

## Braided river benthic diversity at multiple spatial scales: a hierarchical analysis of $\beta$ diversity in complex floodplain systems

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**Abstract.** Despite the global occurrence of braided rivers and the frequency with which they are anthropogenically modified, the benthic diversity of their floodplains and, in particular, lateral and longitudinal patterns in their communities have been neglected. A spatially nested, hierarchical survey was conducted of 11 braided rivers in the South and North Islands of New Zealand to investigate benthic invertebrate diversity at multiple spatial scales. In each river, 6 reaches and up to 5 floodplain habitat types within each reach were sampled. From a total of 203 sites, 145 taxa were identified. Benthic invertebrate diversity was highly variable at the island, river, reach, and habitat scales. Diversity differences between islands were driven by high regional endemism. Diversity at the whole-river scale ranged from 99 taxa in the Wairau River to only 56 in the Waiapu River. At the reach scale, no significant differences in diversity or abundance were found longitudinally down the rivers. At the habitat scale, lateral floodplain habitats, particularly spring creeks, consistently had greater richness and abundance than did adjacent main channel habitats. Comparisons of Whittaker's multiplicative  $\beta$  at different spatial scales revealed that the greatest range and mean value of taxon turnover was among habitats within reaches. Additive partitioning of  $\beta$  diversity indicated that diversity values at the broad spatial scales of reach and river contributed disproportionately to overall diversity. Our results indicate that river managers concerned with maintaining diversity should focus their efforts at the whole-river scale rather than attempting management of smaller units representing local scales. However, at finer scales, lateral floodplain habitats (particularly springs and floodplain ponds) are hot spots of diversity and protection and remediation of these habitats are particularly important.

**Key words:** biodiversity, New Zealand, braided river, floodplain, benthic invertebrates, beta diversity, additive partition, hierarchy, conservation.

Braided rivers are among the most dynamic and complex of all riverine systems (Ward et al. 2002). They are the products of high-energy environments where variable discharge regimes and heavy sediment loads interact to produce dynamic riverscapes (Bristow and Best 1993). Braided rivers typically have extensive floodplains that are hydrologically connected to the river (Brunke and Gonser 1997, Ward et al. 1999, Woessner 2000), spatially and temporally variable in groundwater–surface water exchanges (Stanford and Ward 1993, Brunke and Gonser 1997, Poole et al. 2002), and have a diverse array of habitats that are in a state of continual successional change (Arscott et al. 2000, van der Nat et al. 2003a). These conditions create a complex 3-dimensional mosaic of heterogeneous habitats along the river and across the floodplain with important consequences for spatial

patterns of benthic invertebrate biodiversity (Ward et al. 2002).

Historically, stream ecologists have viewed braided river channels as unstable ecosystems (Percival 1932) with communities characterized by low species diversity (Sagar 1986) and dominated by a few weedy species (Scrimgeour and Winterbourn 1989). However, a more holistic view of the river, which includes lateral habitats of the wider floodplain and underlying groundwaters, in addition to the main braids, has revealed that braided reaches represent hot spots of biodiversity within the greater riverscape (Stanford 1998, Ward et al. 1999, Arscott et al. 2005, Karaus et al. 2005, Gray et al. 2006).

Braided rivers are common in erosion-prone areas of the world and, although the headwaters of many of these rivers might remain relatively free from human modification, their lower reaches include some of the most severely modified river systems on the planet. In most developed regions, few examples of unmodified

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braided floodplain systems remain (Ward et al. 1999). Internationally, both the surface waters and ground waters associated with braided rivers have been targeted by irrigators and municipal water suppliers (Pringle 2001, Hancock 2002, Malmqvist and Rundle 2002, Young et al. 2004), and many major rivers have been impounded for the generation of hydroelectricity (Nilsson et al. 2005). The negative impact of flow regulation on the morphological and successional diversity of braided river floodplain habitats has been highlighted by several workers (Ward and Stanford 1995, Gilvear 2004, Hauer and Lorang 2004, Hohen-sinner et al. 2004). Flow alterations typically reduce channel-forming flows and longitudinal sediment transport, which in turn reduce the rate of channel migration and habitat turnover. The effect of flow regulation truncates the fluvial system and disconnects the river from its floodplain (Hohensinner et al. 2004). These modifications are generally assumed to have deleterious effects on invertebrate diversity in floodplain river systems, although this assumption has rarely been assessed directly (Karaus 2004).

The multiplicative array of pressures acting upon braided river ecosystems has created an urgent need for baseline ecological data. Species are distributed heterogeneously among habitats, landscapes, and regions, and an understanding of how patterns in taxon occurrence vary across space and spatial scales is essential to preserve extant diversity. For example, controversy over the optimal size or design of nature reserves is driven primarily by a failure to account for scaling differences among organisms (Wiens 1989). Hierarchy theory (Allen and Starr 1982, O'Neil et al. 1986) might provide some insights into spatial variation in diversity in lotic systems (Frissell 1986, Poff 1997), particularly in braided river floodplains (Poole 2002, Thorp et al. 2006). Ward et al. (1999) developed a hierarchical framework to apply the concept of  $\beta$  diversity to floodplain rivers. The concept of  $\beta$  diversity in an ecological context was introduced by Whittaker (1960) to quantify changes in taxon composition and abundance across environmental gradients. Gamma diversity (the regional taxon pool) is a function of the number of taxa in each habitat type ( $\alpha$  diversity) and the turnover of taxa between habitats ( $\beta$  diversity). Ward and Tockner (2001) suggested that identification of significant hierarchical levels or domains might help identify factors that constrain or generate biodiversity. Their framework used Whittaker's multiplicative  $\beta$  ( $\gamma = \alpha \times \beta$ ). Recently, the revival of a parallel calculation of  $\beta$ , the additive relationship ( $\gamma = \alpha + \beta$ ), has enabled the partitioning and direct comparison of diversity across multiple spatial scales (Lande 1996, Veech et al. 2002).

Additive partitions have been applied to stream benthic invertebrates (Allan 1975, Stendera and Johnson 2005), plants in agricultural fields (Wagner et al. 2000), arboreal beetles (Gering et al. 2003), and across 3 variably affected floodplain rivers in Europe (Karaus 2004).

Resource and conservation managers are in need of guidance as to the most efficacious use of their resources for the preservation of extant diversity in braided river systems. For example, are the diversity and communities of all braided rivers in a country the same? Within a river, are there predictable reaches that are of greater ecological value than others? Similarly, are particular habitats within braided rivers of greater relative importance to overall system biodiversity? To address these questions, we investigated the spatial distribution of braided river invertebrate diversity by both multiplicative and additive  $\beta$  analysis at 5 spatial scales (New Zealand, North and South islands, river, reach, and floodplain habitat) and discuss the implications of the observed spatial configurations to conservation and resource management.

