

# Food webs in tropical Australian streams: shredders are not scarce

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## SUMMARY

1. Macroinvertebrates were collected in dry and wet seasons from riffles and pools in two streams in tropical north Queensland. Total biomass, abundance and species richness were higher in riffles than in pools but did not differ between streams or seasons.
2. Gut contents of all species were identified. Cluster analysis based on gut contents identified five dietary groups: I, generalist collectors; II, generalist shredders and generalist predators; III, generalist scrapers; IV, specialist shredders; and V, specialist predators. Species were allocated to functional feeding groups (FFGs) based on these dietary groups.
3. Many species were generalist in their diets, but specialist predators and shredders were particularly prominent components of the invertebrate assemblages in terms of biomass and species richness.
4. Community composition (proportions of biomass, abundance and species richness of the different FFGs) varied between habitat types, but not between streams or seasons, although differences between riffles and pools varied with season.
5. Comparison of the fauna of 20 streams showed that our study sites were similar to, or not atypical of, low-order streams in the Queensland wet tropics.

*Keywords:* functional feeding groups, gut content analysis, latitude, macroinvertebrates

## Introduction

Food webs in forest stream ecosystems are typically driven by allochthonous organic inputs, mainly leaf litter, as the main energy source (Kaushik & Hynes, 1971; Vannote *et al.*, 1980). In streams, leaf litter is readily leached, colonized and decomposed by microorganisms, and consumed by macroinvertebrate shredders (Gessner, Chauvet & Dobson, 1999). These processes lead to production of fine particulate organic matter (FPOM), which is consumed by a suite of collector organisms. The shredders and collectors are thus the major primary consumers in forest streams, providing the main link between the organic inputs and the predatory invertebrates and vertebrates.

The phenomenon of leaf processing by macroinvertebrate shredders has been extensively studied in temperate streams, where a numerically important shredder guild, comprising especially stoneflies and caddisflies, exists. Leaf decomposition rates have been shown to depend on a range of factors, including physicochemical characteristics of the water, the conditioning of leaves by microbial colonization, and feeding preferences of shredders (Graça, 2001). Much of this activity takes place in the cooler seasons, following major leaf fall in the autumn and continuing processing of accumulated litter through winter.

These patterns have been particularly well described in the temperate zone but, as is often the case, there are fewer published studies on tropical systems. Tropical rainforest streams may receive comparable leaf litter inputs to their temperate counterparts (Benson & Pearson, 1993; Dobson *et al.*, 2002), but some differences exist. For example, in the Australian wet tropical rainforests, the peak of litter fall occurs in

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the warmer seasons, but there is continuous supply of litter throughout the year (Benson & Pearson, 1993). In tropical forests, species diversity of the riparian vegetation is much higher than in temperate zones, and many tree species may contain substantial quantities of toxic compounds (Nolen & Pearson, 1993), so that litter quality and processing rates might be expected to differ between tropical and temperate systems.

There has been little comparison of leaf processing across latitudes, but recent literature suggests that shredders are scarce in tropical streams (Dobson *et al.*, 2002). Most of the common shredder taxa from temperate systems are lacking in the tropics, including filipalpiid stoneflies (Taeniopterygidae, Nemouridae, Leuctridae and Capniidae) and some caddisflies (Limnephilidae and Sericostomatidae). Moreover, it has been suggested that shredding may be less important in tropical systems because there are alternative decomposition pathways for leaves, such as faster microbial processing due to higher temperatures (Irons *et al.*, 1994), and because of the high concentration of toxic compounds in leaves (Wantzen *et al.*, 2002). However, there is evidence that shredders are not as scarce in the Australian tropics as in other tropical areas and that much litter processing is carried out by macroinvertebrates (Pearson *et al.*, 1989; Pearson & Tobin, 1989; Nolen & Pearson, 1993), although processing rates can differ substantially between leaf species (Pearson & Tobin, 1989), and microbial processing can be very important (Pearson *et al.*, 1989; Pearson & Connolly, 2000).

Theories of ecosystem function have typically been derived from detailed studies of temperate systems (Boyero, 2000), and consideration of tropical systems has been either excluded, or included as an interesting anomaly, despite the tropics occupying the largest land area of the world's climatic regions (Dobson *et al.*, 2002). In particular, there have been few studies of the functioning of tropical stream ecosystems, or of the detail of food webs, that would allow systematic comparisons. For example, the allocation of species to functional feeding groups (FFGs) in the tropics usually relies on information from related temperate species, and almost no analysis of gut contents or mouthparts of tropical species has been performed. Exceptions include Hearnden & Pearson (1990), who examined diets of tropical Australian mayflies as part of a study of niche partitioning (Hearnden & Pearson,

1991). Similarly, comparisons of food web statistics among streams are mostly concerned with temperate systems (e.g. Jaarsma *et al.*, 1998; Schmid-Araya *et al.*, 2002).

In this study, we examined the community composition and diets (gut contents) of macroinvertebrate communities in riffles and pools of two Australian tropical rainforest streams in order to: (1) describe food webs and compare them with webs from streams elsewhere, both with respect to their binary characteristics and to the importance of the major links; (2) determine the relative abundance of the different FFGs in comparison with published data from other tropical and temperate streams, and confirm that shredders are not scarce in Australian tropical rainforest streams; and (3) examine the spatial and temporal variation of the relative numbers of the different FFGs.

## Methods

### *Study sites*

The study sites were Birthday Creek (18°59'S, 146°10'E) and Camp Creek (18°58'S, 146°10'E), third-order upland rainforest streams, located near the township of Paluma at about 800 m a.s.l. in the Burdekin River catchment, north-eastern Queensland. The climate of the area consists of hot moist summers and cool-warm drier winters. Approximately 70% of annual rainfall occurs during the wet season (December–March), although rainfall is typically recorded in every month.

Two riffles and two pools were sampled in each stream. Physical characteristics of sampling sites are summarised in Table 1. Both streams consist of a series of alternating riffles and pools, with granite rock and stones dominating the substratum, interspersed with patches of sand and leaf litter, and substantial accumulation of leaf litter in pools and the slower parts of riffles. Base-flow width, depth and current velocity were greater in the wet season (February), which also experienced minor spates during the study period, but no major flooding.

### *Field methods*

Each study site was sampled in the late dry season (October–November 1996) and the wet season (Feb-

**Table 1** Physical characteristics of the study sites in Birthday Creek and Camp Creek. Ranges shown for channel width, water depth and maximum current velocity represent maximum base-flow values for October and February respectively.

	Birthday Creek				Camp Creek			
	Riffle 1	Riffle 2	Pool 1	Pool 2	Riffle 1	Riffle 2	Pool 1	Pool 2
Riffle/pool length (m)	10	15	9	26	6	9	9	30
Channel width (m)	1–2	1–5	3–6	5–7	2–3.5	2.5–4	3–5	6–8
Water depth (cm)	10–50	10–50	10–30	50–100	20–50	15–50	70–150	1–150
Max current vel (cm s <sup>-1</sup> )	40–100	25–50	1–5	0–1	20–50	20–50	0–1	0–1
% Canopy cover	60	5	80	60	80	60	85	60
Substratum composition*								
% Boulder	30	0	0	10	15	25	20	25
% Cobble	60	85	80	10	75	20	25	20
% Gravel	5	5	10	5	5	5	5	5
% Sand	5	10	10	75	5	50	50	50

\*Excluding leaf litter.

ruary 1997). For each study site and sampling occasion, three benthic samples were taken at random 50 × 50 cm locations from each pool and riffle, using a 250 µm mesh dip net. In riffle samples, the substratum sampled was stones, sand and leaf litter; in the pool samples, leaf litter predominated. Samples were preserved in 70% ethanol and invertebrates were later sorted and identified in the laboratory.

#### *Spatial and temporal variation of community structure*

Community structure was described by total biomass, abundance and species richness. Variation of each of these variables between habitat types, streams and seasons was assessed through a three-way ANOVA. Variables were log-transformed when necessary in order to meet parametric assumptions. Non-metric multidimensional scaling (NMDS) on log-transformed data, using the PC-ORD package (McCune & Mefford, 1999), was used to plot habitats and seasons in species space. Yield–effort curves were drawn and jack-knife estimates of species richness were calculated using PC-ORD to indicate the representativeness of the samples.

#### *Dietary analysis*

Macroinvertebrates were weighed using a Sartorius micro balance. All individuals were separated to species or morphospecies. Diets were described by analysis of gut contents. Ten individuals of each species from each replicate subsample were analysed, unless fewer individuals were collected, in which case

all individuals were analysed. The total number of individuals analysed per species ranged from 1 (very rare species) to 94 (see Appendix 1), with an average of 21 individuals per species. Guts were removed and mounted in polyvinyl lactophenol to create a semi-permanent slide, which was examined under a compound microscope.

