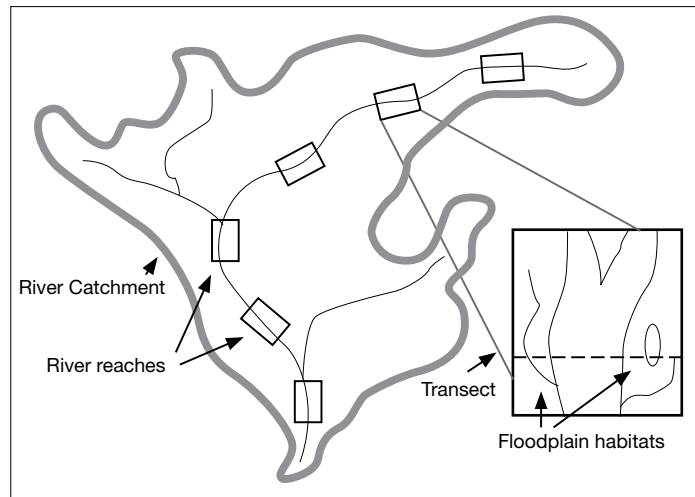
<sup>f</sup> Catchment vegetation assigns rivers to one of seven categories representing the predominant land-cover of the catchment.

<sup>g</sup> 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<sup>2</sup>, 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<sup>2</sup> area within each habitat. Quantitative pond samples were taken using a modified Surber sampler (0.11 m<sup>2</sup>, 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.

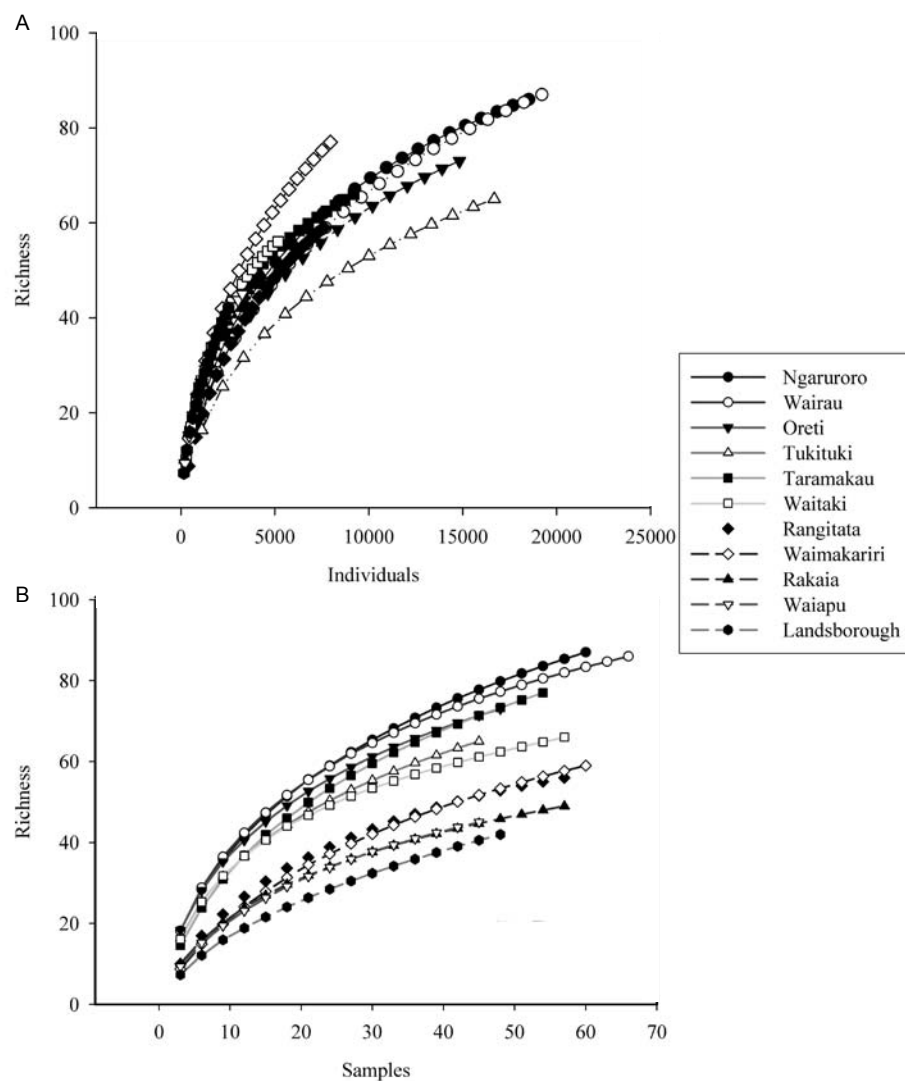
Saturation analysis was used to estimate the proportion of the total taxonomic richness that had been collected by sampling. Total taxonomic richness was estimated by functional extrapolation of the species accumulation curve using the Michaelis Menten means (MMMeans) total richness estimator. The actual 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<sup>1</sup>) 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).



<sup>1</sup> 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
	<b>Eigenvalues</b>	<b>0.165</b>	<b>0.132</b>	<b>0.114</b>
	<b>% sp/env</b>	<b>17.9</b>	<b>32.2</b>	<b>44.5</b>
	Longitude	0.1368	<b>0.8613</b>	0.0925
	Latitude	0.1125	<b>0.8325</b>	-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	<b>0.6958</b>
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	<b>0.6915</b>	-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
	<b>Eigenvalues</b>	<b>0.15</b>	<b>0.121</b>
	<b>% sp/env</b>	<b>40.9</b>	<b>74</b>
	Longitude	-0.0294	<b>0.9437</b>
	Hill	0.4745	<b>0.7472</b>
	Cold and extremely wet	<b>-0.684</b>	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.

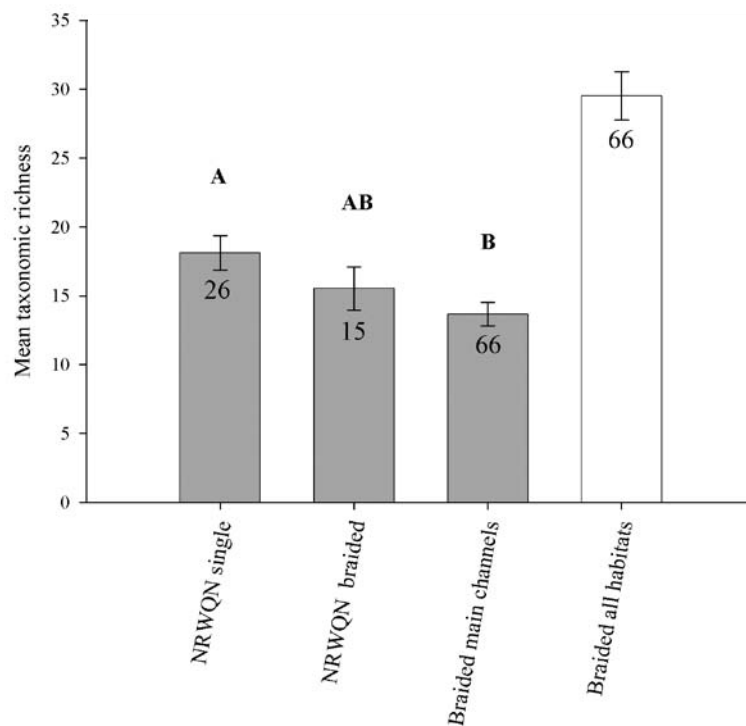


Figure 4. Taxonomic richness of single channel and braided rivers. Shaded bars represent invertebrate richness calculated from the main channels of single channel rivers (National Rivers Water Quality Network (NRWQN) data) and braided rivers (data from NRWQN and this survey). The open bar is taxonomic 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 18520 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 fluvialis* 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.