## Methods

### *Study area*

New Zealand is a mountainous country with  $>1/2$  its surface consisting of steep, valley-dissected terrain. The alpine spine of New Zealand is aligned perpendicular to the prevailing westerly air flow. Consequently, frequent, extreme, and unpredictable orographic precipitation characterizes the hydrology of New Zealand's rivers and streams. Furthermore, sediment yields for some West Coast rivers are among the highest recorded in the world (Griffiths 1979). Braided rivers are a product of these climatic and topographical conditions, which, along with relatively low levels of anthropogenic impacts, have bequeathed New Zealand with  $>163$  rivers having braided reaches that comprise 248,000 ha of floodplain habitat (Wilson 2001).

### *Site selection, characteristics, and sampling procedure*

Eleven rivers were sampled, 3 in the North Island and 8 in the South Island, distributed in proportion to the abundance of braided rivers within New Zealand (Wilson 2001) (Fig. 1A). The rivers ranged in mean discharge from 44 m<sup>3</sup>/s (Waiapu River) to 370 m<sup>3</sup>/s (Waitaki River) (Table 1), and catchment area ranged from 998 km<sup>2</sup> (Taramakau River) to 11,887 km<sup>2</sup> (Waitaki River). Rivers were further characterized according to hydrology, climate, and vegetation cover

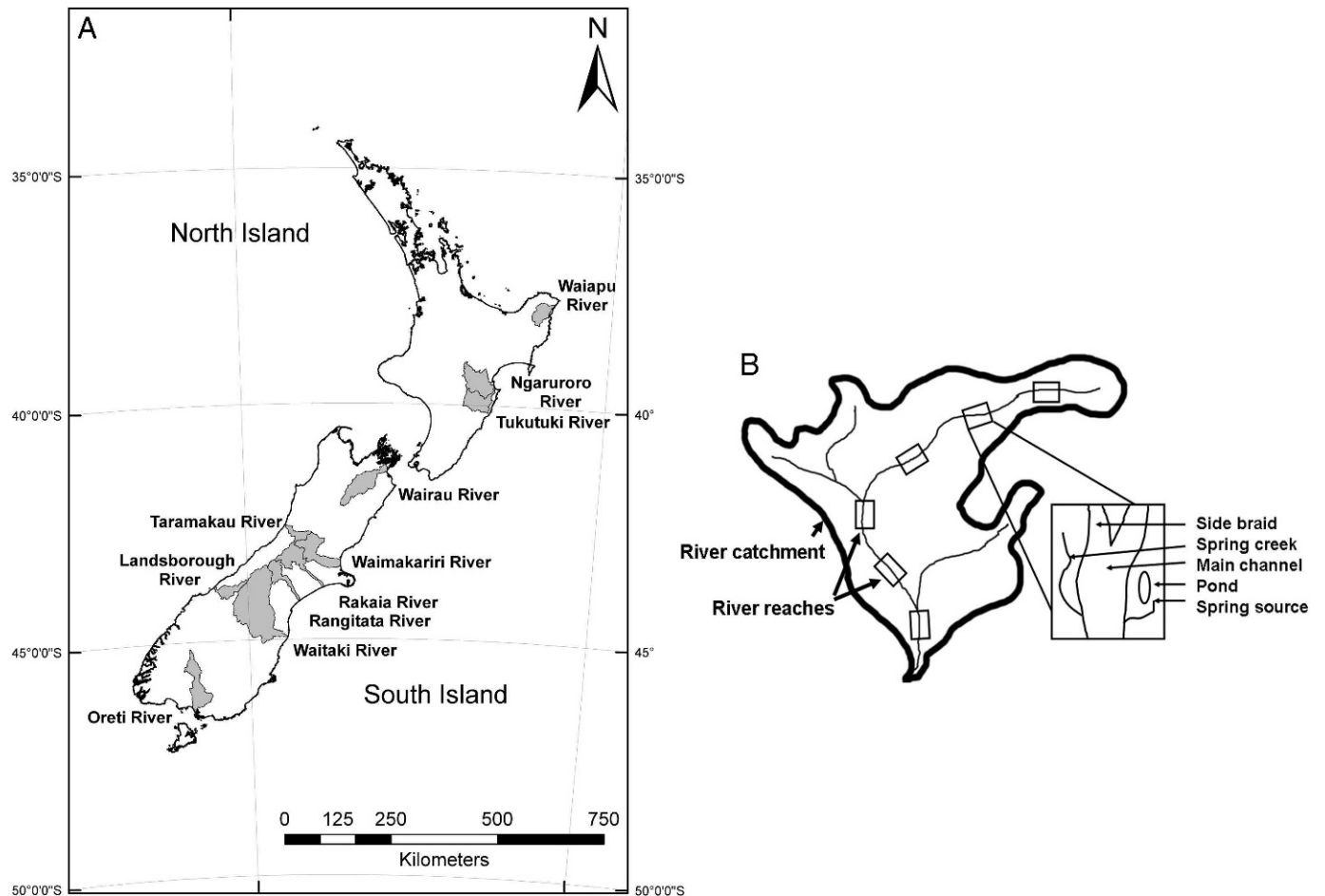


FIG. 1. A.—Eleven braided river catchments included in the survey, 3 in the North Island and 8 in the South Island. B.—Six reaches in each catchment and up to 5 floodplain habitats in each reach were sampled.

TABLE 1. Catchment characteristics of the 11 braided rivers considered in our study. Rivers are ordered north to south, and rivers 1 to 3 are on the North Island. The FRE3 value represents the annual frequency of flows  $>3\times$  the median flow (Clausen and Biggs 1997).

Catchment	Region	Catchment area (km <sup>2</sup> )	River order <sup>a</sup>	Mean discharge (m <sup>3</sup> /s) <sup>b</sup>	FRE 3 excedence	Rain d/y <sup>b</sup>	Catchment vegetation <sup>c</sup>
Waiapu	East Cape	1574	6	82	7.1	19.3	Pasture
Ngaruroro	Hawkes Bay	2009	6	46	10.4	10	Pasture
Tukutuki	Hawkes Bay	2495	6	44	10	7.98	Pasture
Wairau	Nelson-Marlborough	3574	7	99	11.5	13.3	Indigenous forest
Taramakau	West Coast	998	6	150	22.6	64.7	Indigenous forest
Waimakariri	Canterbury	3541	7	128	15.3	17.2	Scrub/tussock
Rakaia	Canterbury	2830	7	175	14.3	24.1	Bare ground
Rangitata	Canterbury	1809	6	109	10.9	26.2	Bare ground
Landsborough	West Coast	1341	6	277	24	81.7	Indigenous forest
Waitaki (upper)	Canterbury	11,887	7	370	9.4	52.1	Bare ground
Waitaki (lower)	Canterbury				0.6	14.1	Scrub/tussock
Oreti	Southland	3513	7	62	13.4	4.9	Pasture

<sup>a</sup> River order (Strahler 1957)

<sup>b</sup> Variables derived from Freshwater Environments of New Zealand (Wild et al. 2005) database correspond to the lowest segment of each river system