Guts of each individual were assumed to be 100% full, and percentages of the different food types were estimated using a graticule with a 10 × 10 grid. Gut contents were divided into six categories: fine particulate organic matter (FPOM) – particles <50 µm), coarse particulate organic matter (CPOM – particles from 50 µm to 1 mm), vascular plant tissue (VPT – particles >1 mm), algae (ALG), animal tissue (AT – including whole prey and fragments of exoskeleton) and mineral material (MM).

Each species was allocated to a dietary group according to its diet, and assisted by cluster analysis, which was performed using Ward's clustering method (JMP 4.0.1 software; SAS Institute Inc., Cary, NC, U.S.A.), using the average percentage of each food type for all the individuals studied. Given that dietary groups were identified visually from the cluster, differences among groups were confirmed with a MANOVA (the dietary group being the independent variable, and the arcsin [ $\sqrt{(x/100)}$ ] transformed percentages of each food type the dependent variables). As the MANOVA result was significant, independent ANOVAs were performed with single food types as independent variables, followed by Fisher's PLSD *post hoc* tests to identify which groups differed in gut contents for each food type.

### *Spatial and temporal variation of community functional composition*

Functional composition was described in terms of relative biomass, abundance and species richness of the different FFGs – scrapers, shredders, collectors and predators, following Cummins & Klug (1979) – allocated according to the dietary groups resulting from the cluster analysis. We did not attempt to divide collectors into gatherers and filterers, as we did not examine mouthparts.

A Multiple Response Permutation Procedure (MRPP) in PC-ORD was used to compare relative biomass, relative abundance and relative species richness of the different FFGs between habitat types, streams, seasons, and the interaction habitat type  $\times$  season. MRPP essentially acts as a non-parametric MANOVA and is free of some of the assumptions of multivariate normality of MANOVA (Zimmerman, Goetz & Mielke, 1985). A Bonferroni correction was applied to probability values of the 12 MRPP analyses performed (three dependent variables  $\times$  four factors).

The MRPP analysis was also used to compare diets of major taxa, using species as replicates and the six food types (see above) as the multiple variables. Species with more than five guts analysed were grouped into seven major taxa (family or above: Odonata, Ephemeroptera, Leptoceridae, other Trichoptera, Coleoptera, Chironomidae and other Diptera), determined by the number of replicates (species) within them. Major taxa with only single species (Plecoptera, Lepidoptera) were excluded.

### *Food webs*

Food webs were constructed using the data on invertebrate diets, pooled by habitat and month. The detailed data were summarised by identifying all species in the webs that contributed 2% or more of the biomass of each habitat/month combination, then taking the integer of the natural log of the biomass to provide a scale for diagrammatic representation of the relative importance of each species. Species representing <2% of the biomass were lumped as 'other consumers' or 'other predators'. The larger elements of the fauna (crayfish and vertebrates) are omitted from the webs, as they were not adequately sampled. However, estimates of biomass of these species,

derived from separate studies, are included in web descriptions. Importance of dietary components was derived from their occurrence in the guts of the invertebrates (Appendix 1). Food web statistics (links, connectance, etc.) were calculated as descriptors of the four replicates of four webs (Appendix 2).

### *Regional comparison*

To set our study sites in a regional context, their fauna was compared with the fauna from 18 other sites in low-order streams in the Queensland wet tropics from a range of latitudes and altitudes. These sites encompassed the full geographical range of the bioregion, and were collected in a separate sampling program in November 1991 (R.G. Pearson, unpublished data). The comparison was based on six 30  $\times$  30 cm benthic samples collected from two riffles in each of the 20 streams. Samples were preserved and processed as above. Counts of invertebrates from the benthic samples were analysed using NMDS in PC-ORD, and the abundance of shredders was compared using ANOVA on log-transformed data followed by a Tukey test.

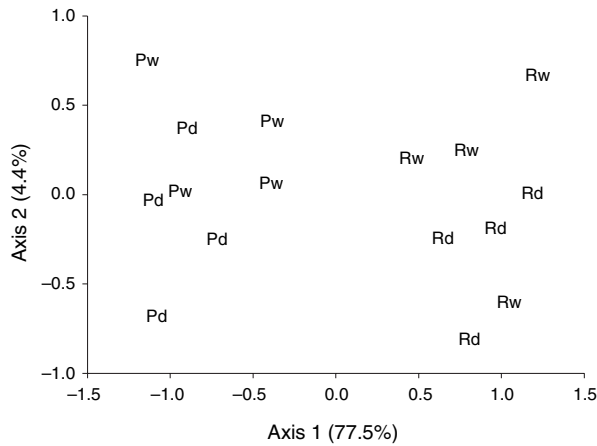
## **Results**

### *Spatial and temporal variation of community structure*

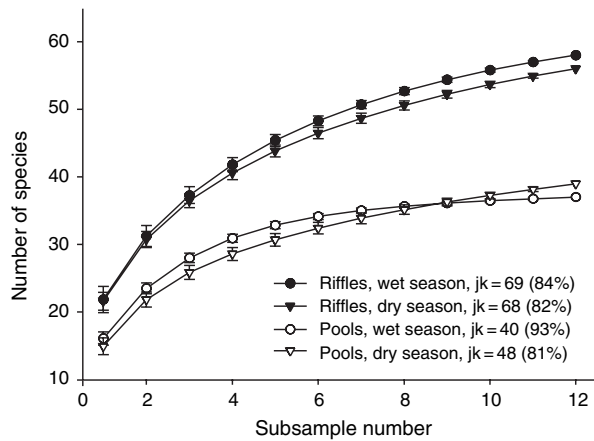
A total of 10 346 individuals from 70 species were collected. Mean invertebrate biomass per sampling site was 14.9 and 16.3 mg in the wet and dry seasons, respectively, and 11.0 and 20.2 mg in pool and riffle habitats, respectively (Appendix 3).

Total biomass and abundance were higher in riffles than in pools (biomass,  $F_{1,8} = 10.97$ ,  $P = 0.0107$ ; abundance,  $F_{1,8} = 24.38$ ,  $P = 0.0011$ ), but did not differ between streams or seasons. Species richness was also higher in riffles ( $F_{1,8} = 30.51$ ,  $P = 0.0006$ ), and higher in Birthday Creek ( $F_{1,8} = 8.45$ ,  $P = 0.0197$ ); the interaction between habitat type, stream and season was significant ( $F_{1,8} = 11.50$ ,  $P = 0.0095$ ), with the difference between riffles and pools much higher in the wet season in Birthday Creek but higher in the dry season in Camp Creek.

Ordination of invertebrate samples by NMDS indicated complete separation by habitat on axis 1, which explained 77.5% of the variance in the data matrix (Fig. 1). There was some evidence of separation by season on axis 2.



**Fig. 1** Non-metric multidimensional scaling ordination of 16 macroinvertebrate samples in Birthday and Camp Creeks. Site labels indicate habitat (R = riffle, P = pool) and season (w = wet season; d = dry season). Percent of variance ( $r^2 \times 100$ ) explained by each axis is indicated. Stress = 11.2.

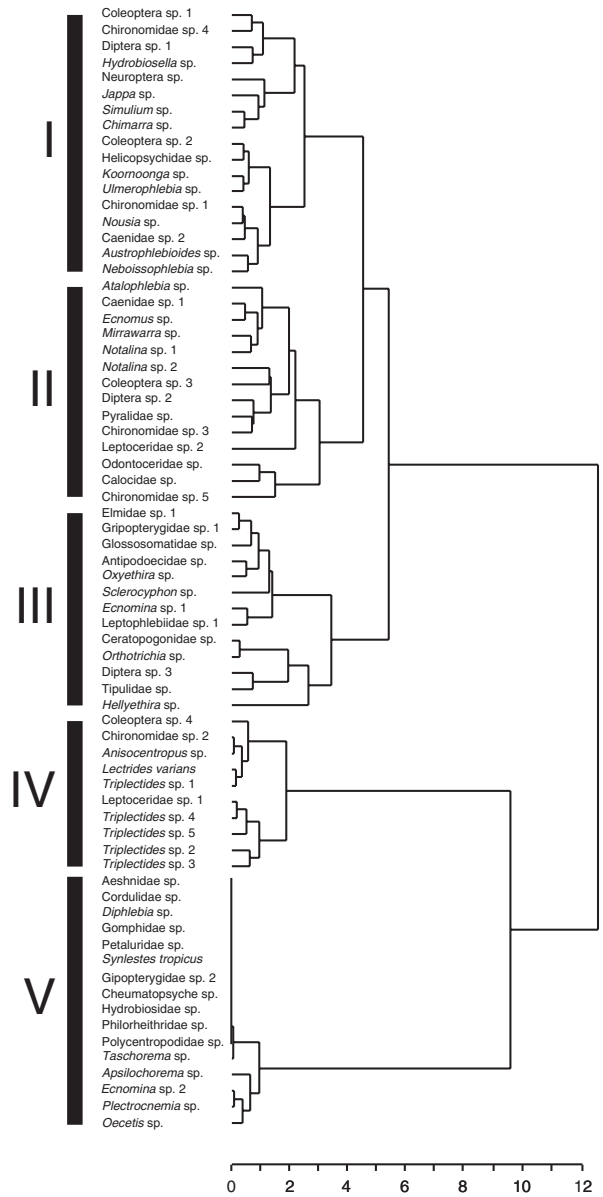


**Fig. 2** Yield-effort curves for species accumulation in riffle and pool samples. Jack-knife estimates of total species complement ( $jk$ ), and actual proportion of jack-knife estimate (%), are shown for each season and habitat.