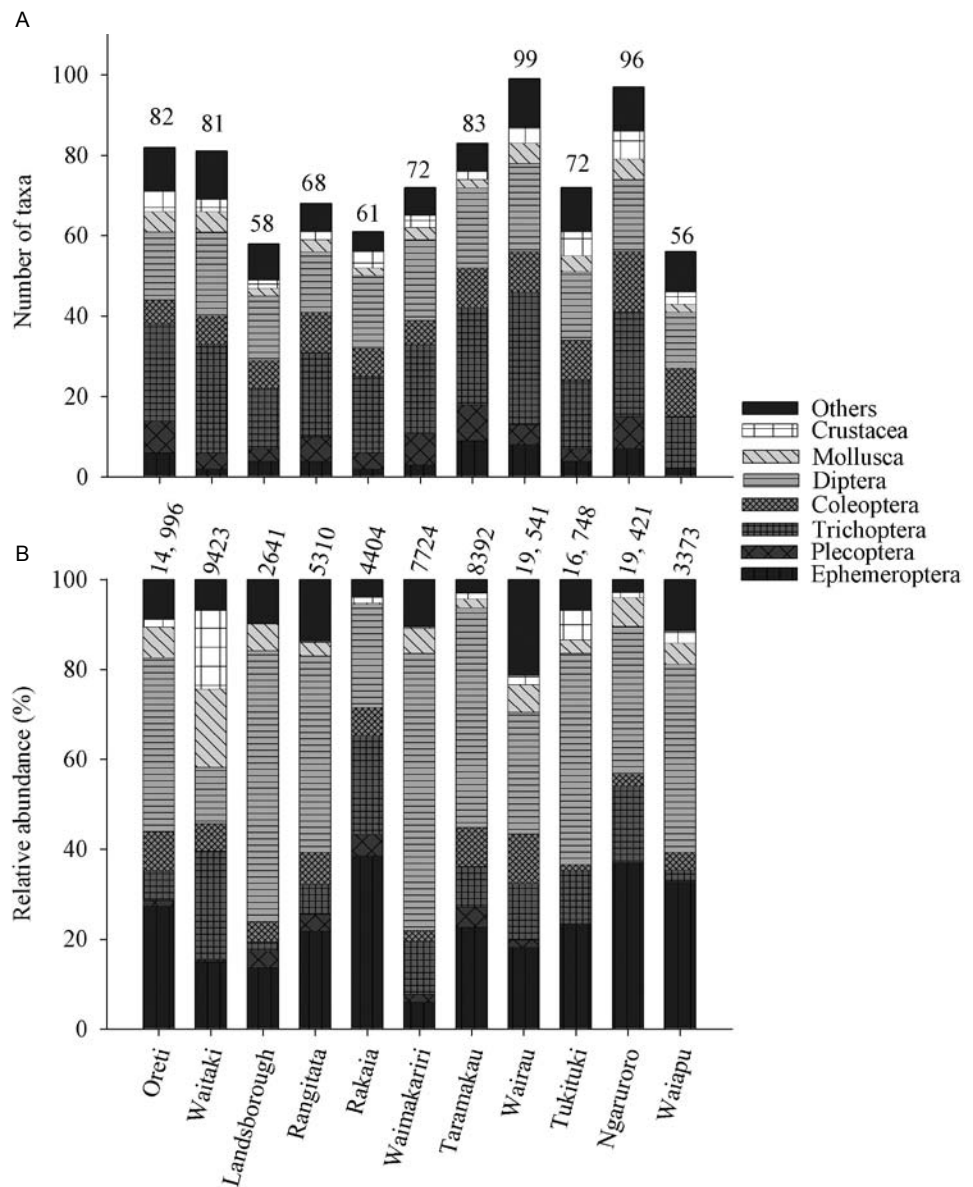
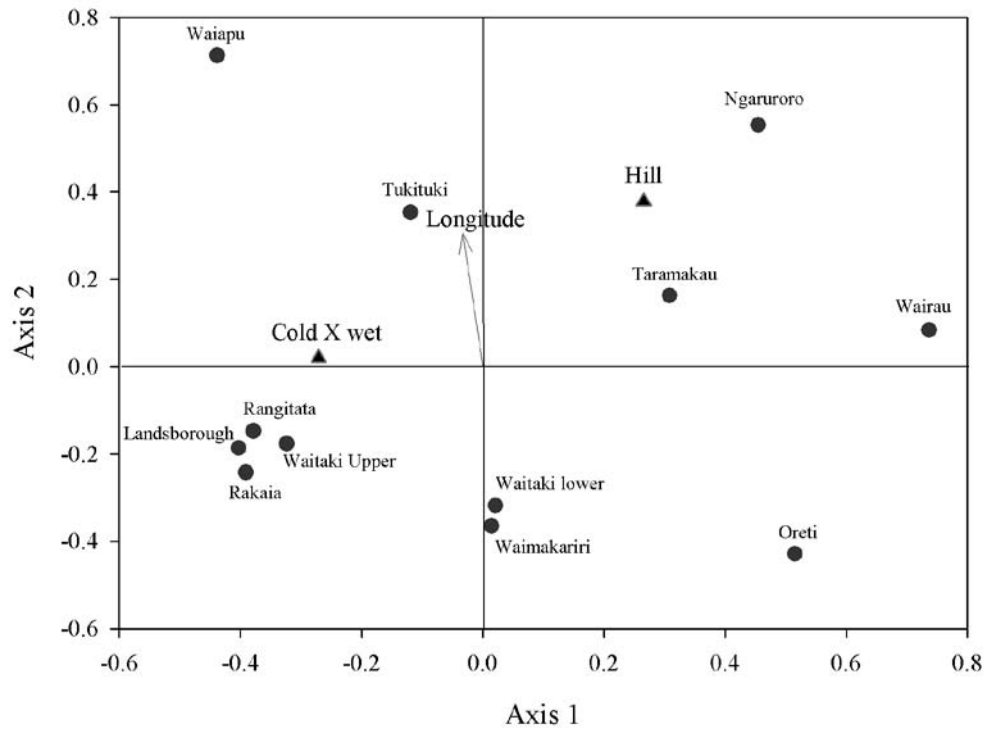


Figure 6. Redundancy Analysis ordination biplot of presence/absence data for braided river invertebrate taxa and three physical variables representing geographical position, climate and topography. Manual forward selection and Monte-Carlo testing (999 permutations) of physical variables were used to 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 ( $r=0.197$ ,  $P>0.05$ ).

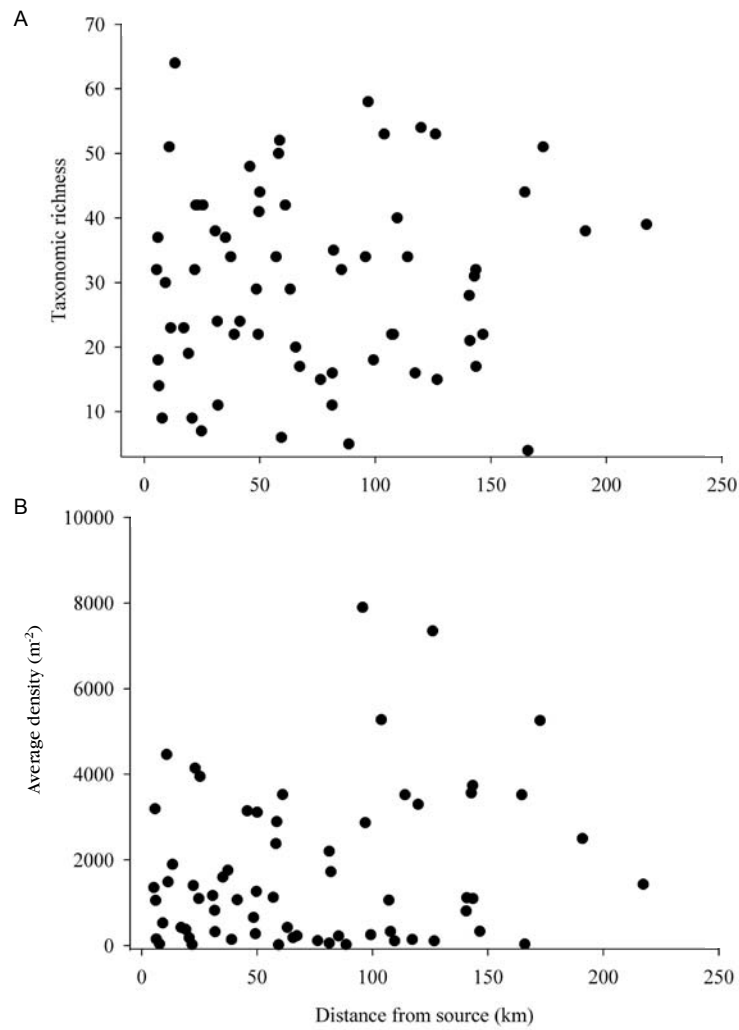


Figure 8. A. Taxonomic richness and B. mean invertebrate density (no./m<sup>2</sup>) for each morphological reach type. Box plots show the median value, 25th and 75th percentiles, and outliers. Sample sizes are shown below the median line. Reach types that are not significantly different (Scheffe's *post hoc* < 0.05) have identical superscript letters. There was a significant difference between reach types in taxonomic richness ( $F=5.805$ , d.f. = 4, 59,  $P=0.001$ ), but not in average density of invertebrates ( $F=1.284$ , d.f. = 4, 59,  $P=0.289$ ). Because only two rivers had low lateral, unconfined reaches, this reach type could not be considered statistically.

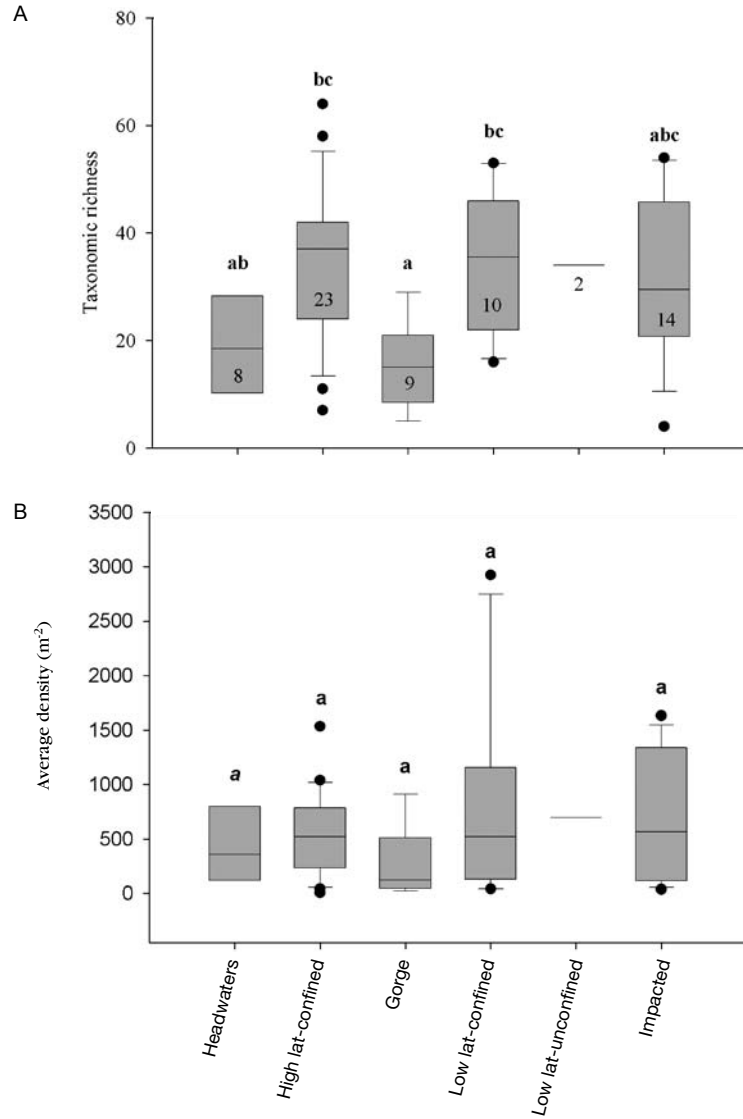
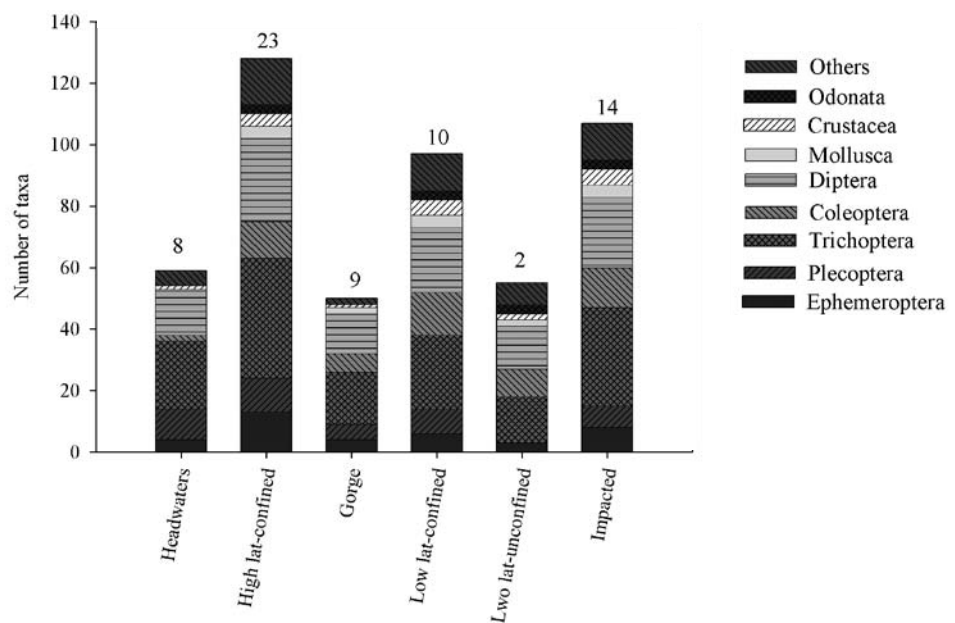