<sup>c</sup> Catchment vegetation assigns rivers to 7 categories representing the predominant land cover of the catchment (from River Environment Classification; Snelder et al. 2005)

categories, which were derived from the Freshwater Environments of New Zealand database (Wild et al. 2005) and the River Environment Classification (Snelder et al. 2005). The Waitaki River is highly modified in its lower reaches by a series of impoundments. Therefore, for the sake of characterization, the river was considered to consist of separate entities above and below the dams (Table 1). Rivers were characterized hydrologically using the average number of floods/y that were  $>3\times$  the median flow of the river (FRE3), a criterion that is ecologically relevant to stream biota (Clausen and Biggs 1997). Values ranged from an average of 24 events/y in the Landsborough River to 0.6 in the regulated lower Waitaki River. FRE3 values were generally lower for North Island rivers than South Island rivers, which have more alpine catchments. Rain days per year was highest in rivers on the west coast of the South Island, e.g., the Landsborough and Taramakau rivers, and lowest in the Oreti River in the south of the South Island. In general, South Island rivers experienced more rain days per year than did North Island rivers. Predominant catchment vegetation cover in the North Island was pasture. However, in South Island, catchment vegetation in the northern and western regions was dominated by indigenous forest, whereas catchment vegetation in east coast rivers was mainly scrub and bare ground.

Six reaches,  $\sim 1$  km long, were selected at intervals along each river (Fig. 1B). The uppermost reach was in the steeper headwaters, above the point where a distinct floodplain first appears on a 1:50,000 topographical map. In these reaches, the river was generally 3<sup>rd</sup>–4<sup>th</sup> order (Strahler 1957). The lowest reach was close to the river mouth, beyond estuarine and brackish water zones and above tidal influence. Intermediate reaches were distributed evenly between the uppermost and lowermost reaches. Where present, a gorge reach was included. Anthropogenic impacts generally increased downstream, although variation was considerable among rivers.

A single transect at the approximate midpoint of each reach was established across the entire floodplain. Transects were approximately straight and perpendicular to the main channel. All habitats visible from the transect line were assessed and the most successional mature example of each of 5 habitat types (when present) was sampled (Fig. 1B). Habitat types were main channel, a side braid or secondary channel (with upstream and downstream connection to the main channel), a floodplain pond, a spring source, and a spring creek  $\geq 50$  m downstream from the source of another spring-fed stream.

Biological samples were collected during baseflow conditions between December 2006 and April 2007 and consisted of 3 Surber samples (0.11 m<sup>2</sup>, mesh size 250  $\mu$ m) and a single extensive kick-net (mesh size 250  $\mu$ m) sample (collected with the protocol described in Stark et al. 2001). Kick netting was done for 5 min over a  $\sim 3$ -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  $\mu$ m), where the sampling quadrat was completely enclosed by mesh and invertebrates were washed and agitated into the net by hand.

Samples were preserved in 70% ethanol in the field, concentrated on a 250- $\mu$ m-mesh sieve in the laboratory, and sorted under 40 $\times$  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 and guides of Winterbourn (1973), Chapman and Lewis (1976), Cowley (1978), McLellan (1991, 1998), Winterbourn et al. (2000), Smith (2001), Scarsbrook et al. (2003), and a description by Percival (1945).

### Analysis

For each habitat, invertebrate data from the 3 Surber samples were summed, and for every new taxon found only in the kick-net sample, a single individual was added to the combined taxon list. All subsequent analyses of diversity were done on this data set. However, species accumulation curves and comparisons of abundance were based on quantitative data only. Differences between taxonomic richness and density in habitats and reaches were assessed in SYSTAT (version 10; SPSS, Chicago, Illinois) with ANOVA and Bonferroni post hoc tests. Log( $x$ ) transformations were made when necessary after checking data for normality and residuals for homogeneity of variance.

Species accumulation curves were used to estimate the efficiency of sampling effort at different spatial scales. A species accumulation curve displays the number of observed species as a function of sampling effort (usually samples or individuals). In theory, the curve will reach an asymptote when no further increase in sampling effort returns any new species. Taxon accumulation curves were produced with EstimateS (version 7.5; <http://purl.oclc.org/estimates>).

Whittaker's multiplicative  $\beta$ , regional richness =  $\alpha \times \beta$  (Whittaker 1960), traditionally has been used to quantify rates of change along an environmental gradient (Veech et al. 2002, Magurran 2004), but its

use has been criticized. Specifically, Vellend (2001) showed that Whittaker's  $\beta$  and its derivatives are independent of the distributions of taxa on spatial or environmental gradients, and therefore that  $\beta$  does not reflect "true species turnover" along a gradient. However, in the context of our study, where spatial gradients are of secondary interest to underlying taxonomic heterogeneity, use of the multiplicative suite of  $\beta$  measures is appropriate. Harrison et al. (1992) modified Whittaker's original formula for  $\beta$  diversity to remove the effect of variable  $\alpha$  levels, which influence patterns in  $\beta$ . Therefore, their measure was adopted to remove the variation in  $\alpha$  caused by variable sampling effort at each hierarchical level. Thus, Whittaker's  $\beta_2$  is

$$((\{S/\alpha_{\max}\} - 1/\{N - 1\}))100$$

where  $S$  is richness within the scale of interest +1 and  $\alpha_{\max}$  is the maximum value of  $\alpha$  diversity in the collection of  $N$  habitats/reaches/rivers at that scale. This variation of  $\beta$  measures the amount by which richness at any one spatial scale exceeds the maximum richness of any spatial units nested within it. Values range from 0 to 100, with 0 representing identical diversity and 100 representing total dissimilarity.

The traditional multiplicative  $\beta$  indices produce values of  $\alpha$  and  $\beta$  that are not directly commensurate and, therefore, cannot be compared directly (Veech et al. 2002). When using richness values, taxa are the units of  $\alpha$ , but  $\beta$  is unitless. Furthermore, when using the multiplicative relationship, diversity components are not weighted equally when applied to >1 spatial scale (Gering and Crist 2002). However, the total taxonomic richness in a pooled set of communities/samples/spatial units also can be partitioned into additive components within and among those groups such that total richness and its components have the same units and can be compared directly, e.g., regional richness =  $\alpha + \beta$  (Lande 1996, Crist et al. 2003). Thus, additive partitions can be used to compare directly the contributions across spatial or temporal sampling scales to total richness (Allan 1975, Wagner et al. 2000, Devries and Walla 2001, Fournier and Loreau 2001, Gering et al. 2003, Stendera and Johnson 2005, Ribeiro et al. 2008).

The multiplicative suite of methods and the additive method of calculating  $\alpha$ ,  $\beta$ , and  $\gamma$  are mathematically related measures of diversity (Kiflawi and Spencer 2004, Ricotta 2005), but our use of these indices described different aspects of spatial diversity. Our presentation of Whittaker's relationship was calculated separately at each spatial scale using

richness values. Whittaker's relationship in this context describes heterogeneity in richness values among all habitat units within a spatial scale. The calculation of additive diversity uses abundance data and incorporates all spatial scales and individuals in a single analysis. It essentially describes the greatest spatial scale at which taxa are unique, and hence, which scale contributes most to overall diversity.