Yield-effort curves and jack-knife estimates of species richness indicated that at least 80% of species were collected, with asymptotes being approached for most curves (Fig. 2). Given that species not collected were rare, the webs presented here are good representations of the communities, except for the few much larger species that were not targeted by the sampling methods (crayfish, eel, platypus and kingfisher).

*Dietary analysis*

The cluster analysis based on gut contents of species split species into five dietary groups (Fig. 3).



**Fig. 3** Classification (Ward's method) of species based on the proportion of different food types in their guts. Groups I-III include generalist species (I, mostly collectors; II, mostly shredders and predators and III, mostly scrapers); groups IV-V are specialists (IV, shredders and V, predators).

Although there was some overlap between groups I-III, which included generalist feeders (in contrast to groups IV and V, composed of specialist feeders), there were consistent differences between groups (see below). Further division of groups did not provide any useful information.

Group I was mostly composed of collectors, with an average of 30% of their gut contents comprising

FPOM. However, proportions of 26% of MM, and 16% of CPOM and VPT indicated the existence of some scraping and/or shredding in these species. This group included seven species of Ephemeroptera, three Trichoptera, four Diptera, two Coleoptera and one Neuroptera. Group II was mainly composed of generalist predators and generalist shredders, with their gut contents consisting of 24% AT and 27% VPT. Group II included three species of Ephemeroptera, six Trichoptera, three Diptera, one Coleoptera and one Lepidoptera. Group III was composed of generalist scrapers. Guts of these species contained a high percentage of ALG (average 28%), as well as large amounts of FPOM (average 41%) and small amounts of MM (average 7%). This group included one species of Ephemeroptera, one Plecoptera, six Trichoptera, three Diptera and two Coleoptera. Group IV was composed of specialist shredders, with an average of 86% of their gut contents being VPT. This group included eight species of Trichoptera, one Diptera and one Coleoptera. Group V was composed of the specialist predators, with an average of 96% of their gut contents being AT. This group consisted of one species of Plecoptera, nine Trichoptera and six Odonata. Identification of prey of insect predators was not attempted, but in general, these predators were observed to be catholic in their diets, selecting prey by size rather than by species.

Differences among dietary groups in gut contents for each food source are shown in Fig. 4. The MANOVA showed the existence of significant differences in diet among the five dietary groups (Wilk's  $\lambda_{24,211} = 0.001$ ,  $P < 0.0001$ ), and the ANOVAs showed that dietary groups differed in gut contents for every food source: FPOM,  $F_{4,65} = 59.27$ ,  $P < 0.0001$ ; CPOM,  $F_{4,65} = 66.80$ ,  $P < 0.0001$ ; VPT,  $F_{4,65} = 104.04$ ,  $P < 0.0001$ ; ALG,  $F_{4,65} = 27.65$ ,  $P < 0.0001$ ; AT,  $F_{4,65} = 217.83$ ,  $P < 0.0001$ ; MM,  $F_{4,65} = 82.69$ ,  $P < 0.0001$ .

#### *Spatial and temporal variation of community functional composition*

The allocation of species to FFGs was the following: scrapers and collectors were species from groups III and I, respectively; shredders were all the species from group IV and some species of group II (those with no AT in their gut contents); predators were all the species from group V and some species of group II (those with AT in their gut contents).

Fig. 5 shows the proportions of each of the four FFGs in each benthic sample, according to biomass, abundance and species richness. There was some variation between samples, but in general, predators or shredders dominated in terms of biomass and species richness, while collectors were numerically prominent, especially in riffles. Shredders occurred in both habitats but were most abundant in pools.

The MRPP analysis (Table 2) shows that relative biomass, abundance and species richness of the different FFGs all varied between habitat types, but not between streams and seasons; however, the interaction between habitat and season was significant in all cases.

The MRPP analysis of diet across the seven taxa indicated highly significant differences ( $T = -7.76$ ,  $P < 0.0001$ ). The source of the differences among taxa was identified by using MRPP between pairs of taxa (Table 3). Unsurprisingly, the Odonata showed the greatest difference in diet from the other taxa, and the Leptoceridae and Ephemeroptera differed strongly from most other taxa. Taxa showing more overlap were the non-leptocerid Trichoptera, Chironomidae and Coleoptera.

#### *Food webs*

The composition of the community by dietary groups (Fig. 5) and the food webs (Fig. 6) indicate the prominence of predators, and the relatively high abundance of the detritivores, especially shredders.

In the pools in the dry season (Fig. 6a), the primary consumers were dominated by three shredder species (*Atalophlebia* sp., Leptoceridae sp. 1 and *Lectrides varians*), and VPT contributed a major proportion of the dietary intake of these consumers. FPOM and a combination of dietary components were predominant in two further taxa (*Ulmerophlebia* sp. and *Nousia* sp.). Many taxa had some of every non-animal food in their guts, such that most could be regarded as generalist feeders. The 'other consumer' group included 25 taxa, each of which contributed <2.0% of the sample biomass. Three odonate and one chironomid species dominated the predator group, with two other species having lower biomass.

In the pools in the wet season (Fig. 6b), the shredder *Atalophlebia* sp. was again predominant, but other shredders were less evident, and generalist collectors and scrapers were more abundant, again demonstra-

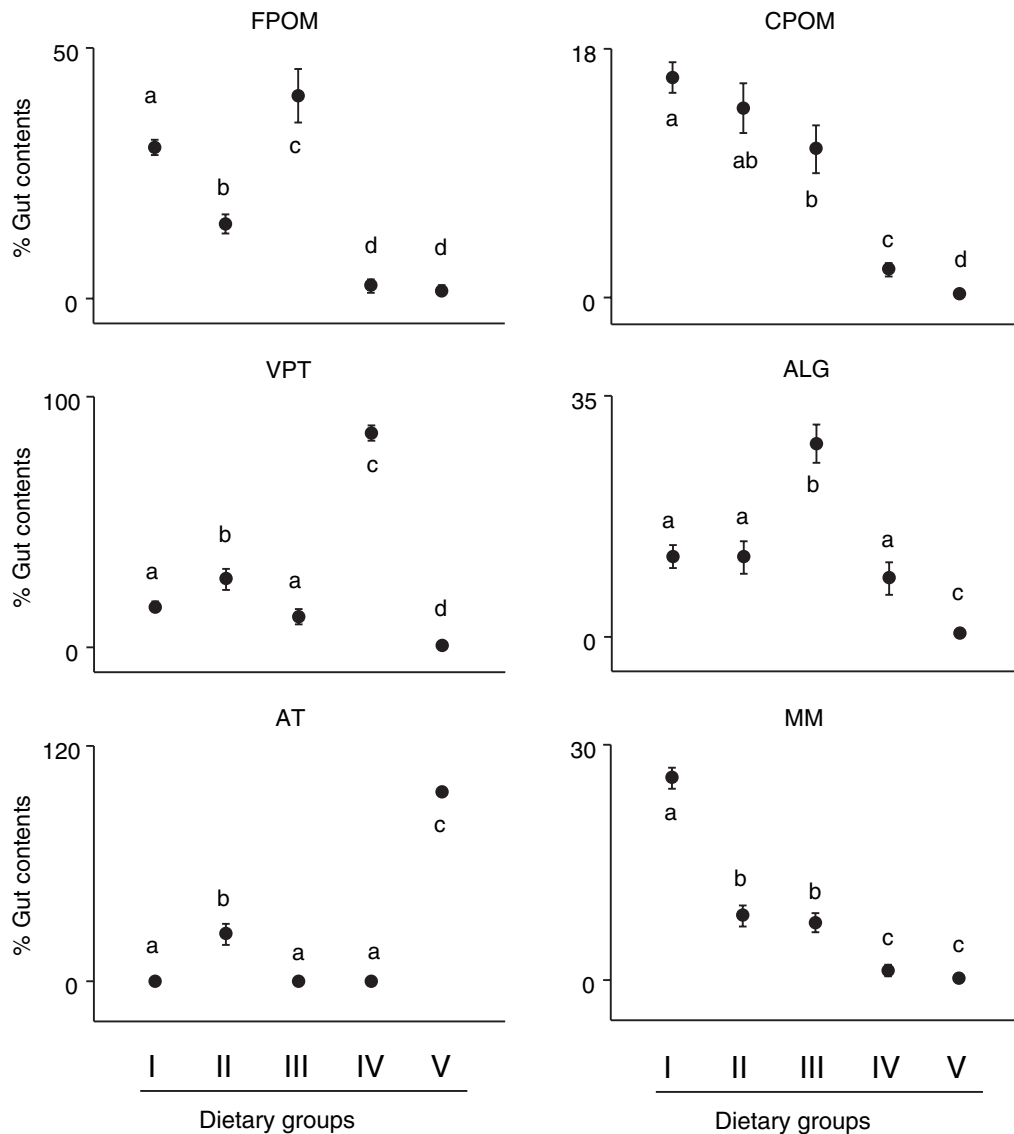


Fig. 4 Average percentage of each food source in the gut contents of dietary groups I–V. Different labels (a–d) indicate significant differences among dietary groups.