Figure 9. Numbers of ordinal (and above) taxa found in each of the six reach types. The number of sampling sites included in each category is given above each column.



### 3.2.4 Habitat scale

Both taxonomic richness and density varied significantly among habitat types (Fig. 10). Lateral habitats (ponds, spring creeks and spring sources) were more diverse than main channels, with side braids having intermediate richness; spring creeks had the highest mean taxonomic richness (Fig. 10A). A similar pattern was found for density, with ponds and spring creeks having higher densities of invertebrates than main channels and side braids, whereas spring sources had intermediate densities (Fig. 10B). All habitats showed considerable variation in both richness and density. Saturation analysis indicated that 86–97% of taxa were sampled in each habitat type (Appendix 3).

Most ordinal groups were represented in each habitat type, with the exception of Odonata, which were absent from the main channels of braided rivers (Fig. 11). All other groups were present in each habitat type in similar proportions. Orthocladiinae and Chironominae midges and Elmidae beetles were consistently among the ten most common taxa within each habitat type (Table 4). The ephemeropteran *Deleatidium* was ubiquitous in all habitats except ponds. Common taxa limited to a single habitat type included the plecopterans

Figure 10. A. Taxonomic richness and B. average density (no./m<sup>2</sup>) in five habitat types sampled across six reaches of 11 braided rivers. Box plots show the median value, 25th and 75th percentiles, and outliers. Habitat types that are not significantly different (Scheffe's *post hoc*  $P < 0.05$ ) have identical superscript letters. Density was log transformed to meet assumptions of normality, but actual values are shown on the plot. There were significant differences between habitat types in both taxonomic richness ( $F = 9.743$ , d.f. = 4, 196,  $P < 0.001$ ) and average density ( $F = 5.114$ , d.f. = 4, 196,  $P < 0.001$ ).

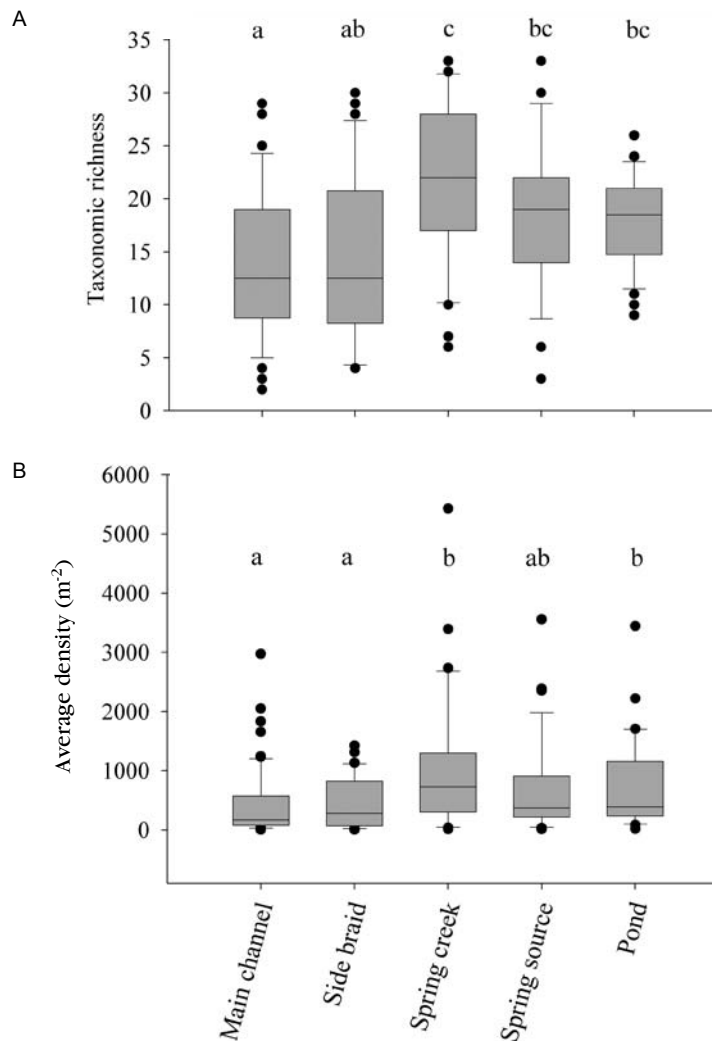


Figure 11. Numbers of ordinal (and above) taxa found in each of five habitat types in the 11 braided rivers studied. Total richness is shown above each column.

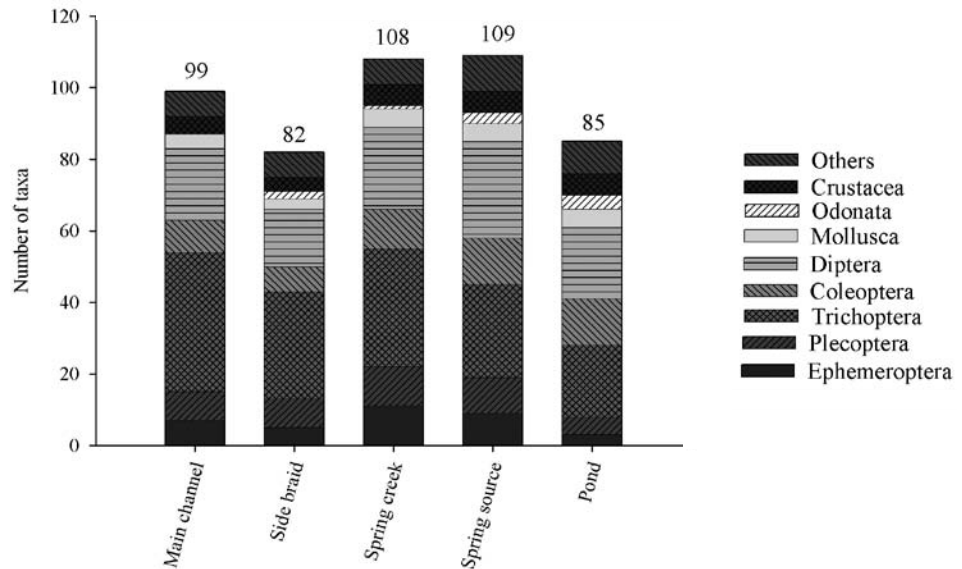


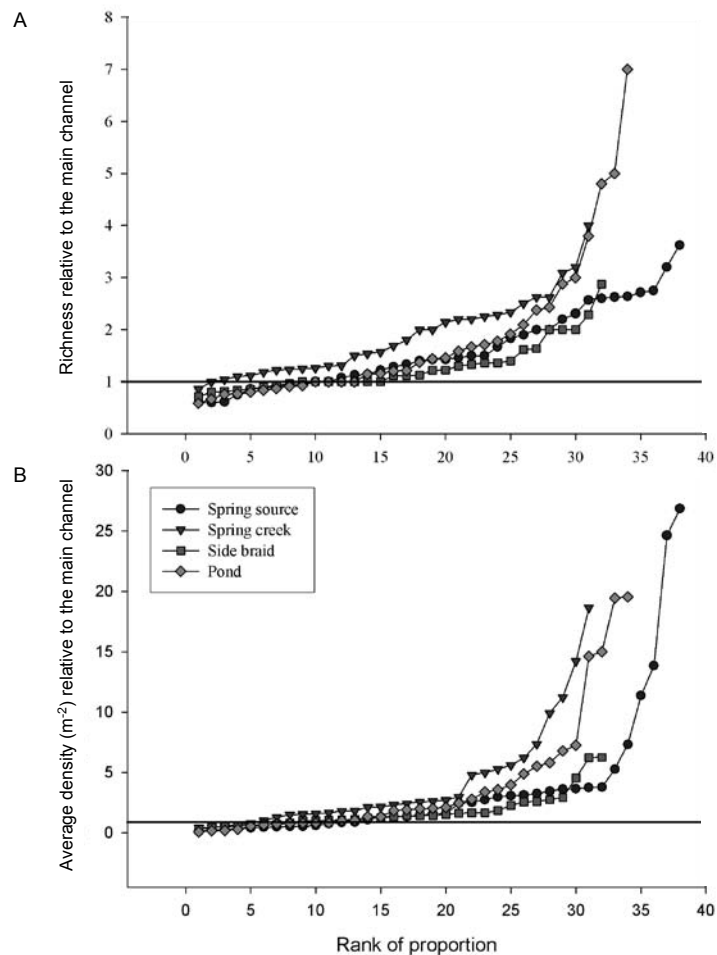
TABLE 4. THE TEN MOST COMMONLY OCCURRING TAXA WITHIN EACH HABITAT TYPE. The percentage of habitats in which they were found and the number of those habitats sampled are shown.