Until recently, the use of additive partitioning was primarily descriptive, and statistical methods for testing null hypotheses were lacking. However, the development of an empirical approach, on the basis of randomization, permits a more rigorous evaluation of the arrangement of diversity components across scales (Crist et al. 2003). We used individual-based randomization with the software package PARTITION (Crist et al. 2003) to assess the significance of components. The numbers of individuals and taxa in samples are determined by the random replacement of individuals at the lowest level, while preserving the original species abundance and sample-size distributions. This process was repeated 10,000 times and each randomized data set was then partitioned into its additive components. The probability ( $p$ -value) that a diversity component greater or less than the observed value could have been obtained by chance is obtained from the proportion of null values that are greater or less than the observed value (Crist et al. 2003).

PARTITION calculates the additive components of diversity using taxonomic richness and Shannon and Simpson diversity. As a heterogeneity measure, the Shannon index emphasizes taxonomic richness, but takes into account the degree of evenness in species abundances such that greater values are obtained when the abundances of separate species are equal. In contrast, Simpson's index is a dominance measure weighted toward the abundances of the most common taxa rather than the number of different taxa (Magurran 2004). Taxa were defined as rare or common on the basis of their proportional abundance throughout the entire study (Gering et al. 2003). Rare taxa represented <0.05% of the total number of individuals collected, and common taxa represented >0.05% of individuals. Diversity partitions were done on all rare and common taxa.

## Results

We identified 145 taxa from a total of 203 sites using the combined quantitative and qualitative data set (Appendix; available online from: <http://dx.doi.org/10.1899/08-136.1.s1>); 61 were common taxa and 84 were rare. Most individuals (63%) belonged to 5 taxa,

of which the leptophlebiid mayfly *Deleatidium* and Orthocladiinae (Chironomidae) comprised 44% of all individuals. Chironominae, the gastropod *Potamopyrgus antipodarum*, and Elmidae (Coleoptera) complete the list of the 5 most common taxa overall. Of the 145 taxa, 37 (25%) were unique to the South Island and 9 (6%) were only found in the North Island. Twenty-six taxa were represented by  $\leq 5$  individuals. Among these 26 taxa 8 were represented by single individuals: Trichoptera (3), Plecoptera (1), Odonata (1), Diptera (2), and Coleoptera (1).

River scale

Taxonomic richness ranged from 56 taxa in the Waiapu River to 99 taxa in the Wairau River, and represented 38% and 68% of the entire taxon pool, respectively (Fig. 2A). The 5 rivers with the highest taxonomic richness were in 5 separate geographic regions. All ordinal groups were represented in each river system with the exception of Plecoptera, which were absent from the Waiapu River. Most rivers were dominated by trichopteran taxa, except the Landsborough and Waiapu rivers, which had a greater number of dipteran taxa. The proportions of ordinal groups were similar among rivers despite considerable variation in overall richness. Total number of individuals ranged from ~19,500 in the Wairau and Ngaruroro rivers to <3500 in the Landsborough and Waiapu rivers (Fig. 2B). In terms of relative abundance of individuals, all rivers were dominated by Diptera, except the Ngaruroro, Rakaia, and Waitaki, which contained proportionally more ephemeropterans. The Waitaki River was unusual in having a high proportion of Crustacea (17%), predominantly the amphipod *Paracalliope fluviatilis*, which dominated the impounded lower reaches. This amphipod normally is associated with stable, weedy streams (Chapman and Lewis 1976), but was abundant in the main channel of this modified river.

Reach scale

Taxonomic richness and density did not differ significantly along the river systems (taxonomic richness:  $F_{5,60} = 0.485, p = 0.787$ ; density:  $F_{5,60} = 0.407, p = 0.842$ ; Fig. 3A, B). However, both metrics were highly variable both within and among individual rivers.

Habitat scale

Richness and density varied significantly among habitat types (taxonomic richness:  $F_{4,196} = 9.743, p < 0.001$ ; density:  $F_{4,196} = 5.114, p = 0.001$ ; Fig. 4A, B).

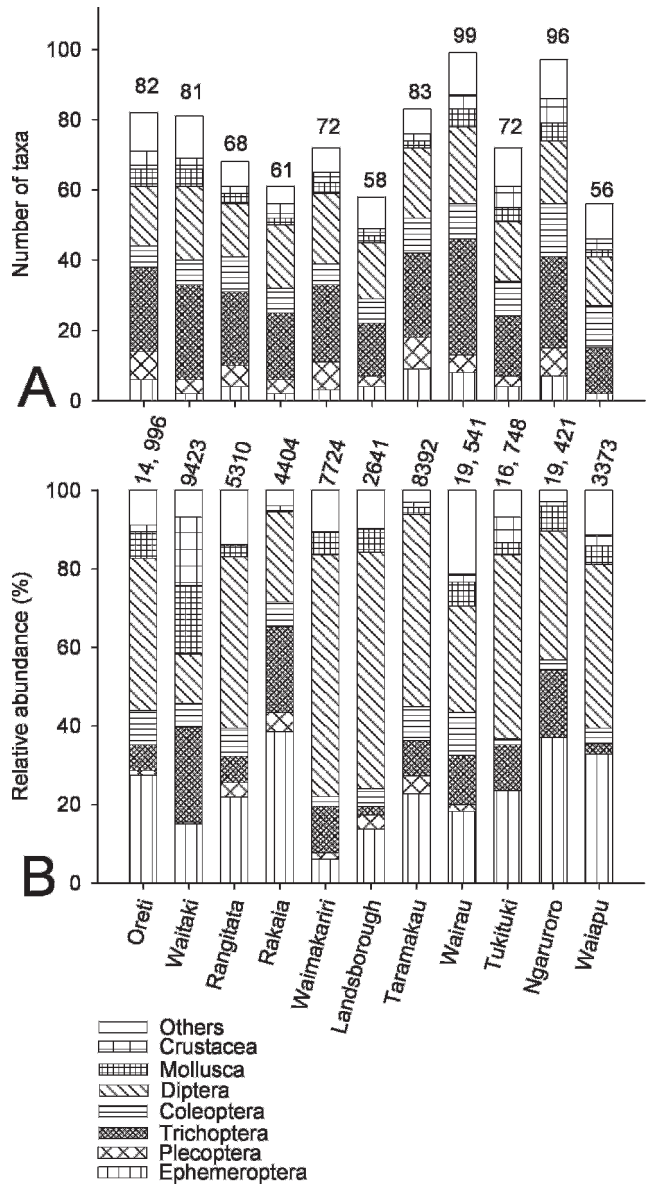


FIG. 2. A.—Taxonomic richness of ordinal (or higher) groups for rivers sampled during austral summer between December 2006 and April 2007. Total taxonomic richness is shown above each bar. B.—Relative abundance of ordinal (or higher) groups collected in each river. Total number of individuals is shown above each bar.