ting a complex of generalist taxa. Predators were more abundant than in the dry season, with four odonate and one chironomid species representing >2% of the biomass, but maintaining similar relative numbers between the seasons. In the pools, therefore, shredders and collectors were predominant in both seasons, but with some shift in emphasis from the dry to the wet season.

In the riffles in the dry season (Fig. 6c), a mixed fauna was predominant, with a filter feeder (*Simulium* sp.), a shredder (*Triplectides* sp. 6) and a generalist collector (Coleoptera sp. 3) most abundant, followed

by four other generalist collector species and 37 species each representing <2.0% of the biomass. Predators were abundant, dominated by Aeshnidae sp. and three other species, with nine species representing <2.0% of the biomass.

In the riffles in the wet season (Fig. 6d), only five taxa represented >2.0% of the biomass, all having a generalist diet. Three of the more common taxa in the dry season were not common in the wet season, and one extra species, *Atalophlebia* sp., became relatively more abundant. The predators were a major component of the fauna, with a similar suite of species predominant.

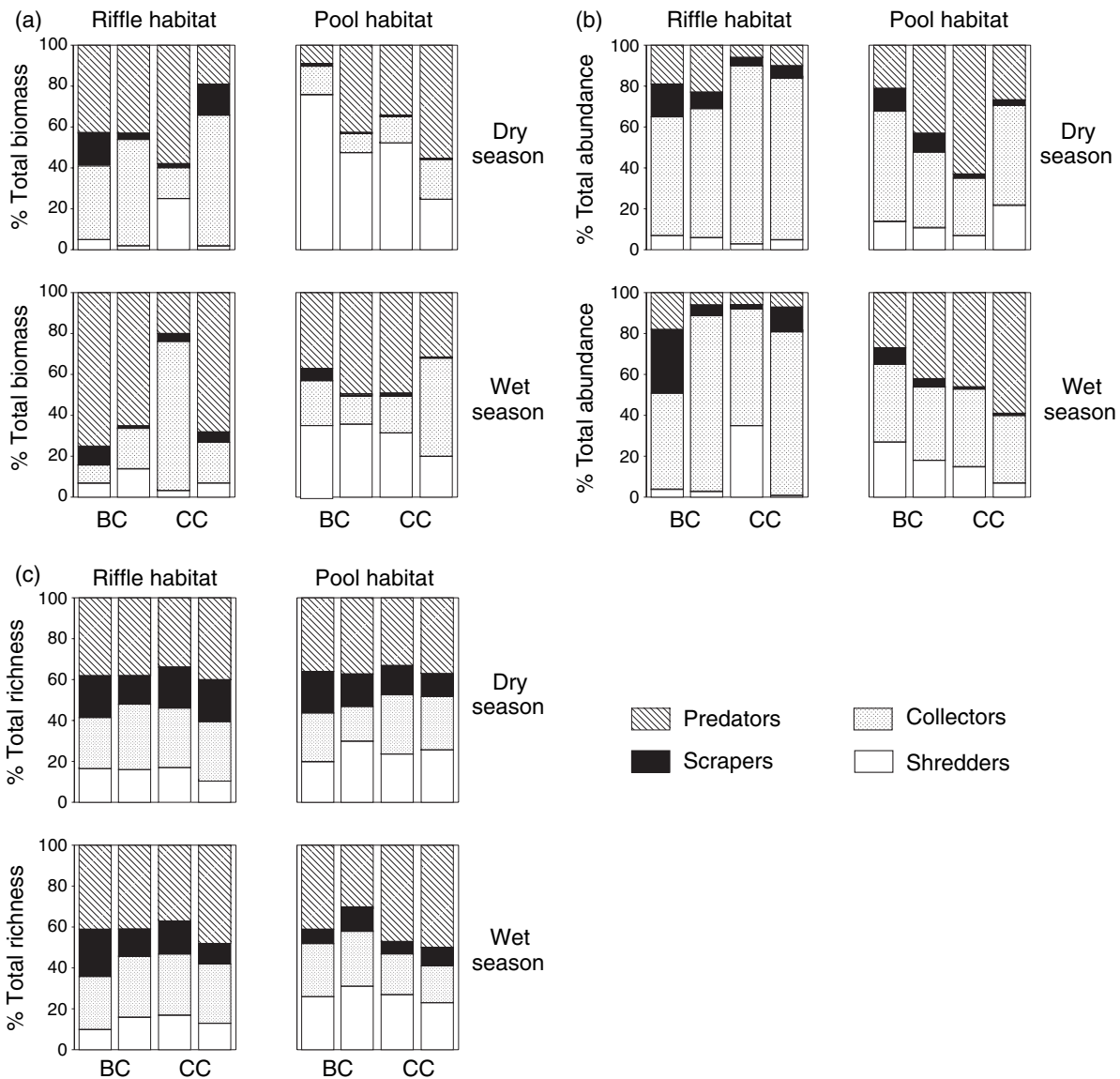


Fig. 5 Percentage composition of each functional group at each site (two riffles and two pools at each stream) and season (dry and wet): (a) biomass, (b) abundance, (c) species richness. BC, Birthday Creek; CC, Camp Creek.

Table 2 Results of Multiple Response Permutation Procedure (*T*-statistic and *P*-values) showing differences in relative biomass, relative abundance, and relative species richness of the different functional feeding groups between streams, habitat types, and seasons, and the interaction between habitat type and season. Significant effects after applying a Bonferroni correction are in bold.

Factor	Biomass		Abundance		Richness	
	<i>T</i>	<i>P</i>	<i>T</i>	<i>P</i>	<i>T</i>	<i>P</i>
Stream	0.70	0.731	0.18	0.442	0.27	0.508
Habitat	-4.22	<b>0.003</b>	-6.90	<b>4E-04</b>	-6.66	<b>2E-04</b>
Season	0.31	0.541	0.71	0.745	-1.24	0.111
Habitat × season	-2.61	<b>0.015</b>	-3.26	<b>0.007</b>	-4.41	<b>6E-04</b>



**Table 3** Results of Multiple Response Permutation Procedure analysis of seven taxa by six food types: lower left cells show *T*-statistic; upper right cells show *P*-value

	Ephemeroptera	Leptoceridae	Trichoptera (other)	Chironomidae	Diptera (other)	Coleoptera	Odonata
Ephemeroptera	–	0.0007	0.0090	0.0334	0.0015	0.0046	0.0003
Leptoceridae	–6.3874	–	0.0065	0.1981	0.0029	0.0039	0.0013
Trichoptera (other)	–3.6337	–3.6597	–	0.9412	0.1997	0.1992	0.0028
Chironomidae	–2.2373	–0.8212	–1.1238	–	0.3212	0.2727	0.0228
Diptera (other)	–3.9748	–4.7341	–0.6650	–0.3795	–	0.7079	0.0009
Coleoptera	–3.5833	–4.6152	–0.6581	–0.4283	0.6349	–	0.0010
Odonata	–8.0516	5.9102	–5.1627	–2.4920	–6.4256	–6.2542	–

A materials budget was not possible because of a lack of concomitant estimates of throughput of organic matter such as leaf litter. For the macroinvertebrates, the quantitative estimates of relative biomass across seasons and habitats are: predators 40.6%, shredders 24.2%, scrapers 5.8%, and other detritivores 29.4%. These estimates are based on the relative proportion of riffle and pool habitat being about 50% each (R.G. Pearson, unpublished data). Inclusion of estimated biomass of the crayfish, *Cherax depressus* Riek, attributed equally to shredding and collecting (J. Coughlan & R.G. Pearson, unpublished data), tadpoles (mostly *Litoria genimaculata* (Horst), which are scrapers and collectors – R.G. Pearson, unpublished data) and vertebrate predators (mostly the eel *Anguilla reinhardti* Steindachner with negligible contribution by Platypus *Ornithorhynchus anatinus* (Shaw) and Azure kingfisher *Ceyx azureus* Latham), based on observations of the study sites over several years (R.G. Pearson, unpublished data), resulted in the following proportions: invertebrate predators 26.7%, shredders 15.9%, scrapers 3.8%, other detritivores 19.3%, crayfish 4.9%, tadpoles 20.4% and vertebrate predators 9.0%. Predators therefore represented about 36% of the overall animal biomass in the stream.