MAIN CHANNELS		SIDE BRAIDS		PONDS		SPRING CREEKS		SPRING SOURCES	
TAXON	%	TAXON	%	TAXON	%	TAXON	%	TAXON	%
<i>Zelandobius</i> spp.	44	<i>Austrosimulium</i>	47	<i>Oxyethira</i>	53	<i>Potamopyrgus</i>	65	<i>Molophilus</i>	55
Tanypodinae	50	<i>Oxyethira</i>	50	<i>Berosus</i>	56	Tanypodinae	68	<i>Paraleptambopus</i> spp.	55
<i>Pycnocentodes</i>	52	<i>Aoteapsyche</i> spp.	53	Ostracoda	56	<i>Psiloborema</i>	71	<i>Oxyethira</i>	61
<i>Aoteapsyche</i> spp.	55	<i>Psiloborema</i>	53	<i>Xanthocnemis</i>	59	Chironominae	71	Chironominae	61
Chironominae	55	<i>Pycnocentodes</i>	56	Elmidae	68	<i>Oxyethira</i>	74	Tanypodinae	63
<i>Psiloborema</i>	56	Chironominae	59	Oligochaeta	71	<i>Pycnocentodes</i>	74	Elmidae	71
<i>Eriopterini</i>	71	<i>Eriopterini</i>	75	Chironominae	79	Oligochaeta	74	<i>Eriopterini</i>	71
Elmidae	74	Elmidae	88	<i>Sigara</i>	79	Elmidae	84	Oligochaeta	71
Orthoclaadiinae	94	<i>Deleatidium</i>	100	Orthoclaadiinae	91	<i>Deleatidium</i>	97	<i>Deleatidium</i>	89
<i>Deleatidium</i>	100	Orthoclaadiinae	100	Tanypodinae	91	Orthoclaadiinae	97	Orthoclaadiinae	89
<b>Number of sites</b>	<b>66</b>		<b>32</b>		<b>34</b>		<b>31</b>		<b>38</b>

*Zelandoperla* and *Zelandobius*, which were found only in main channels, and Muscidae (Diptera), which were only common in spring creeks. The beetle *Berosus*, a zygopteran *Xanthocnemis*, a corixid *Sigara* and ostracods were all common in ponds.

Over 70% of lateral habitats had greater invertebrate taxonomic richness than their associated main channel (Fig. 12A). All spring creeks except one had more taxa than their associated main channels, while ponds, spring sources and side braids were more variable in relative taxonomic richness, with 26%, 24% and 25% of sites, respectively, having a lower diversity than the main channel. Three ponds had over four times as many taxa as the nearby main channel. Similarly, 73% of lateral habitats had higher total invertebrate density than their associated main channel (Fig. 12B). Eighty-four percent of spring creeks had a greater density of individuals than their associated main channels, and most spring sources, ponds and side braids also displayed greater relative density than their main channels (66%, 68% and 75%, respectively).

Figure 12. A. Taxonomic richness and B. average density (no./m<sup>2</sup>) in four lateral habitats of the 11 braided rivers studied as a proportion of richness/density in the main channel. Values greater than 1 (horizontal line) signify higher relative diversity in the lateral habitat than the main channel within that reach. All sites within each habitat type are ranked in order of increasing lateral habitat relative richness/density.



### 3.3 SPATIALLY RESTRICTED TAXA

Of the 144 taxa identified in our survey, 16 were found in only one river, 19 were found in two rivers and 15 were found in three (Figs 13 & 14, Table 5). Thus, 35% of taxa were only found in three or fewer river systems. These taxa were also represented by few individuals, comprising only 0.8% of all individuals. Taxa found in three or fewer rivers included 9 Ephemeroptera, 3 Plecoptera, 18 Trichoptera, 5 Diptera, 7 Coleoptera, 5 Crustacea, 1 Polychaeta, 1 Odonata, 1 Tricladida and 1 Nematomorpha (Table 5). The Tukituki River had the lowest number of spatially restricted taxa (4), while the neighbouring Ngaruroro River had the highest number (18) (Fig. 14A).

Only 13% of taxa were found in all 11 rivers. However, they comprised 80% of all individuals collected and included *Deleatidium*, Elimidae beetles, Chironominae, Orthoclaudiinae, Tanypodinae and Eriopterini. The spring/groundwater-associated *Paraleptamphopus* spp. and the pond-dwelling *Sigara* were also present in every river.

There was also variability in the number of taxa restricted to particular reach types (Fig. 14B). The highest numbers of spatially restricted taxa were found in the high lateral input, confined reaches and in impacted reaches further downstream in the rivers. Gorges contained very few rare taxa. Overall, braided (high lateral confined, low lateral confined, low lateral unconfined and impacted) reaches contained more spatially restricted taxa than non-braided reaches including headwater reaches.

Numbers of rare taxa were relatively evenly distributed across habitat types, with the exception of side braids (Fig. 14C). Although spring sources, creeks and ponds contained the highest number of rare taxa (16–21), 15 rare taxa were also found in main channels. The caddisfly *Neurochorema confusum* was only found in main channels, whereas ten other Trichoptera, two Ephemeroptera, a Plecoptera and a Diptera were found in main channels plus one other habitat type.

Figure 13. Numbers of taxa found only in 1, 2, 3 ... 11 rivers (histograms) and the percentage of all taxa found represented by them (closed circles).

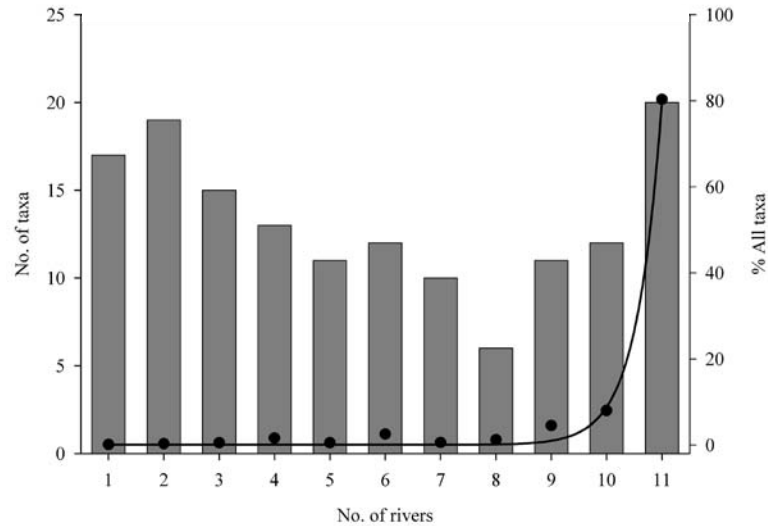


Figure 14. Numbers of taxa found in A. three or fewer river systems, B. two or fewer reach types and C. two or fewer habitat types.

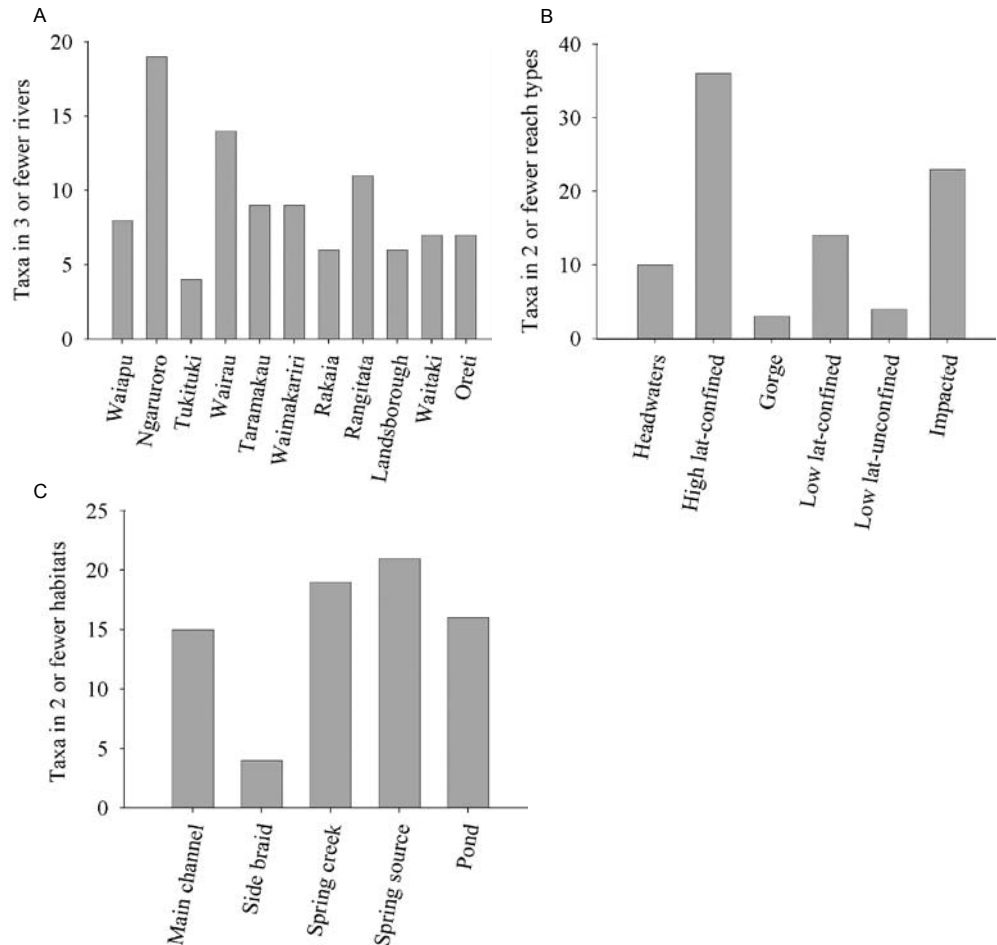




TABLE 5. SPATIALLY RESTRICTED TAXA FOUND ONLY WITHIN 1, 2 OR 3 BRAIDED RIVERS.