Thus, spring sources, spring creeks, and ponds had greater richness than did main channels, whereas side braids had intermediate diversity. Spring creeks had the highest mean taxonomic richness. Ponds and spring creeks had significantly higher densities than did main channels and side braids.

We calculated the proportional richness of each lateral habitat relative to its associated main channel and then ranked sites within each habitat type for

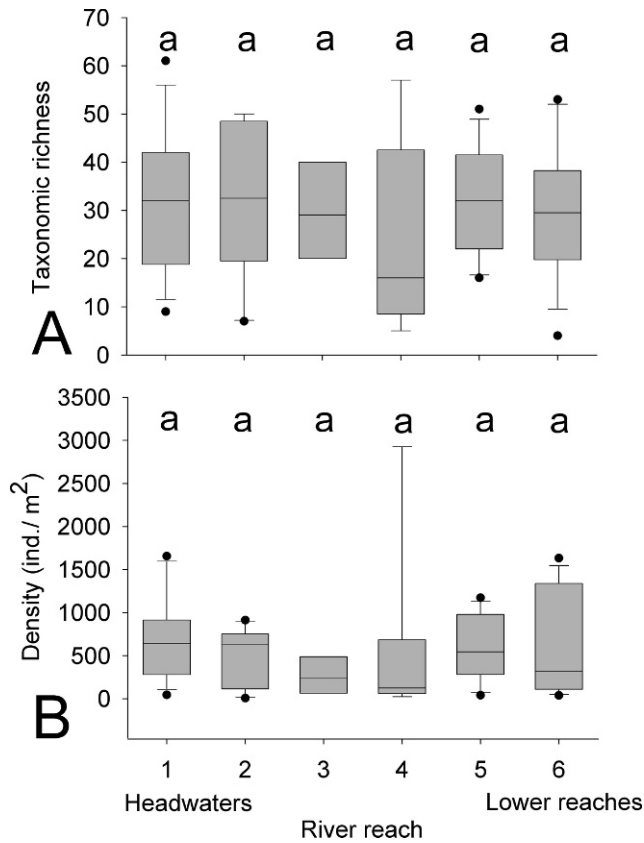


FIG. 3. Reach-scale taxonomic richness (A) and invertebrate density (B). Boxes show medians and 25<sup>th</sup> percentiles, whiskers show the 75<sup>th</sup> percentile, and dots show outliers. Plots with the same letter are not significantly different (Bonferroni post hoc test,  $p > 0.05$ ).

clearer presentation (Fig. 5A). Sites with a proportional richness  $>1$  had more taxa than did the adjacent main channel. Over 70% of lateral floodplain habitats had greater invertebrate richness than did their associated main channel. All spring creeks (except 1) had more taxa than did their associated main channel, but ponds, spring sources, and side braids were more variable in relative taxonomic richness with 74, 76, and 75% of sites, respectively, having a higher diversity than did the main channel. Three ponds had  $>4\times$  as many taxa as did the nearby main channel. Taxonomic richness in lateral habitats never was  $<1/2$  the richness found in the main channel, a result that suggested that main channels might represent the lower limit for floodplain diversity in braided rivers. Of the lateral habitats, 73% contained a higher density of invertebrates than did their associated main channel (Fig. 5B). Specifically, 84% of spring creeks, 66% of spring sources, 68% of ponds, and 75% of side braids had higher densities than did the main channel.

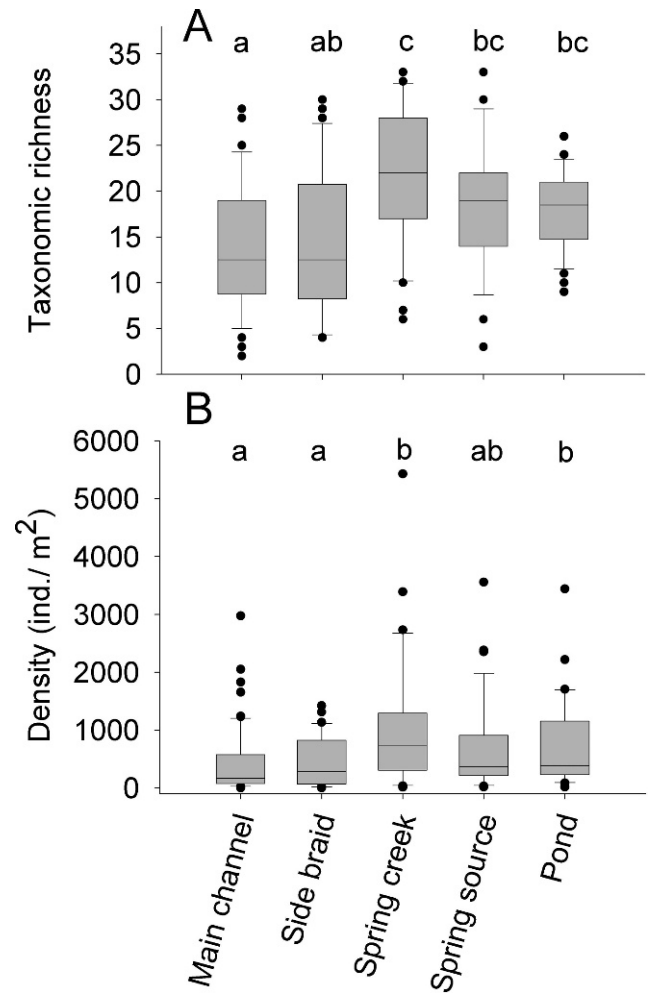


FIG. 4. Floodplain habitat-scale taxonomic richness (A) and invertebrate density (B) in 5 habitat types sampled across 6 reaches of 11 braided rivers. Boxes show medians and 25<sup>th</sup> percentiles, whiskers show the 75<sup>th</sup> percentile, and dots show outliers. Plots with the same letter are not significantly different (Bonferroni post hoc test,  $p > 0.05$ ). Density was  $\log(x)$  transformed to meet assumptions of normality required by a parametric ANOVA, but actual values are shown on the plot.

*Sampling efficiency*

Taxon accumulation curves for individual rivers did not reach asymptotes, results that indicate that our sampling within rivers was unlikely to have encompassed their full taxonomic diversity (Fig. 6). In contrast, the accumulation curve for the South Island approached an asymptote indicating that the 151 samples from 8 rivers provided a strong estimate of total taxonomic richness. The North Island curve (3 rivers) followed a similar trajectory as did that for the full survey of 11 rivers.