Several food-web statistics show substantial consistency between samples (Appendix 2). Connectance was closely correlated with species richness in both habitats, across samples (Fig. 7).

#### Regional comparison

The NMDS of 20 riffle sites from the Queensland wet tropics bioregion showed that the sites for this study – Birthday and Camp Creeks – fell within the group on both axes (Fig. 8). The abundance of shredders in Birthday and Camp Creeks similarly fell within the overall range across the wet tropics sites (Table 4).

The arrangement of sites according to the ordination and the abundance of shredders bore no relationship to latitude, altitude or stream order (Table 4). Birthday and Camp Creeks therefore supported invertebrate communities that were similar to, or not atypical of, low-order streams in the Queensland wet tropics.

#### Discussion

This is the first study that assigns tropical stream invertebrate species to FFGs based on direct observation (gut content analysis) rather than on existing information for temperate species, as advocated by Cohen *et al.* (1993). This is important because taxonomically related species may have different diets in tropical and temperate areas. For example, Dobson *et al.* (2002) found that the tropical African baetid *Acanthiops* was a shredder, while baetids in northern temperate streams are usually grazers. Although the FFG classification is usually based on feeding modes, and therefore analysis of mouthparts, rather than diet, feeding modes and diet are usually correlated (Plague & Wallace, 1998).

The allocation of species to FFGs allowed us to identify differences in functional composition of communities between habitat types, seasons and streams. The proportions of the different FFGs, in terms of biomass, number of individuals, and number of species, differed between habitat types (these differences varying with season), but not between streams or between seasons. Similarly, total macroinvertebrate biomass, abundance and species richness varied between habitat types (being higher in riffles than in pools), but showed no seasonal variation. Thus there was substantial uniformity in the community structure across streams and seasons, reflecting the stability of the physical environment, except after

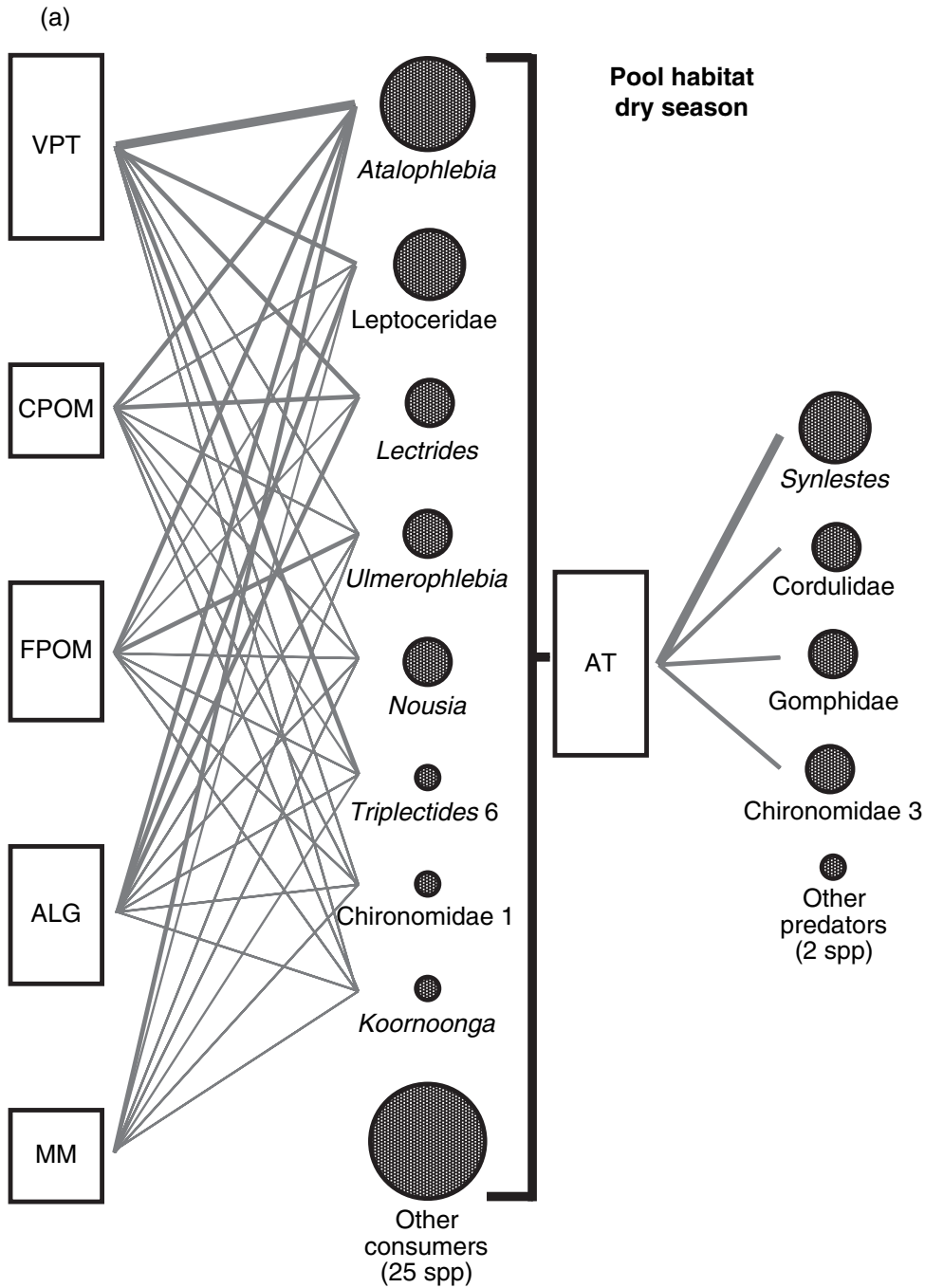


Fig. 6 Food webs for two habitats and two seasons in Birthday and Camp Creeks (combined). Size of each food-source box determined by proportion of biomass of consumers including item in diet; size of primary consumer and predator circles determined from log of the biomass of each taxon or group; size of connecting lines determined from relative proportion of each food source in the diet of each taxon. All taxa representing >2% of the biomass are identified; others are represented by the 'other' circles.

major floods (Rosser & Pearson, 1995). Differences between the communities of pool and riffle habitats are consistent with studies elsewhere (e.g. Brown & Brussock, 1991), and are due to the habitat preferences

of the component species. For example, in Australian tropical streams, mayflies show distinct habitat preferences, with flow being an important determining factor (Hearnden & Pearson, 1991; Christidis, 2004).