TAXON	ORDER	WAIAPU	NGARURORO	TUKITUKI	WAIKAI	TARAMAKAU	WAIMAKARIRI	RAKAI	RANGITATA	LANDSBOROUGH	WAITAKI	ORETI
<b>Restricted to 1 river</b>												
<i>Enomina zealandica</i>	Trichoptera	0	0	0	0	0	0	0	0	0	0	1
<i>Edpercivalia</i>	Trichoptera	0	0	0	0	0	0	0	1	0	0	0
<i>Enochrus</i>	Coleoptera	0	1	0	0	0	0	0	0	0	0	0
<i>Ichthybotus</i>	Ephemeroptera	0	1	0	0	0	0	0	0	0	0	0
<i>Ischnura</i>	Odonata	1	0	0	0	0	0	0	0	0	0	0
Nematomorpha		0	0	0	0	0	0	0	0	1	0	0
<i>Ochlerotatus antipodeus</i>	Diptera	0	0	0	0	0	1	0	0	0	0	0
<i>Oecetis unicolor</i>	Trichoptera	0	0	0	0	0	0	0	0	1	0	0
<i>Paraleptambopus caeruleus</i>	Amphipoda	0	0	0	0	0	0	0	0	0	0	1
Podaena	Coleoptera	0	0	0	0	0	0	0	1	0	0	0
<i>Prorhynchus</i>	Rabbitophora	0	0	0	0	0	0	0	0	0	1	0
Staphylinidae	Coleoptera	0	0	0	0	1	0	0	0	0	0	0
<i>Taraperla bowesi</i>	Plecoptera	0	0	0	0	0	1	0	0	0	0	0
<i>Tiphobiosis</i>	Trichoptera	0	0	0	0	0	0	0	1	0	0	0
<i>Triplectides cephalotus</i>	Trichoptera	0	1	0	0	0	0	0	0	0	0	0
<i>Zelandobius edensis</i>	Plecoptera	0	0	0	0	0	0	0	1	0	0	0
<b>Restricted to 2 rivers</b>												
<i>Ameletopsis</i>	Ephemeroptera	0	1	0	0	1	0	0	0	0	0	0
<i>Antiporus femoralis</i>	Coleoptera	1	1	0	0	0	0	0	0	0	0	0
<i>Austroclima</i>	Plecoptera	0	0	0	1	0	0	0	0	0	0	1
<i>Costachorema callistum</i>	Trichoptera	0	0	0	0	1	0	0	0	0	1	0
<i>Cruregens fontanus</i>	Isopoda	0	1	1	0	0	0	0	0	0	0	0
<i>Hydrobiosella</i>	Trichoptera	1	0	0	0	0	0	0	0	0	1	0
<i>Hydrobiosis chalcodes</i>	Trichoptera	0	0	0	1	0	0	0	0	0	1	0
<i>Hydrobiosis barpidiosa</i>	Trichoptera	0	1	0	0	0	0	0	0	0	1	0
<i>Hydrobiosis neadelphus</i>	Trichoptera	0	0	0	1	0	0	0	1	0	0	0
<i>Hydrobiosis torrentis</i>	Trichoptera	0	0	0	0	1	1	0	0	0	0	0
<i>Hyphydrus elegans</i>	Trichoptera	1	0	1	0	0	0	0	0	0	0	0
<i>Mauitulus</i>	Ephemeroptera	0	0	0	1	1	0	0	0	0	0	0
<i>Nesameletus austrinus</i>	Ephemeroptera	0	0	0	0	0	0	0	1	1	0	0
<i>Neurochorema confusum</i>	Trichoptera	0	1	0	1	0	0	0	0	0	0	0
<i>Oniscigaster wakefieldi</i>	Ephemeroptera	0	0	0	1	0	0	0	0	0	0	1
<i>Paracymus</i>	Coleoptera	1	1	0	0	0	0	0	0	0	0	0
Ptilodactylidae	Coleoptera	0	1	0	1	0	0	0	0	0	0	0
<i>Triplectidina</i>	Trichoptera	0	1	0	1	0	0	0	0	0	0	0
<i>Zephlebia</i>	Ephemeroptera	0	0	0	1	1	0	0	0	0	0	0
<b>Restricted to 3 rivers</b>												
<i>Beraeoptera roria</i>	Trichoptera	0	1	0	0	0	1	0	1	0	0	0
Copepoda		0	0	0	0	0	1	1	0	0	0	1
<i>Corynocera</i>	Diptera	0	0	0	0	0	1	1	0	1	0	0
<i>Cristaperla</i>	Plecoptera	0	1	0	0	0	0	1	1	0	0	0
<i>Hydrobiosis frater</i>	Trichoptera	0	0	0	0	0	0	1	1	0	1	0
<i>Hydrobiosis silvicola</i>	Trichoptera	0	0	0	0	0	1	1	1	0	0	0
<i>Namanereis tiriteae</i>	Nereididae	1	1	1	0	0	0	0	0	0	0	0
<i>Neozephlebia</i>	Ephemeroptera	0	1	0	0	1	0	0	0	1	0	0
<i>Oniscigaster distans</i>	Ephemeroptera	0	0	0	1	1	0	0	0	0	0	1
<i>Paracrangonyx</i>	Isopoda	1	1	0	1	0	0	0	0	0	0	0
<i>Paratya</i>	Atyidae	0	1	1	0	0	0	0	0	1	0	0
<i>Pelecorhynchidae</i>	Diptera	0	1	0	0	0	1	1	0	0	0	0
<i>Ptilorheithrus agilis</i>	Trichoptera	0	0	0	1	0	0	0	1	0	0	1
Psychodidae	Diptera	1	0	0	1	1	0	0	0	0	0	0
<i>Trillochorema</i>	Trichoptera	0	0	0	1	0	1	0	0	0	1	0

## 4. Discussion

### 4.1 COMPARISON OF DIVERSITY BETWEEN BRAIDED AND SINGLE CHANNEL RIVERS

New Zealand braided rivers have been considered to have depauperate invertebrate communities (Percival 1932; Gray & Harding 2007). Previous studies of main channel invertebrates have shown communities dominated by a low number of 'weedy' species, which show refuge-seeking behaviours, flexible life histories and rapid recolonisation mechanisms (Scrimgeour & Winterbourn 1989; Sagar & Glova 1992). In the main channel of the lower Rakaia River, Canterbury, Sagar (1986) found that 96% of invertebrates were larvae of the mayfly *Deleatidium*, and only identified 33 other taxa over 3 years of sampling. Thus, richness and density were described as low. Furthermore, richness and density were strongly negatively related to antecedent flooding. Regular substrate-moving floods are a feature of braided rivers and extreme physical disturbance is thought to reduce taxonomic richness, particularly of more sedentary species. In contrast, single channel rivers tend to have more stable substrates, permanent location of wetted areas and offer greater refuge for more sedentary taxa.

Our analysis of the main channels of braided and single channel rivers supported the above generalisations. However, it was found that the inclusion of hydrologically connected lateral floodplain habitats extended their diversity considerably (Gray et al. 2006; Gray & Harding 2009). In fact, our results indicate that by not sampling a full range of habitats, we may underestimate the diversity within floodplain rivers by 50%. The braided reaches of rivers should therefore be considered to be biodiversity hotspots within the riverscape. If monitoring or biodiversity assessment projects are to correctly determine the biodiversity of braided rivers, it is important that the full range of habitat types present are considered.

### 4.2 TAXONOMIC RICHNESS, DENSITY AND ASSEMBLAGE DIVERSITY ACROSS SPATIAL SCALES

#### 4.2.1 Catchment scale

The 11 rivers included in this survey showed marked variation in taxonomic richness and density, as well as contrasting assemblages that were related to geographical position and topographical hydrology. The five rivers with the highest taxonomic diversity occurred in five separate regions of New Zealand, suggesting that high braided river diversity is an intrinsic feature of the rivers themselves rather than a product of regional variation in taxonomic richness. Interestingly, the rivers with the highest diversity were not necessarily those with the least impacted catchments, a pattern that has been observed previously in a number of aquatic and terrestrial systems (Englund & Malmqvist 1996; Karaus 2004; Luck 2007; Pautasso & Fontaneto 2008). Patterns in regional species

richness are difficult to explain, but dispersal ability and historic opportunities to disperse coupled with regional productivity, habitat diversity plus current and historic land-use impacts are all important (Rosenzweig 1995; Harding et al. 1998). A large-scale survey of New Zealand by Harding & Winterbourn (1997) indicated that climate, geomorphology, biogeography and vegetation cover influence both diversity and community composition. Catchment units have previously been ranked according to their level of human disturbance using the Waters of National Importance (WONI) analysis (Chadderton et al. 2004). This analysis gave each catchment a single natural heritage score, which incorporated measures of environmental representativeness, the presence of threatened species and connectivity to nationally important wetlands, but did not include aquatic invertebrate data due to a lack of available information. Using this analysis, rivers such as the Landsborough in South Westland and Rakaia in Canterbury scored highly in terms of natural heritage (WONI), whereas our data indicate that they would rank poorly in terms of benthic invertebrate richness and the presence of rare taxa. In contrast, the Ngaruroro River in Hawke's Bay scored poorly using WONI but had high invertebrate richness and the greatest number of spatially restricted taxa of any river in our survey. The Wairau River in Marlborough had the greatest taxonomic richness of the braided rivers included in our survey and a high number of spatially restricted taxa, and also scored highly in the WONI analysis. These results highlight the fact that it is not necessarily the most pristine catchments that contain the greatest diversity.

#### 4.2.2 Longitudinal and reach scales

We found no consistent relationship between invertebrate diversity or density and distance along the 11 braided rivers, and no relationship between invertebrate density and reach type. In contrast, Arscott et al. (2005) found weak peaks in diversity at both ends of the Tagliamento River, Italy, and an increase in density downstream. Our results also conflict with the basic tenets of the River Continuum Concept (RCC) (Vannote et al. 1980), which predicts that the highest diversity should be found in the middle reaches of rivers due to increased environmental heterogeneity, and that diversity should be lower in headwaters and lower reaches. However, the RCC considers river orders 1-13, whereas our rivers ranged from order 3 to 7 and therefore can be considered 'middle reaches' in the RCC terminology.