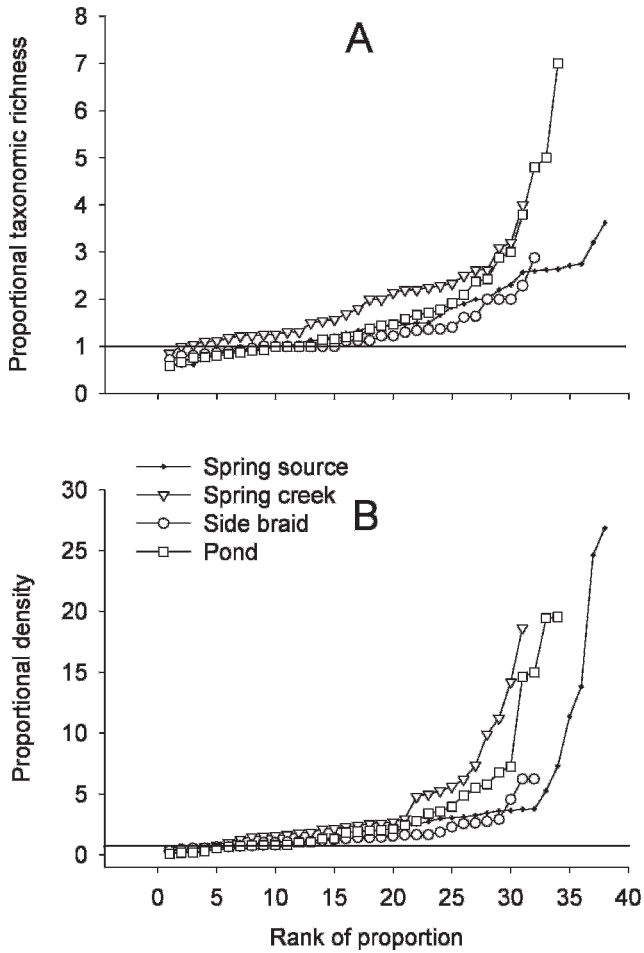


FIG. 5. Taxonomic richness (A) and invertebrate density (B) in lateral floodplain habitats expressed as a proportion of values in their associated main channel. Each point in A represents values from 3 Surber samples and a kick-net sample; each point in B represents values from 3 Surber samples. Proportions have been ranked within each habitat type for clearer presentation.

*Whittaker's  $\beta$  diversity*

The richness ( $\alpha$ ) of hierarchical units increased with increasing spatial scale, i.e., at higher levels of the hierarchy (Fig. 7A). The range and variability of taxonomic turnover ( $\beta_2$ ) also varied across spatial scales (Fig. 7B) and was highest among floodplain habitats at the reach scale. This result indicated that floodplain habitats were more different from each other in taxonomic richness than were units at higher levels of the hierarchy. Taxonomic turnover between islands was marginally higher than mean turnover within an island and reflected the high number of taxa endemic to each island. Thus, of the 145 taxa, 25% were unique to the South Island and 6% were only found in the North Island.

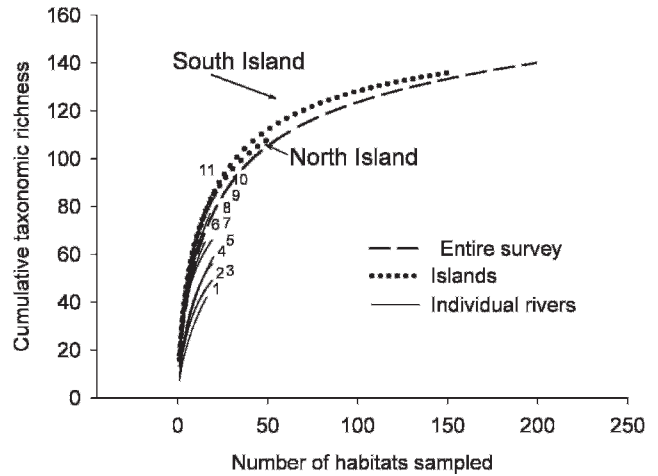


FIG. 6. Taxonomic richness accumulations curves from 201 braided river habitats, sampled across 11 rivers, 2 islands (North and South islands), and all data combined. Rivers are: 1) Landsborough, 2) Waiapu, 3) Rakaia, 4) Rangitata, 5) Waimakariri, 6) Tukituki, 7) Waitaki, 8) Oreti, 9) Taramakau, 10) Wairau, and 11) Ngaruroro.

*Additive diversity partitioning*

Additive partitions for the island ( $\beta_4$ ) and river ( $\beta_3$ ) scales were consistently greater than expected for total, rare, and common taxa (Table 2). Concomitantly, the within-habitat ( $\alpha$ ) component was consistently less than expected. These patterns were evident across all taxonomic groups and indices despite the fact that the  $\alpha$  component of common taxa was a substantial proportion (28%) of overall diversity (Fig. 8) and a large proportion of the Shannon (54%) and Simpson (74%) diversity (Fig. 9). Higher values of Shannon's index are obtained when both richness and evenness are high, whereas Simpson's index is weighted toward the abundance of dominant taxa (Fig. 9). The differences between  $\alpha$  values for richness and Shannon's and Simpson's indices are a measure of the extent to which communities are dominated by common taxa.

We also found differences in the relative proportions and significances of diversity values between all taxa, rare taxa, and common taxa across the hierarchical model (Fig. 8). For the entire community, the observed  $\beta_2$  (turnover among reaches) was not significantly different from the expected proportion derived from randomization (Table 2). However, for rare taxa,  $\beta_2$  was less than expected, and for common taxa, it was greater than expected (Table 2). The result for rare taxa suggests that turnover of rare taxa is low among reaches within rivers. In contrast, turnover of common taxa was greater than expected, a result that suggested that composition of communities varied

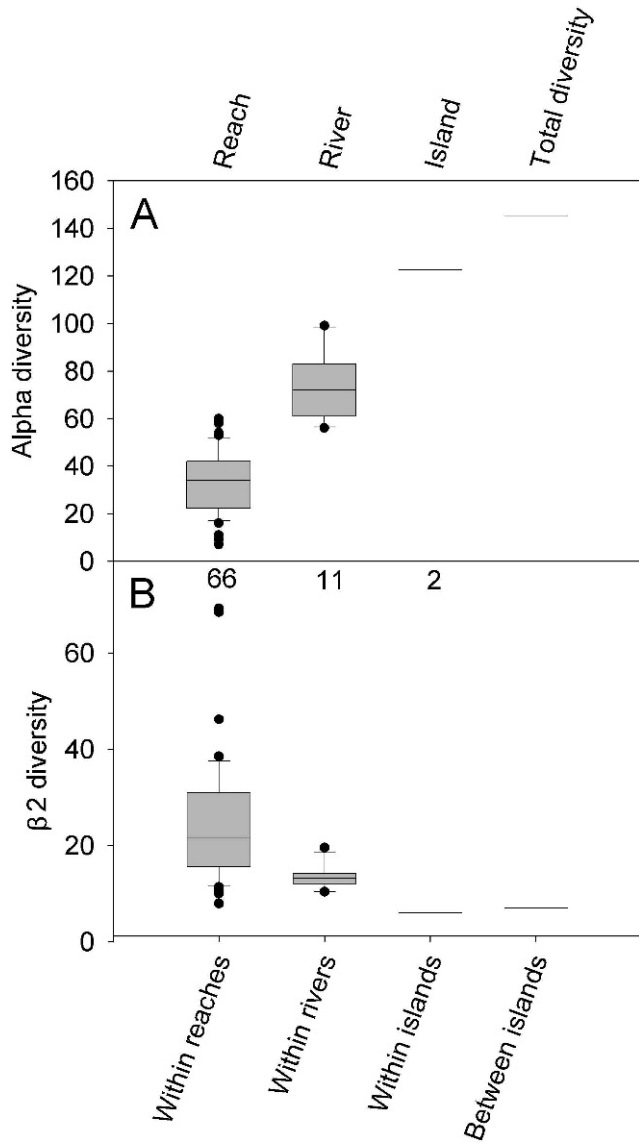


FIG. 7. Alpha richness (A) and Whittaker's  $\beta_2$  (B) for benthic invertebrates at 4 spatial scales. Boxes show medians and 25<sup>th</sup> percentiles, whiskers show the 75<sup>th</sup> percentile, and dots show outliers. The number of  $\beta$  calculations at each scale is marked along the midline of the graph.