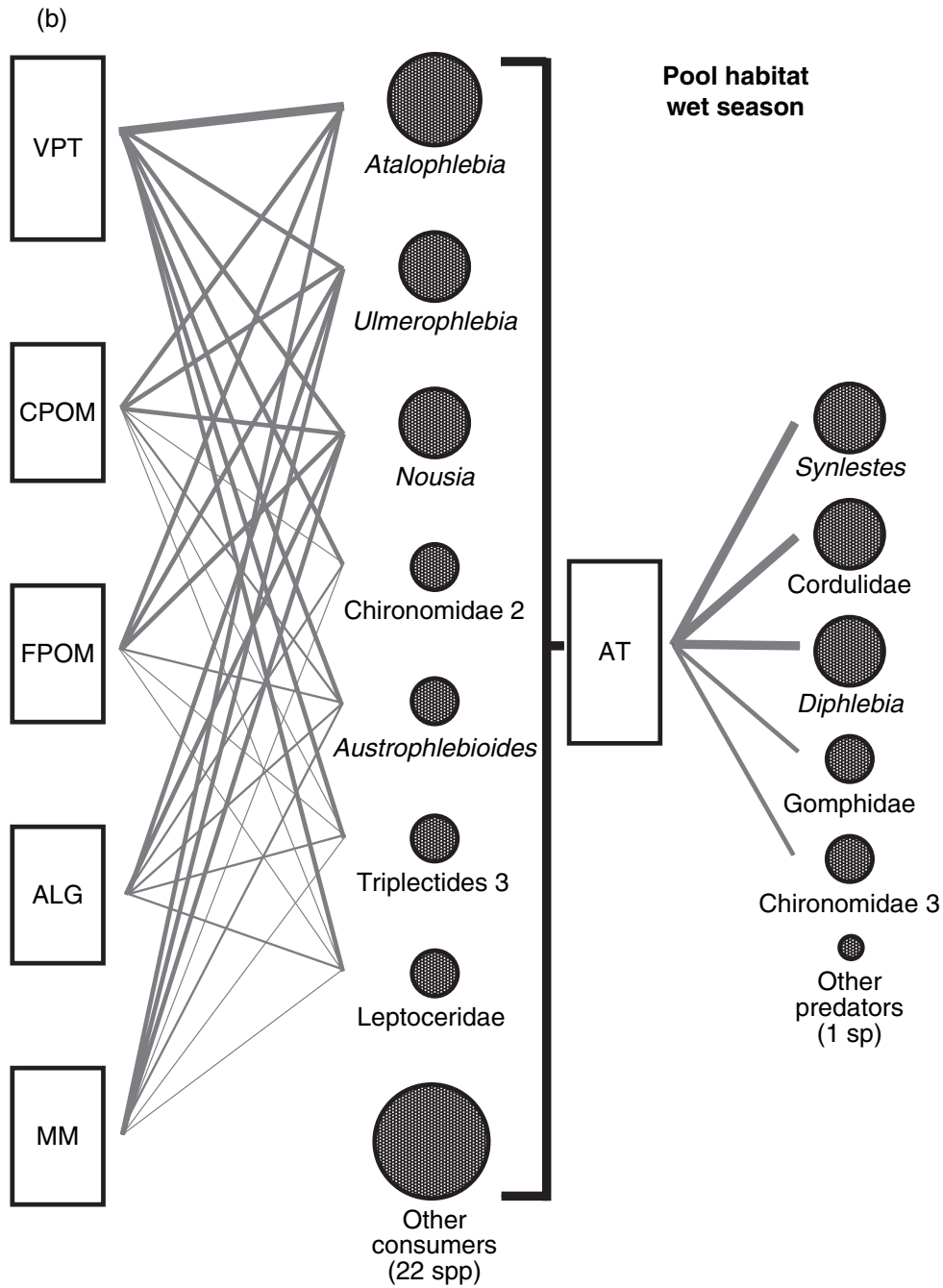


Fig. 6 (Continued)

Many species were shown to be generalist feeders, with varying proportions of detrital material as well as algae, animal material and/or mineral material in their guts. Two groups of species were specialists, namely the specialist predators and shredders. Whether these relationships are maintained at a higher taxonomic level is of interest from ecological

and evolutionary perspectives. The specialist predators, Odonata, and shredders, Leptoceridae, were shown to be very different in their diets as a group from the rest of the fauna; the Ephemeroptera, too, separated from some groups. Otherwise, there was substantial overlap. Given that the Trichoptera, Coleoptera and Chironomidae are known to include

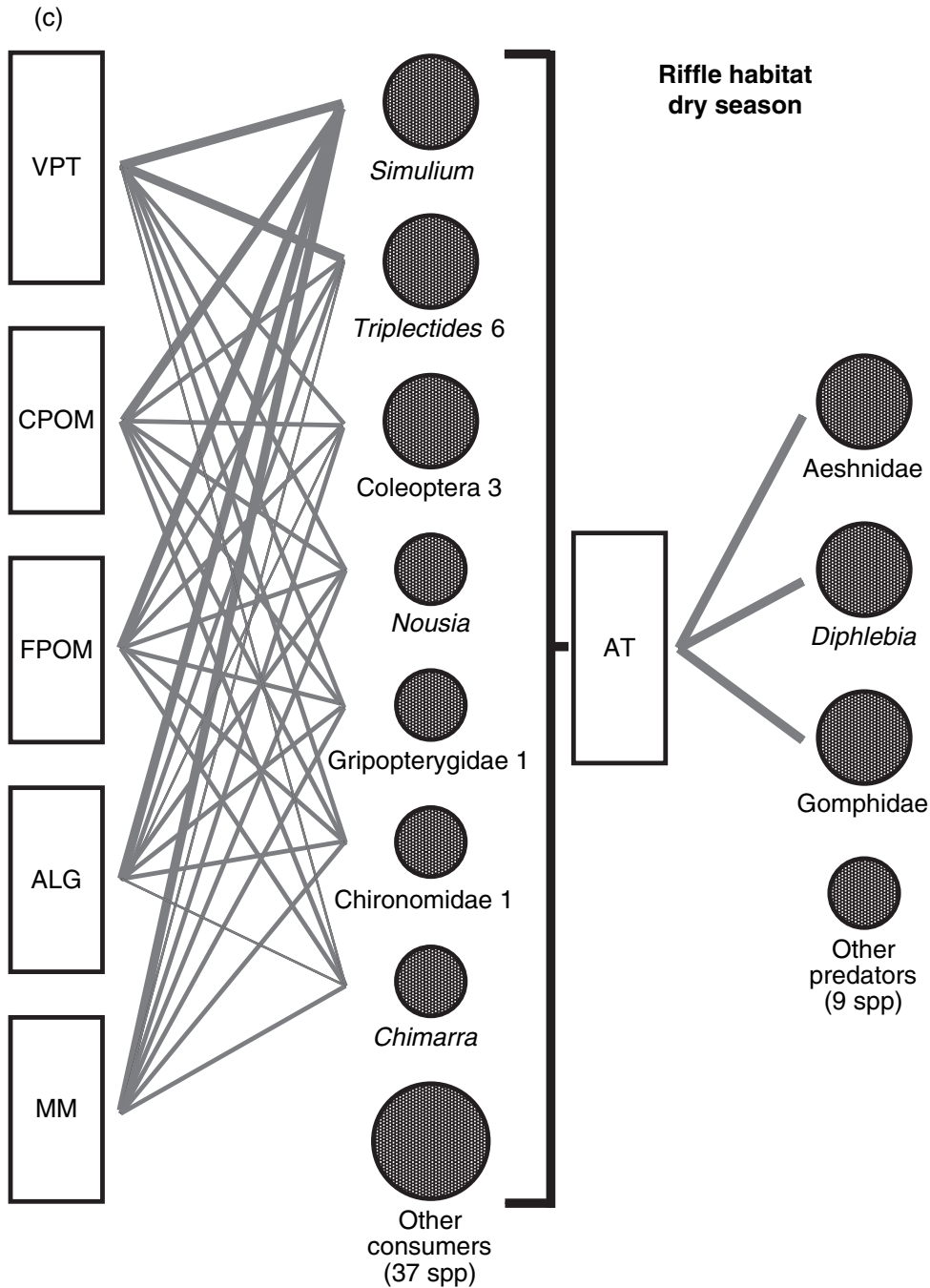


Fig. 6 (Continued)

species with very different feeding modes, this is unsurprising. This analysis would be of greater interest if more groupings at the family level were available (i.e. if more families had sufficient species for comparison). For example, it might be predicted that several families of Trichoptera would separate

from other groups, as there are specialist families within the order – predators, shredders, filterers, etc. Taxonomic fidelity to particular diets might be predicted as phylogeny, form and function are usually closely related although not always, as Dobson *et al.* (2002) have pointed out for baetids.