The RCC considers only single channel rivers, whereas the flood-pulse concept (FPC; Junk 1999) extends this concept to include the intermittently inundated floodplain. In large tropical rivers, the primary driver of riverine diversity is thought to be annual inundation of the floodplain; thus, the lower reaches of large rivers should support the highest diversity as they have the largest floodplains. The original concept was developed for rivers with predictable seasonal patterns of floodplain inundation. However, the concept has also been extended to include the floodplain habitats of temperate rivers by including information derived from near-natural proglacial, headwater and lowland floodplains (Tockner et al. 2000). This extension explicitly considers expansion-contraction cycles occurring well below bank-full. Tockner et al. (2000) suggested that diversity might be greatest at intermediate levels of flood and flow pulse, but that there is insufficient evidence to make universal predictions about longitudinal patterns. The role of floodplain inundation and expansion-contraction cycles was assessed in a braided

glacial river in Switzerland by Malard et al. (2006), who found that changes in size, composition and configuration of water bodies affected biodiversity. However, the role of inundation was only considered within a single reach of the Val Roseg River and so cannot be extrapolated along an entire river.

We did not observe any obvious longitudinal diversity patterns in braided rivers, although we did observe some species replacement. Therefore, the predictions of the flood-pulse concept did not appear to apply. The RCC and FPC were proposed for pristine river systems, whereas most of the rivers included in our survey had channelised lower reaches and extensive modifications of their catchments to support pastoral agriculture in particular. The lowland reaches of many New Zealand rivers once incorporated swamps, wetlands, springs and complex groundwater/surface water exchange patterns that no longer exist (Park 2002). A good example of this is the Waimakariri River in Canterbury, which formerly had a diverse lower floodplain extending laterally from its present day mouth to Lake Ellesmere/Te Waihora (Pawson 2002).

#### **4.2.3 Habitat**

Previous studies in New Zealand and elsewhere have found that groundwater-fed channels often contain higher invertebrate richness and density than other floodplain habitats (McCabe 1998; Digby 1999; Burgherr et al. 2002; Gray et al. 2006). This finding contrasts with that of Arscott et al. (2005), who found that invertebrate richness in the braided Tagliamento River, Italy, was lower within three groundwater-fed channels than in the main channel. Furthermore, they found that the density of invertebrates in groundwater-fed channels was intermediate between that of the main channel (high) and a side braid (low). Presumably, in rivers or reaches of rivers where disturbance events are insufficiently intense or frequent to suppress taxonomic richness and density, main channel invertebrate assemblages may be similar to those in lateral habitats. This might account for the high relative invertebrate richness values seen in some main channel habitats in our survey. Conversely, lateral habitats may be regularly disturbed resulting in richness and density in some reaches remaining low relative to the main channel. This might be the case in a channelised river where a minor flood event impacts the entire floodplain habitat assemblage, e.g. the lower Waimakairi River or in the groundwater-fed channels of the Tagliamento River sampled by Arscott et al. (2005).

The lateral habitats sampled in our survey, particularly the spring creeks, had consistently greater taxonomic richness of invertebrates than their adjacent main channels. Therefore, this appears to be a general property of New Zealand braided rivers. The density of invertebrates was also greater in lateral habitats than in the main channels of any given river or reach. These findings have important implications for the bird and fish species that feed within the floodplain. Specifically, the food resource available from a braided river in terms of its capacity to support bird and fish species cannot be assumed from invertebrate density measurements in the main channels alone.

Any discussion of benthic invertebrate communities, particularly in disturbance-driven systems such as braided rivers, must be qualified with some mention of hydrology (Scrimgeour & Winterbourn 1989; Tockner et al. 2006). In general, increased disturbance from substrate-moving flows are associated with a decline in

invertebrate richness and shift in community composition (Death & Winterbourn 1995; Townsend et al. 1997). Floods can be described in terms of timing, duration, magnitude, recurrence and predictability (Poff et al. 1997; Olden & Poff 2003). Each of these factors impacts invertebrate communities and the interpretation of these results. Although all the rivers in this survey were sampled during baseflow conditions, patterns in antecedent flooding must be considered. Seasonal timing of floods—primarily spring in alpine sourced rivers versus winter in foothill rivers (Duncan & Woods 1992)—creates variation in the successional recovery state of different rivers. Thus, foothill rivers sampled in summer have had longer to recover than alpine rivers. Floods of increasing duration and magnitude result in a commensurately greater impact on invertebrate communities, which may be prevented from complete recovery by the recurrence of further flood events. Comparison of river richness values (Fig. 5) and the hydrological data in Table 1 illustrates this relationship. In general, rivers with a greater number of floods and fewer days since the last flood had lower richness, e.g. the Landsborough River. However, antecedent hydrology is not the only environmental factor influencing richness in rivers, particularly when lateral habitats, which may be unaffected by flooding, contribute so highly. The environmental drivers of braided river invertebrate communities and richness will be explored more thoroughly in a subsequent publication.

#### 4.3 SPATIALLY RESTRICTED TAXA

The biodiversity of a habitat or river is not measured solely by the number of taxa present. Rather, consideration needs to be given to which specific taxa are present. Rare or endemic taxa might be accorded a greater conservation value than those that are common, analogous to the way that certain taxa have a higher value when calculating biotic indices such as the Macroinvertebrate Community Index (MCI) (Stark 1985). Regions of high local biodiversity and endemism characterise the New Zealand stream fauna (Harding & Winterbourn 1997; Boothroyd 2000; Harding 2003). For example, trichopteran diversity is highest in central regions and lower at northern and southern extremes of the country (Forsyth & Lewis 1987), Plecoptera are most diverse in the northwest and southwest of the South Island (McLellan 1991), and the diversity of Ephemeroptera declines from north to south (Boothroyd 2000). Furthermore, locally restricted distributions are also common, e.g. among species of *Zelandobius* (Plecoptera) (McLellan 1993). Consequently, many New Zealand taxa have limited distributions, and in some cases these taxa account for diversity differences between habitats, streams and regions, and dictate their conservation values.

The findings of this study suggest that rare taxa are found in all braided rivers and that some of them are endemics. This makes intuitive sense due to the high level of local endemism and restricted distributions nationally. Any regionally based sampling design is liable to reveal taxa unique to that region. However, the majority of taxa found to be spatially restricted were not local endemics, but simply rare. One exception is *Namanereis tiriteae*, a polychaete worm thought to be stygobiotic (subterranean dwelling), which prior to this survey was thought to be restricted to the upper Manawatu River and some easterly flowing streams in Hawke's Bay (Winterbourn 1969; Scarsbrook et al. 2003). The discovery of a

specimen in the Waiapu River extends this polychaete's known range northwards towards East Cape, but the species still appears to be restricted primarily to the east coast of the North Island (Gray et al. 2009). Another example of a regionally endemic braided river taxon is a novel species of Plecoptera found in the upper Rangitata River. *Zelandobius edensis* Gray has subsequently been confirmed as a new species within the confusus-group and has been formally described (Gray 2009). The damselfly *Ischnura aurora* is common in lakes and ponds of northern New Zealand, and was found in a pond within the floodplain of the Waiapu River during our survey. However, this species is a moderately recent immigrant to New Zealand whose potential range expansion may not yet be complete.

The distribution of taxa across the 11 regionally stratified braided rivers we examined indicates that braided rivers contain taxa that are restricted in their spatial occurrence. In some cases, these taxa are likely to be restricted to gravel bed streams (e.g. *Namanereis triteae*), whereas other taxa have also been recorded from other stream types (e.g. the trichopteran *Ecnomina zealandica*). Some taxa that may occur commonly in non-braided streams were found to be rare in the braided rivers (e.g. the burrowing mayfly *Ichthybotus* and the amphipod *Paraleptamphopus caeruleus*).

Rare and restricted taxa also appeared to show an affinity for the braided reaches of rivers as opposed to gorges and headwater channels. Braided reaches are more likely to contain the habitats required by these taxa due to their high physical heterogeneity. Given the broad range of physical habitats considered in our survey, it is not surprising that a number of taxa specific to those habitat types were identified. However, it is particularly interesting that main channel habitats contained comparable numbers of rare taxa to lateral habitats, despite the latter having greater diversity and density of invertebrates. This result affirms and extrapolates on that of Gray et al. (2006), who found that 5 out of 100 taxa were restricted to the main channel of the Upper Waimakariri River.

These insights indicate that it is not easy to identify rivers, reaches or habitats with the greatest biodiversity values. Rare taxa are distributed across all rivers, and most reach types and habitats. Therefore, a holistic approach to river management is almost certainly required.

#### 4.4 IMPLICATIONS FOR CONSERVATION MANAGEMENT

Taxonomic richness and the presence of rare taxa varied considerably across spatial scales, whereas density varied significantly at the river and habitat scales only. The most predictable feature of the braided river systems analysed appeared to be the disproportionate contribution of lateral floodplain habitats to diversity. In the context of understanding dynamic floodplain systems, these results have two main implications.

Firstly, rivers are hierarchical in nature. Habitats are physically nested within reaches, which are themselves nested within rivers within a catchment, and the physical attributes of habitats are regulated by factors operating at greater spatio-temporal scales (Poff 1997). However, local geological and other idiosyncrasies create a discontinuous longitudinal continuum and propagate

physical heterogeneity along rivers, so that physical heterogeneity provides a diversity of habitat for a diversity of organisms and processes to exist. Events within the catchment will have implications for conditions within the river, reach and eventually habitat, within the constraints of local factors.

There is a high degree of inter-dependence between habitats within a reach, mediated by hydrological connectivity, which is a defining feature of floodplain systems (Woessner 2000; Poole et al. 2002, 2004). Consequently, impacts that occur at any given location have the potential to propagate effects to all habitats both up and downstream, and laterally. Our current understanding of braided river floodplains supports the contention that habitats exist in a balance described as a shifting habitat mosaic (Arscott et al. 2000, 2002; Latterell et al. 2006; Malard et al. 2006). Despite high turnover of floodplain elements, the relative proportions of habitats remain constant. Furthermore, constant rates of habitat turnover result in an array of habitats at different successional stages (Ward et al. 2002). The high biodiversity and invertebrate density of braided rivers is dependent upon the physico-chemically diverse, three-dimensional mosaic of successional variable habitats available (Stanford & Ward 1993; Gray et al. 2006). Perturbations within a catchment, river or reach have the potential to alter this equilibrium. Flow alteration and channelisation in particular have been implicated in drastic alterations to the floodplain habitat mosaic and consequent alterations to the biodiversity of floodplains (Ward & Stanford 1995; Claret et al. 1999; Brunke 2002; Hancock 2002; Gilvear 2004; Hauer & Lorang 2004; Hohensinner et al. 2004; Choi et al. 2005). Thus, spatio-temporal hierarchical controls and hydrological connectivity must be made an integral part of management strategies. Units of a river system cannot be treated as discrete entities; rather, the biodiversity of a single reach or habitat is very much a function of the entire catchment.