significantly among reaches. Diversity among all taxa was spread relatively equitably between  $\beta_2$  and  $\beta_3$ , whereas for rare taxa, it was allocated to  $\beta_3$  and for common taxa, to  $\beta_2$  (Fig. 8).

**Discussion**

Braided rivers are regarded as hostile environments that should be characterized by depauperate aquatic invertebrate communities (Percival 1932, Tockner et al. 2006). Studies done in the main channel of braided

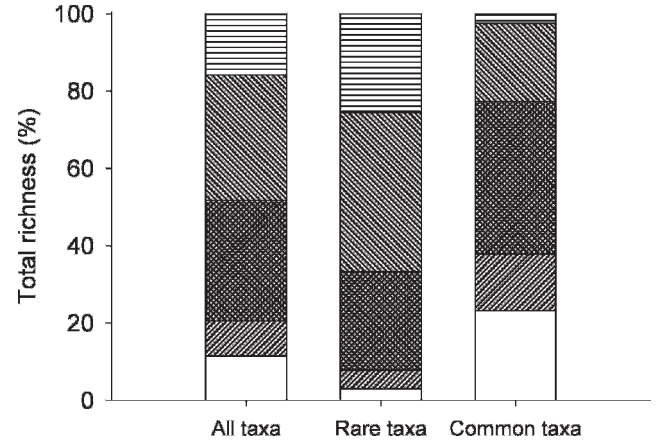


FIG. 8. Percentage of total benthic invertebrate richness explained by  $\alpha$  and  $\beta$  at 4 spatial scales. The contribution of each spatial scale to total richness was determined by additive partitioning. The total numbers of taxa are shown above each bar.

rivers have found communities dominated by a low number of weedy species that have refuge-seeking behaviors, flexible life histories, and rapid recolonization mechanisms (Scrimgeour and Winterbourn 1989, Sagar and Glova 1992, Arscott et al. 2003a, b). However, recent research incorporating lateral floodplain habitats has demonstrated potentially high richness and productivity of these habitats within the greater riverscape (Karaus 2004, Gray et al. 2006) and shows that floodplains might have high overall richness that can be important regionally (Burgherr et al. 2002, Tockner and Stanford 2002). The high species richness of some braided river floodplains appears to be the result of high floodplain habitat heterogeneity maintained by a shifting habitat mosaic driven by fluvial dynamics (Arscott et al. 2002, van der Nat et al. 2003a). Floodplains maintain high hydrological connectivity between a 3-dimensional array of physically and successional diverse aquatic habitats (Stanford 1998, Poole et al. 2002, Ward et al. 2002, Hauer and Lorang 2004). However, consistency in patterns of diversity and abundance across multiple reaches, rivers, and regions has not been considered.

The 11 rivers in our survey showed marked variation in taxonomic richness and absolute and relative abundances of macroinvertebrates. The variation in taxonomic richness reflects, to some degree, the high level of regional endemism of New Zealand stream invertebrates (Harding et al. 1997, Boothroyd 2000). However, the primary influence on river community structure is more likely to be the physical characteristics of each river system than endemism (Winterbourn et al. 1981). Thus, the 11 rivers differed in terms of catchment-scale variables, such as mean

TABLE 2. Significance tests of observed diversity estimates against null estimates derived from 10,000 additive partition randomizations. Values were partitioned among islands ( $\beta_4$ ), rivers ( $\beta_3$ ), reaches ( $\beta_2$ ), and habitats ( $\beta_1$ ), and within habitats ( $\alpha$ ). Significance was determined at the 0.05 level. + = diversity greater than expected, - = diversity lower than expected, ns = not significant. Simpson and Shannon diversity were not tested for common and rare taxa only.

Group	Level	Richness	Simpson	Shannon
Entire community	$\beta_4$	+	+	+
	$\beta_3$	+	+	+
	$\beta_2$	ns	+	+
	$\beta_1$	-	+	+
	A	-	-	-
Rare taxa	$\beta_4$	+		
	$\beta_3$	+		
	$\beta_2$	-		
	$\beta_1$	-		
	A	-		
Common taxa	$\beta_4$	+		
	$\beta_3$	+		
	$\beta_2$	+		
	$\beta_1$	-		
	A	-		

discharge, flow regime, climate, and vegetation characteristics. Direct linkages are difficult to quantify, but numerous conceptual models and field-based studies have indicated biological responses to catchment-scale variables (Poff 1997, Harding et al. 1998, Townsend et al. 2003, 2004, Death and Joy 2004). In particular, antecedent flooding has a strong effect on invertebrate community structure in the main channels of braided rivers in New Zealand and Italy (Sagar 1986, Arscott et al. 2003b).

The braided river reaches included in our study showed no consistent longitudinal patterns in richness or density, which were highly variable both within and among reaches. This result suggests that community structure (richness and abundance) might be more strongly regulated by physicochemical conditions at the reach scale within rivers than by predictable changes along the river. In a study of Trichoptera diversity in 2 headwater floodplains, Arscott et al. (2003a) suggested that both habitat and the Trichoptera assemblage were dependent on reach-scale factors that were uncoupled from position in the longitudinal continuum. A predictable downstream pattern in diversity might occur in a single-channel river (Vannote et al. 1980), but such a pattern is likely to be confounded in braided rivers by the influence of discontinuities, such as gorges, that alternate with physically diverse braided reaches, much like "beads on a string" (Stanford and Ward 1993, Ward and