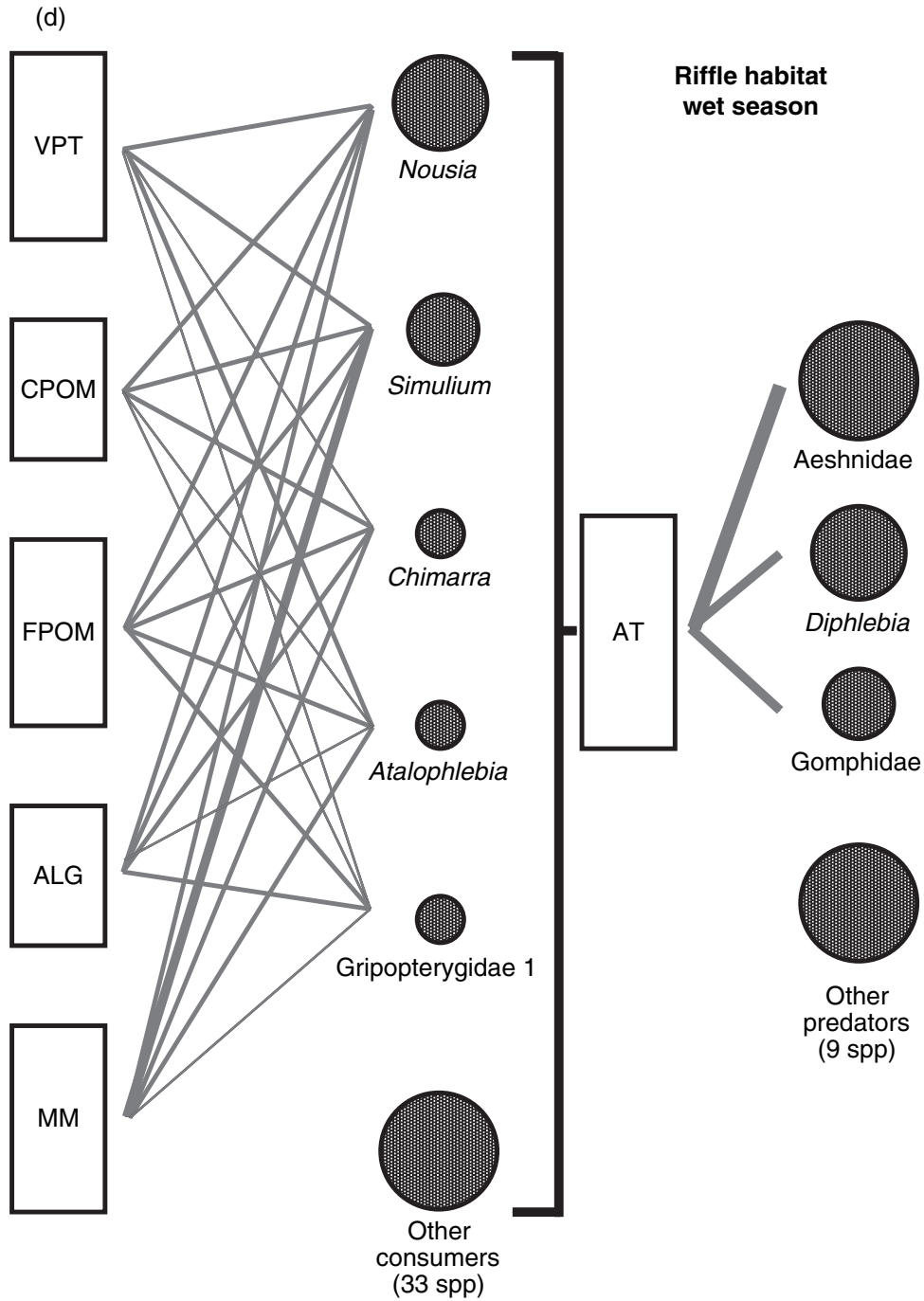
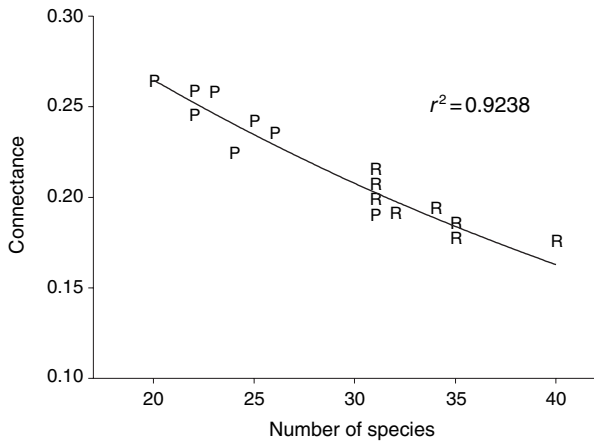


Fig. 6 (Continued)

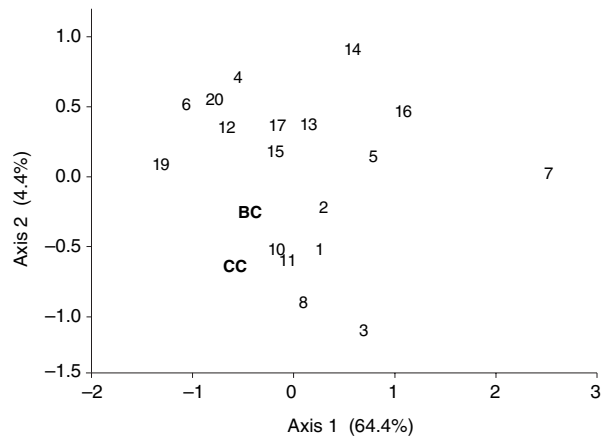
Macroinvertebrate shredders were abundant in the study sites, comprising about 24% of the total macroinvertebrate biomass, not including the crayfish. This pattern contrasts with recent reports of the scarcity of shredders in tropical streams (e.g. Dobson *et al.*, 2002 and references therein). However, it is

unclear whether previous reports were accurate, because they did not analyse diets or mouthparts of all species in the community, as we did in this study. For example, Dobson *et al.* (2002) examined the mouthparts of the 44% of all species (plus gut contents of 25% of those species) from tropical



**Fig. 7** Connectance of food webs for pool and riffle samples across two streams and two seasons. ‘Species’ (X-axis) includes all taxa and food items (Appendix 2).  $R^2$  value is for an exponential decay model,  $y = a \times e^{-bx}$ , where  $a = 0.430$  and  $b = 0.024$ .

African streams, and relied on the literature to allocate other species to FFGs. Their results indicated that shredders were scarce, but they pointed out that they could have allocated species to FFGs incorrectly. Further, shredder abundance can be temporally and spatially patchy (Table 4; Pearson, Benson & Smith, 1986; Pearson *et al.*, 1989). Nevertheless, the African



**Fig. 8** Non-metric multidimensional scaling ordination of macroinvertebrate samples from 20 Queensland Wet Tropics sites, based on six sample units per site. Site numbers are identified in Table 3, except sites for current study: BC, Birthday Creek and CC, Camp Creek. Per cent of variance ( $r^2 \times 100$ ) explained by each axis is indicated. Stress = 15.6.

streams had no typical shredders present – neither the stoneflies typically reported from northern hemisphere nor the caddisflies from Australia and elsewhere.

Scarcity of shredders may be more a biogeographical than a simple latitudinal/climatic issue, as it has

**Table 4** Density of shredders (mean numbers/0.1 m<sup>2</sup> ± SE,  $n = 6$ ) in 20 Queensland wet tropics streams, December 1993. ANOVA showed significant differences among streams ( $F_{1,19} = 2.512, P = 0.002$ ); Tukey HSD test identified three groups, a–c, with significance of differences between sites in Group a and Group c as indicated. Approximate altitude and stream order derived from 1 : 100 000 maps.

Stream	Latitude (S)	Longitude (E)	Altitude (m)	Stream order	Shredder density	Tukey group ( $P$ )
1 Gap	15°49'	145°20'	150	2	0.00 ± 0.00	a (0.025)
2 Emmagen	16°03'	145°27'	20	4	0.00 ± 0.00	a (0.025)
3 Windmill	16°34'	145°16'	900	2	0.00 ± 0.00	a (0.025)
4 Allan	16°37'	145°30'	350	3	0.00 ± 0.00	a (0.025)
5 Malbon-Thompson	17°09'	145°54'	100	2	0.00 ± 0.00	a (0.016)
6 Woobadda	15°58'	145°22'	20	4	0.17 ± 0.17	a (0.016)
7 Middle	17°03'	145°51'	40	2	0.17 ± 0.17	a (0.016)
8 Goddard	18°13'	145°49'	500	3	0.17 ± 0.17	a (0.016)
9 Camp	18°58'	146°10'	850	2	0.17 ± 0.17	a (0.016)
10 Lorna Doone	15°47'	147°17'	300	2	0.50 ± 0.35	b
11 Yuccabine	18°12'	145°46'	600	3	0.67 ± 0.34	b
12 Baird	16°06'	145°20'	260	3	0.83 ± 0.55	b
13 Breach	17°06'	145°39'	700	3	1.17 ± 0.49	b
14 N. Johnstone tributary	17°26'	145°41'	500	3	1.17 ± 0.55	b
15 Pixies	17°47'	145°41'	60	3	1.17 ± 0.81	b
16 Kauri	17°06'	145°36'	900	1	1.67 ± 1.11	b
17 Charappa	17°42'	145°40'	620	3	2.33 ± 1.25	b
18 Birthday	18°59'	146°10'	800	3	2.00 ± 1.84	b
19 Rifle	16°40'	145°28'	440	3	4.33 ± 2.22	b
20 Shoteel	16°56'	145°37'	450	2	5.17 ± 2.10	c

been reported for streams in both tropical and temperate parts of the world. For example, Thompson & Townsend (2000) found that shredders contributed only 4% of the total number of species in New Zealand streams, compared with a world average of 11%. Dobson *et al.* (2002) reported fewer than 5% of shredders for all but one of the Kenyan streams they sampled (one had about 10%), compared with 10–40% shredders for different places in Europe. Winterbourn (1995) suggested that the low supply and retention of coarse organic matter are responsible for the paucity of shredders in New Zealand streams but that is not the case in some tropical streams with low numbers of shredders, which have high biomass of coarse detritus (Dobson *et al.*, 2002). In our study streams, shredders made up 15% of species richness in riffles and 26% in pools (average, 20%). The community composition matched the pattern for shaded temperate streams (Vannote *et al.*, 1980), with low numbers of scrapers and much higher numbers of shredders and other detritivores, because of allochthonous material being the main source of organic input. Allochthonous material is of similar importance in other Queensland wet tropics streams (Pearson *et al.*, 1989).