Secondly, because diversity is spatially and hierarchically variable, conservation managers need to ensure that assessments of biodiversity incorporate hierarchical scales and spatial variability. It is not sufficient to categorise biotic richness or density of a river or reach by taking samples from a limited number of habitats or reaches. The apparently stochastic nature of the spatial distribution of invertebrate communities in braided rivers requires laterally and longitudinally stratified sampling. Otherwise, there is a strong possibility of spurious conclusions being drawn based on inadequate spatial sampling.

## 5. Conclusion

A total of 163 river systems in New Zealand have braided reaches, which account for a total floodplain habitat area of 248 400 ha. The majority of these rivers occur in Canterbury and on the West Coast of the South Island.

Braided rivers have been regarded as species depauperate 'biological deserts' when compared to more stable, single channel streams (Percival 1932). However, when the complete, hydrologically linked habitat assemblage of a floodplain river is considered, the inverse is true. The floodplain reaches of some New Zealand braided rivers can rightly be considered biodiversity hotspots in the greater riverscape, and lateral habitats may contain about 50% of the diversity of the river.

Total taxonomic richness of the 11 braided rivers included in this study was highly variable, but the composition of invertebrate assemblages corresponded broadly to geographical location, source of flow and climate. No consistent longitudinal reach-scale patterns were observed; however, braided reaches contained greater invertebrate diversity than either gorges or headwaters. The braided rivers in this survey did not conform to the theoretical concepts with respect to longitudinal diversity patterns, and it appeared that richness was regulated at the scale of the individual reach in those rivers. The five habitat types considered in this survey all showed highly variable richness values between reaches and rivers. However, the richness of lateral floodplain habitats (spring sources, spring creeks, ponds and side braids) within a specific reach was almost always greater than in the associated main channel, particularly in the case of spring creeks.

A number of taxa were both spatially and numerically rare, and such taxa were found in all rivers, most reaches and most habitats included in our survey. Some of these taxa are regionally endemic and confined to gravel bed streams, but the majority are known throughout the country whilst still being considered rare.

The hierarchical structure and high levels of connectivity that define braided rivers must be incorporated into management strategies. Braided river biodiversity is a function of the constantly shifting habitat assemblage of floodplains, which in turn is regulated by elements nested within the entire catchment, e.g. factors that affect flow and sediment input/transport at the catchment scale, and channel migration at the reach scale.

An assessment of the biodiversity and productivity values of braided rivers needs to incorporate a range of spatial scales in the study design. Because of high levels of variation between rivers, reaches and habitats, extrapolation of findings among these scales should be made with caution.



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# Appendix 1

## REACH TYPES

Figure A1.1. Headwaters. Main channel of the upper Waiapu River, East Cape. Note steep gradient and banks, and the absence of a floodplain or any lateral aquatic habitats.



Figure A1.2. High lateral input, confined reach. The Clyde River at the confluence with the Frances River, Rangitata River system, Canterbury. Note large shingle fans and bedrock bluffs, which influence floodplain topography.



Figure A1.3. Gorge reach.  
The Rangitata gorge,  
Canterbury.



Figure A1.4. Low lateral  
inputs, confined reach. The  
Ngaruroro River opposite the  
'Pig Sty', Hawke's Bay.



Figure A1.5. An impacted reach. The lower Waimakariri River, north of Christchurch, channelised by stopbanks.



# Appendix 2

## PRESENCE/ABSENCE OF INVERTEBRATE TAXA IN THE 11 BRAIDED RIVERS INCLUDED IN OUR STUDY

	WAIAPU	NGARURORO	TUKITUKI	WAIRAU	TARAMAKAU	LANDSBOROUGH	WAIMAKARIRI	RAKAIA	RANGITATA	WAITAKI	ORETI
<b>Ephemeroptera</b>											
<i>Ameletopsis</i>	0	1	0	0	1	0	0	0	0	0	0
<i>Atalopblebtoides</i>	1	1	1	0	1	0	1	0	1	0	0
<i>Austroclima</i>	0	0	0	1	0	0	0	0	0	0	1
<i>Coloburiscus</i>	0	1	1	1	1	0	0	0	1	0	1
<i>Deleatidium</i>	1	1	1	1	1	1	1	1	1	1	1
<i>Ichthybotus</i>	0	1	0	0	0	0	0	0	0	0	0
<i>Mauiulus</i>	0	0	0	1	1	0	0	0	0	0	0
<i>Nesameletus austrinus</i>	0	0	0	0	0	1	0	0	1	0	0
<i>Nesameletus ornatus</i>	0	1	1	1	1	1	1	1	0	1	1
<i>Oniscigaster distans</i>	0	0	0	1	1	0	0	0	0	0	1
<i>Oniscigaster wakefieldi</i>	0	0	0	1	0	0	0	0	0	0	1
<i>Zepblebia</i>	0	0	0	1	1	0	0	0	0	0	0
<i>Neozepblebia scita</i>	0	1	0	0	1	1	0	0	0	0	0
<b>Plecoptera</b>											
<i>Austroperla cyrene</i>	0	1	1	0	1	1	0	0	0	0	1
<i>Cristaperla</i>	0	1	0	0	0	0	0	1	1	0	0
<i>Megaleptoperla diminuta</i>	0	0	1	0	1	0	0	0	0	1	1
<i>Megaleptoperla grandis</i>	0	1	0	0	1	0	1	0	0	0	1
<i>Spaniocerca</i>	0	1	0	1	1	0	1	0	1	1	0
<i>Stenoperla prasina</i>	0	1	0	0	1	0	1	0	0	0	1
<i>Stenoperla maclellani</i>	0	1	0	1	1	0	1	0	0	0	1
<i>Taraperla howesi</i>	0	0	0	0	0	0	1	0	0	0	0
<i>Zelandobius</i>	0	1	0	1	1	1	1	1	1	1	1
<i>Zelandobius pilosus</i>	0	0	0	1	1	0	1	1	1	0	1
<i>Zelandoperla</i>	0	1	1	1	1	1	1	1	1	1	1
<b>Trichoptera</b>											
<i>Aoteapsyche</i>	1	1	1	1	1	1	1	1	1	1	1
<i>Beraeoptera roria</i>	0	1	0	0	0	0	1	0	1	0	0
<i>Costachorema psaroptera</i>	0	0	0	1	1	0	0	0	1	0	1
<i>Costachorema callistum</i>	0	0	0	0	1	0	0	0	0	1	0
<i>Costachorema xanthoptera</i>	0	0	0	1	0	0	1	0	1	1	1
<i>Edpercivalia</i>	0	0	0	0	0	0	0	0	1	0	0
<i>Ecnomina zealandica</i>	0	0	0	0	0	0	0	0	0	0	1
<i>Hudsonema alienum</i>	0	0	0	1	1	1	0	1	0	1	1
<i>Hudsonema amabile</i>	0	1	1	1	1	1	0	1	1	1	1

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	WAIAPU	NGARURORO	TUKITUKI	WAIRAU	TARAMAKAU	LANDSBOROUGH	WAIMAKARIRI	RAKAIA	RANGITATA	WAITAKI	ORETI
<i>Hydrobiosella</i>	1	0	0	0	0	0	0	0	0	1	0
<i>Hydrobiosis chalcodes</i>	0	0	0	1	0	0	0	0	0	1	0
<i>Hydrobiosis charadraea</i>	1	1	1	1	1	1	1	1	0	1	0
<i>Hydrobiosis clavigera</i>	1	0	0	1	1	0	0	0	0	1	1
<i>Hydrobiosis copis</i>	0	1	0	1	1	0	0	0	0	1	1
<i>Hydrobiosis frater</i>	0	0	0	0	0	0	0	1	1	1	0
<i>Hydrobiosis harpidiosa</i>	0	1	0	0	0	0	0	0	0	1	0
<i>Hydrobiosis neadelphus</i>	0	0	0	1	0	0	0	0	1	0	0
<i>Hydrobiosis parumbripennis</i>	1	1	1	1	1	1	1	1	1	1	1
<i>Hydrobiosis silvicola</i> grp	0	0	0	0	0	0	1	1	1	0	0
<i>Hydrobiosis spatulata</i>	0	0	0	1	1	1	0	1	0	0	0
<i>Hydrobiosis soror</i>	1	1	1	1	0	0	0	0	0	1	1
<i>Hydrobiosis torrentis</i>	0	0	0	0	1	0	1	0	0	0	0
<i>Hydrobiosis umbripennis</i>	1	1	1	1	1	1	1	1	1	1	1
<i>Hydrochorema tenuicaudatum</i>	1	1	1	1	1	0	0	1	1	0	1
<i>Helicopsyche</i>	0	0	1	1	1	1	1	0	0	0	0
<i>Neurochorema confusum</i>	0	1	0	1	0	0	0	0	0	0	0
<i>Neurochorema</i>	0	1	0	1	0	0	0	1	0	0	1
<i>Oecetis unicolor</i>	0	0	0	0	0	1	0	0	0	0	0
<i>Oeconesus</i>	0	1	0	1	1	0	1	0	0	1	0
<i>Olinga feredayi</i>	1	1	1	1	1	0	1	1	1	0	1
<i>Oxyethira</i>	1	1	1	1	1	1	1	1	1	1	1
<i>Paroxyethira eatoni</i>	0	1	1	1	1	1	1	1	1	1	1
<i>Paroxyethira hendersoni</i>	0	1	1	1	0	1	1	1	0	1	1
<i>Ptilorbeithrus agilis</i>	0	0	0	1	0	0	0	0	1	0	1
<i>Plectrocnemia maclachlani</i>	1	1	1	1	1	0	1	0	0	1	1
<i>Polyplectropus</i>	0	1	1	1	1	0	1	0	0	1	1
<i>Psilochorema</i>	1	1	1	1	1	1	1	1	1	1	1
<i>Pycnocentria evecta</i>	0	1	1	1	1	0	1	1	1	1	1
<i>Pycnocentria funerea</i>	0	1	0	1	0	0	1	0	1	1	0
<i>Pycnocentrodes</i>	0	1	1	1	1	1	1	1	1	1	1
<i>Traillochorema</i>	0	0	0	1	0	0	1	0	0	1	0
<i>Tiphobiosis</i>	0	0	0	0	0	0	0	0	1	0	0
<i>Triplectides obsoletus</i>	1	1	0	1	1	1	1	1	0	1	1
<i>Triplectides cephalotes</i>	0	1	0	0	0	0	0	0	0	0	0
<i>Triplectidina</i>	0	1	0	1	0	0	0	0	0	0	0
<b>Coleoptera</b>											
<i>Antiporus femoralis</i>	1	1	0	0	0	0	0	0	0	0	0
<i>Antiporus strigosulus</i>	1	1	1	1	1	1	0	1	1	0	1
<i>Berosus</i>	1	1	1	1	1	1	1	1	1	1	1
Elmidae	1	1	1	1	1	1	1	1	1	1	1
<i>Enochrus</i>	0	1	0	0	0	0	0	0	0	0	0
<i>Huxelhydrus syntheticus</i>	1	1	1	1	1	1	1	1	1	0	1
Hydraenidae	1	1	1	1	1	0	0	0	1	0	1
<i>Hyphydrus elegans</i>	1	0	1	0	0	0	0	0	0	0	0
Hydrophilidae	1	1	1	0	0	0	0	0	0	1	0