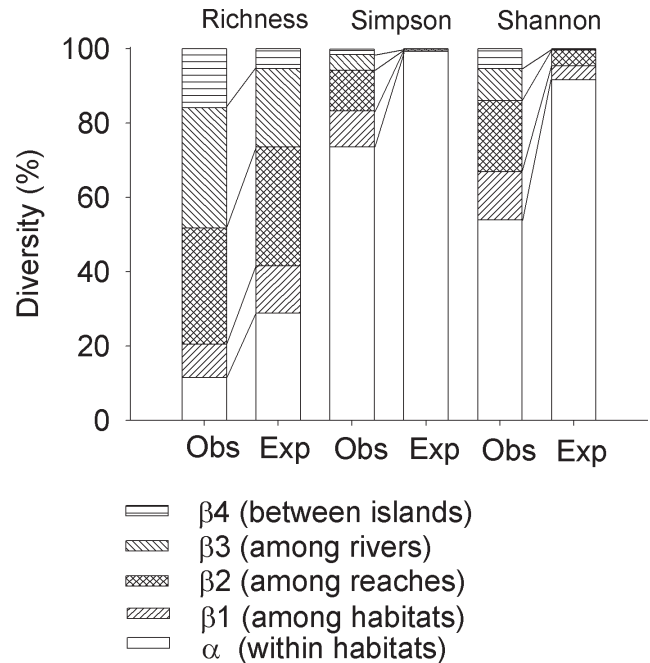


FIG. 9. Percentage of total richness and Shannon and Simpson diversity explained by  $\alpha$  and  $\beta$  components of richness at 4 spatial scales. Observed (obs) and expected (exp) components were calculated by additive partitioning of diversity. Expected components were based on the distributions of 10,000 individual-based randomizations. Linking lines illustrate the relationship between observed and expected components.

Stanford 1995). Hence, the reach-specific morphology of braided rivers has been linked to the degree of constriction by valley sides and the presence of protruding bluffs and tributary fans (Stanford and Ward 1993). Characteristics of floodplain vegetation also have been strongly implicated as influencing floodplain morphology, particularly channel form and diversity (Huang and Nanson 1997, Millar 2000, Gran and Paola 2001). Furthermore, large woody debris derived from eroded floodplain vegetation has been linked to habitat diversity within a river reach and tends to be more prominent in the headwaters, at least of the braided Tagliamento River, Italy (Gurnell et al. 2002, van der Nat et al. 2003b).

Several previous studies have reported that groundwater-fed floodplain channels had higher invertebrate richness than did main channels (McCabe 1998, Burgherr et al. 2002, Gray et al. 2006). These findings contrast with those of Arscott et al. (2005), who found that invertebrate richness was lower in 3 groundwater-fed channels than in the main channel of the Tagliamento River. In rivers where disturbance events are insufficiently intense or frequent to suppress taxonomic richness, such as many

impounded rivers, main-channel diversity values might be similar to or greater than values in lateral habitats (Karaus 2004). Low levels of disturbance might account for the relatively high invertebrate richness seen in some main-channel habitats in our study. Conversely, some lateral habitats might have been recently disturbed, with the result that diversity values were similar to or lower than those in the adjacent main channel. Recolonization of discrete lateral habitats, such as ponds and springs, might be slower than in the main channel because they lack upstream colonists.

Our finding that Whittaker's  $\beta$  values were greater within reaches than at any larger scale is indicative of the diversity of habitat conditions known to occur across the floodplains where strong gradients in environmental conditions are found between main channels and lateral habitats (Arscott et al. 2000, 2001, Karaus et al. 2005, Tockner et al. 2006, Gray and Harding 2007). Consequently, different habitats support distinct assemblages of invertebrates, including taxa that are unique to them (Gray et al. 2006). The high level of turnover among habitats within reaches emphasizes the importance of lateral habitats to overall braided river diversity.

Additive diversity partitioning showed that  $\beta$  diversity was consistently greater at larger spatial scales and confirmed that there were strong regional effects on the richness and composition of braided-river communities. These differences might be caused partly by regional endemism, but they also might be driven by catchment-scale physical characteristics of each river. The partitioning results for all taxa combined were similar to those for rare taxa, a result that suggested that rare species were driving patterns of the entire community. This result is not surprising because rare species accounted for 58% of all taxa found. The large number of rare taxa found in our study produced the relatively large, broad-scale components of diversity in the partitions, as exemplified when rare taxa were removed for the common taxa analysis. These rare taxa were unique to the broadest scale of the analysis to which they were allocated.

Despite the sampling intensity of our study, accumulation curves did not approach an asymptote at the reach or river scale and suggest that we did not quantify the entire diversity of any river system. This finding has implications for the design of conservation inventories that seek to produce a comprehensive list of taxa present in a region or system of interest. The best way to achieve such a goal is through intensive sampling of a limited area, but some rare taxa that would be found in a more spatially intensive

survey are still likely to be missed (Gering et al. 2003). The disproportionate accumulation of rare taxa at broad spatial scales and the failure to saturate accumulation curves suggest that obtaining complete inventories is an unrealistic goal.

Contrasting patterns of diversity partitioning between taxon richness and Simpson's and Shannon's indices can be explained by patterns of taxon rarity and abundance. The contrast between partitioning of richness and dominance/evenness illustrated the extent to which small spatial scales were dominated by common taxa, a finding consistent with existing knowledge of braided-river communities, particularly the main channels of New Zealand rivers (Scrimgeour and Winterbourn 1989).

#### *Implications for conservation management*

Our findings have 2 major implications for the preservation of extant biodiversity in braided river systems. First, the disproportionate contribution of broad spatial scales to overall diversity suggests that a focus on the large scale is most appropriate for the retention of rare taxa. Overall diversity will be best protected by safeguarding whole reaches and catchments rather than attempts at management of local-scale habitats. This point is particularly pertinent for braided rivers where many of the individual habitats in a reach are naturally transient or regularly disturbed (Reinfelds and Nanson 1993, Arscott et al. 2002). Reach-scale management approaches also must be considered within a holistic framework because of the nonindependence of reaches within a river system and because disturbances, such as impoundment, can be transmitted both up- and downstream (Ward and Stanford 1995, Pringle 1997). Thus, the basic conservation unit needs to be the river and its catchment. The spatial scales of importance for rare taxa (reach and river) also encompass the scales of relevance for common taxa (reach and habitat). Therefore, management targeting the diversity of rare taxa should maintain the overall functionality of stream communities. However, this strategy is almost certainly a false panacea. We might aspire to preserve the entire diversity of an appropriate selection of rivers, but the implications of the complete loss of functionality, the ecosystem services of invertebrate communities, in all unprotected streams require that the 2 issues be kept separate.

Second, a general property of braided rivers is that greater taxonomic richness and invertebrate density occur in lateral habitats rather than main channels. For example, Karaus (2004) found that >50% of overall diversity in the Tagliamento River was

contributed by lateral habitats, and we found that >75% and >73% of lateral habitats contained greater richness and abundance, respectively, than did their associated main channels. In terms of conservation of biodiversity, the value of these lateral habitats cannot be overstated (Arscott et al. 2005).

Last, conservation managers need to ensure that assessments of biodiversity are made at the appropriate spatial scales because of the spatial and hierarchical structure of diversity in braided rivers. Categorizing the diversity of a river system on the basis of the assessment of a single reach or main channel habitat is not sufficient. The spatial diversity of braided rivers requires that sampling be stratified laterally and longitudinally to reduce the possibility of drawing spurious conclusions.

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