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	WAIAPU	NGARURORO	TUKITUKI	WAIRAU	TARAMAKAU	LANDSBOROUGH	WAIMAKARIRI	RAKAIA	RANGITATA	WAITAKI	ORETI
<i>Liodessus deflectus</i>	1	1	1	1	1	0	0	0	1	1	0
<i>Liodessus plicatus</i>	1	1	1	1	1	1	1	1	1	1	0
<i>Paracymus</i>	1	1	0	0	0	0	0	0	0	0	0
<i>Podaena</i>	0	0	0	0	0	0	0	0	1	0	0
Ptilodactylidae	0	1	0	1	0	0	0	0	0	0	0
<i>Rbantus suturalis</i>	0	1	0	1	1	1	1	1	1	1	1
Staphylinidae	0	0	0	0	1	0	0	0	0	0	0
Scirtidae	1	1	1	1	1	1	1	1	1	1	0
<b>Diptera</b>											
<i>Aprobila</i>	1	1	1	1	1	1	1	0	1	1	1
<i>Austrosimulium</i>	0	1	1	1	1	1	1	1	1	1	1
Ceratopogonidae	1	1	1	1	1	1	1	1	1	1	1
<i>Corynocera</i>	0	0	0	0	0	1	1	1	0	0	0
Chironominae	1	1	1	1	1	1	1	1	1	1	1
<i>Culex</i>	1	0	1	1	0	1	1	0	1	1	0
Diamesinae	1	1	1	1	1	1	1	0	1	1	1
Empididae	0	0	0	1	0	0	1	0	0	1	1
<i>Ephydrella aquaria</i>	0	0	1	1	1	0	1	0	0	0	0
Eriopterini	1	1	1	1	1	1	1	1	1	1	1
Hexatomi	1	1	1	1	1	1	0	1	1	1	1
<i>Paratimnophila skusei</i>	0	1	1	1	0	1	1	0	0	1	1
<i>Limonia</i>	0	1	0	1	1	0	1	1	1	1	0
<i>Molophilus</i>	1	1	1	1	1	1	1	1	1	1	1
Muscidae	1	1	1	1	1	1	1	1	1	1	1
<i>Neocurupira</i>	0	0	0	0	1	1	1	1	1	1	1
<i>Ochlerotatus antipodeus</i>	0	0	0	0	0	0	1	0	0	0	0
Orthoclaadiinae	1	1	1	1	1	1	1	1	1	1	1
<i>Paradixa</i>	0	0	1	1	0	0	1	1	0	1	1
Pelecorhynchidae	0	1	0	0	0	0	1	1	0	0	0
Psychodidae	1	0	0	1	1	0	0	0	0	0	0
<i>Neolimnia</i>	0	1	0	0	0	0	0	0	1	1	1
<i>Scatella</i>	0	1	1	0	1	0	0	1	0	0	0
Stratiomyidae	1	1	0	1	1	1	0	1	0	1	0
Tabanidae	0	1	1	1	1	0	0	0	0	0	0
Tanyderidae	1	0	0	1	1	0	0	1	0	1	1
Tanypodinae	1	1	1	1	1	1	1	1	1	1	1
<i>Zelandotipula</i>	0	0	0	1	1	0	0	1	0	1	0
<b>Mollusca</b>											
<i>Potamopyrgus</i>	1	1	1	1	1	1	1	1	1	1	1
<i>Gyraulus corinna</i>	1	1	1	1	0	0	0	0	0	1	1
<i>Haitia acuta</i>	0	1	1	1	0	0	0	0	1	1	1
<i>Austropeplea tomentosa</i>	0	1	0	1	1	0	1	0	1	1	1
<b>Crustacea</b>											
Copepoda	0	0	0	0	0	0	1	1	0	0	1
Ostracoda	1	1	1	1	0	0	1	1	1	1	1

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	WAIAPU	NGARURORO	TUKITUKI	WAIRAU	TARAMAKAU	LANDSBOROUGH	WAIMAKARIRI	RAKAIA	RANGITATA	WAITAKI	ORETI
<i>Cruregens fontanus</i>	0	1	1	0	0	0	0	0	0	0	0
<i>Pbreotogammarus</i>	0	1	1	1	1	0	0	1	0	0	0
<i>Paraleptambopus caeruleus</i>	0	0	0	0	0	0	0	0	0	0	1
<i>Paracrangonyx</i>	1	1	0	1	0	0	0	0	0	0	0
<i>Paraleptambopus</i> spp.	1	1	1	1	1	1	1	1	1	1	1
<i>Paratya curvirostris</i>	0	1	1	0	0	1	0	0	0	0	0
<i>Paracalliope fluviatilis</i>	0	1	1	0	0	0	0	0	0	1	1
<b>Others</b>											
<i>Namanereis tiriteae</i>	1	1	1	0	0	0	0	0	0	0	0
<i>Anisops wakefieldi</i>	1	1	1	1	1	1	0	1	1	1	1
<i>Archibauliodes diversus</i>	0	1	1	1	1	0	0	0	0	0	1
Tricladida	1	1	1	1	0	0	1	1	1	1	1
Hirudinea	0	0	1	1	0	0	1	0	0	1	1
<i>Microvelia macgregori</i>	1	1	1	1	1	1	0	0	1	1	0
Nematomorpha	0	0	0	0	0	1	0	0	0	0	0
Oligochaeta	1	1	1	1	1	1	1	1	1	1	1
<i>Prorhynchus</i>	0	0	0	0	0	0	0	0	0	1	0
Acari	1	0	1	1	0	0	1	0	1	1	1
<i>Sigara</i>	1	1	1	1	1	1	1	1	1	1	1
<i>Hygraula nitens</i>	0	1	1	1	0	1	0	0	0	1	1
<i>Musculium novaezelandiae</i>	0	1	1	1	0	1	1	1	0	1	1
<i>Ischnura</i>	1	0	0	0	0	0	0	0	0	0	0
<i>Austrolestes colenonis</i>	1	1	0	1	0	1	1	0	1	1	1
<i>Xanthocnemis</i>	1	1	1	1	1	1	1	1	0	1	1
<i>Procordulia</i>	0	1	0	1	1	1	0	0	0	1	1
<b>Total</b>	<b>56</b>	<b>96</b>	<b>72</b>	<b>99</b>	<b>83</b>	<b>58</b>	<b>72</b>	<b>61</b>	<b>67</b>	<b>81</b>	<b>82</b>

# Appendix 3

## SATURATION ANALYSIS

TABLE A3.1. SATURATION ANALYSIS AT THE A. RIVER, B. REACH, AND C. HABITAT SCALE.

Number of samples is the total number of Surber samples taken in each category. Estimated total richness was calculated in EstimateS (Colwell 2005) using the MMMeans extrapolation. Saturation is the percentage of the estimated total that was observed in each category.

A

RIVER	NUMBER OF SAMPLES	NUMBER OF INDIVIDUALS	OBSERVED RICHNESS	ESTIMATED RICHNESS	SATURATION
Waiaapu	45	3264	45	60	75
Ngaruroro	60	19219	87	104	84
Tukituki	45	16678	65	79	82
Wairau	66	18520	86	101	85
Taramakau	54	7953	77	100	77
Waimakariri	60	7600	59	84	70
Rakaia	57	4255	49	60	82
Rangitata	57	5168	56	74	76
Landsborough	48	2531	42	59	71
Waitaki	57	9198	66	77	86
Oreti	48	14831	73	88	83

B

REACH	NUMBER OF SAMPLES	NUMBER OF INDIVIDUALS	OBSERVED RICHNESS	ESTIMATED RICHNESS	SATURATION
Headwaters	36	6188	54	77	70
High lateral, confined	267	42136	115	121	95
Gorge	27	1991	34	48	71
Low lateral, confined	108	24792	85	98	87
Impacted	138	29946	89	98	91

C

HABITAT	NUMBER OF SAMPLES	NUMBER OF INDIVIDUALS	OBSERVED RICHNESS	ESTIMATED RICHNESS	SATURATION
Main channel	198	24722	84	87	97
Side braid	90	10627	63	71	89
Spring creek	93	28757	95	106	90
Spring source	114	22606	102	118	86
Pond	102	22505	74	83	89

***How taxonomically rich are braided rivers?***

*The invertebrate communities of braided rivers have been described as taxonomically depauperate 'biological deserts'. In this study, surveys of 11 braided rivers incorporating habitat, reach and catchment scales showed that they actually support very diverse invertebrate assemblages when all floodplain habitats are included in the analysis. There is no consistent longitudinal pattern in taxonomic richness or density. However, braided reaches are more diverse than headwater or gorge reaches, and the majority of springs and ponds are more diverse than main channels. Lateral floodplain habitats are thus biodiversity hotspots that need to be included in future sampling designs and management strategies.*

Gray, D.; Harding, J.S. 2010: Spatial variation in invertebrate communities in New Zealand braided rivers. *Science for Conservation* 302. 43 p.