It is notable in this study that, while the majority of species in the community were generalists in their mode of feeding, most shredder species were specialists. Of 14 shredder species, 10 were specialists (most of them caddisflies), feeding almost exclusively on coarse detritus, and only four were generalist feeders (two mayflies and two caddisflies), with about half of their gut contents being coarse detritus. On the contrary, the most common shredder taxa in temperate streams (filipalpians stoneflies) have been shown to be generalist feeders. For example, Dangles (2002) examined the diets of 20 putative shredder species and found that only six (all caddisflies) fed exclusively on coarse detritus, while all filipalpians stoneflies were generalists and fed mainly on fine detritus and filamentous algae.

In temperate forest streams, where leaf fall occurs mainly in the autumn (northern hemisphere deciduous forests – e.g. Webster & Benfield, 1986) or summer (Australian temperate forests – e.g. Lake, 1982), shredder species may be adapted to feed on other resources during the rest of the year. In tropical rainforest streams, year-round leaf litter input (Benson & Pearson, 1993) could favour the existence

of specialist shredder species. However, shredders in tropical Australian streams have distinct leaf preferences (Nolen & Pearson, 1993) and each tree species is seasonal in its litter input, so it is possible that shredders switch from species to species in sequence. Nevertheless, the high diversity of tree species in riparian rainforest (Benson & Pearson, 1993) is such that it is unlikely that specialist shredders would need to use foods other than leaf litter. Even after cyclonic winds and floods, when the only detritus is new green leaf litter, shredders are able to feed on the fresh material (Nolen & Pearson, 1993), thereby mobilising new organic inputs and making them available to collectors.

The high biomass and species richness of invertebrate predators in our study streams were also notable. Predators made up about 40% of the total invertebrate biomass and 39% of total species richness. In contrast, Thompson & Townsend (2000) found that predators constituted 25% of total species richness in New Zealand streams, and their review of the world literature indicated an average of about 27% of total species richness made up by predators. The predator species in the food webs included animals ranging widely in size – from chironomids measuring up to 5 mm in length to dragonflies up to 45 mm – and undoubtedly included more than one trophic level. Nevertheless, it is apparent that the processing of organic material and turnover of detritivores must be substantial to support the predator populations. There are no studies of productivity in these streams, although the numbers of small detritivores (indicated by high abundance but low biomass – Fig. 5) would support this observation.

The previously reported high species richness of these tropical streams (Pearson *et al.*, 1986; Lake *et al.*, 1994) is reflected in this study in two FFGs in particular – the shredders and the predators. The challenge to explaining how this diversity is maintained will depend on studies on resource limitations and partitioning of resources that are in short supply. Mayflies in an Australian tropical stream have been shown to have similar diets, but to partition microhabitats (Hearnden & Pearson, 1990, 1991) and it is possible that fine partitioning occurs within the shredder and predator FFGs. For the shredders, differences in leaf preference or microhabitat selection may facilitate partitioning, while for predators partitioning by size of prey and microhabitat is likely. The

high proportion of predator biomass in the streams (even ignoring vertebrates) is probably explained by a relatively high rate of production of prey species, but this warrants further investigation.

Connectance showed the expected relationship with richness, and fell within the range of values recorded for various ecosystems (e.g. Cattin *et al.*, 2004). The close relationship obviated the need for yield–effort curves (recommended by Cohen *et al.*, 1993) for number of links as they would mirror the species–richness curves. However, comparison between this and other webs is hampered by different levels of resolution – in our case, the limitation was in not identifying specifically the gut contents of predators, and therefore placing predators in one trophic level. We know that the larger odonates include in their prey smaller predators such as some of the trichoptera (L. Charlton & R.G. Pearson, unpublished data), which in turn will eat predatory chironomids (McKie, 2002). Therefore, the links indicated (Fig. 6, Appendix 2) could be enhanced by further detailed analysis of predators' gut contents, but we would predict there to be typically two and up to four predator levels (including the rare vertebrate top predators). Our study is further limited by ignoring micro-fauna and by the absence of direct quantitative estimates of organic input to the web. However, the part of the web that is included parallels other stream studies, which tend to focus on the macroinvertebrate fauna (e.g. Poepperl, 2003).

The lack of comprehensiveness is a limitation of most food web descriptions (Cohen *et al.*, 1993). Most studies are also constrained by limitations of the units used to measure interactions. Descriptions of webs based on binary links (i.e. presence or absence of links) lack information on the importance of each link, and may therefore be deceptive. On the contrary, energy-flow descriptions that involve probably the best measure of importance, tend to lump species together because of the difficulty of determining all specific energetic relationships, especially in species-rich communities. Thus the currency of web studies varies substantially. To our knowledge only one study (Hall, Wallace & Eggert, 2000) has attempted to address this problem by integrating binary and flow approaches. A useful exercise would be to attempt several approaches on single communities – using binary and flow-based linkage values, and counts, biomass and energy flow as measures of importance –

to test the influence on the conclusions drawn. In this study we focussed on biomass as a compromise that clearly provides a more accurate picture of importance than do binary links or numeric abundance, given that even among the insects, biomass of individuals varied up to 800-fold. Ideally, productivity studies should support food web descriptions (e.g. Poepperl, 2003) – that is, a combination of flow and binary approaches to webs is preferred (Hall *et al.*, 2000) – as it is clear from this study that rapid turnover of prey is likely to be the source of relatively high predator biomass. Although we did not attempt measures of productivity, we believe that our importance measure (biomass), summarised in the web diagrams, is a better representation of community function than a simple binary web or improvement on it by use of counts (e.g. Kitching, 1987). The summary figures that compare allocation of species, counts and biomass among the FFGs partly demonstrate the contrast between biomass and counts: in particular, the predators accounted for a much greater proportion of the biomass of the invertebrate assemblages than of their numeric abundance. While the textbook pyramid of abundance is not always expected, this apparently top-heavy web is noteworthy. Productivity data are needed to confirm our supposition that it is the high turnover of species at lower trophic levels that sustains this structure.

The importance to the invertebrate community of the larger animals is unclear: crayfish probably contribute a large amount of FPOM through their shredding activity but may also interfere with insect activity (J. Coughlan & R.G. Pearson, unpublished data); the relative biomass of tadpoles suggests that they might compete or interfere with invertebrate collectors; and the large predators, especially eels, could well have a cropping effect on the invertebrate community. However, as platypus and kingfishers are scarce and eels are mostly very large (R.G. Pearson, unpublished data) and take large prey (crayfish, frogs, tadpoles) rather than insects (Hortle & Pearson, 1990), it is likely that the impacts on the invertebrate assemblages are small.

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## Appendices

**Appendix 1** Gut contents of invertebrates from Birthday Creek and Camp Creek, shown as the mean percentage of each food type found in the guts of each species (*n*, number of individuals analysed). FPOM, fine particulate organic matter (<50 µm); CPOM, coarse particulate organic matter (50 µm to 1 mm); VPT, vascular plant tissue (>1 mm); ALG, algae; AT, animal tissue; MM, mineral material. Species are grouped as in the cluster analysis (Fig. 4). Not included are tadpoles, crayfish and vertebrate predators (see text).

	<i>n</i>	FPOM	CPOM	VPT	ALG	AT	MM
<b>Group I: generalist collectors</b>							
<b>Ephemeroptera</b>							
<i>Koornoonga</i> sp.	17	27	21	17	5	0	30
<i>Ulmerophlebia</i> sp.	43	26	17	21	8	0	28
<i>Nousia</i> sp.	91	23	20	22	13	0	22
<i>Austrophlebioides</i> sp.	30	20	24	27	10	0	19
<i>Jappa</i> sp.	4	27	7	25	9	0	32
<i>Neboissophlebia</i> sp.	2	28	20	28	4	0	20
Caenidae sp. 2	3	27	16	20	16	0	21
<b>Trichoptera</b>							
<i>Hydrobiosella</i> sp.	3	38	11	16	11	0	24
<i>Chimarra</i> sp.	47	36	14	9	5	1	35
Helicopsychidae sp.	19	35	18	9	10	0	28
<b>Diptera</b>							
Chironomidae sp. 1	94	23	17	29	12	0	19
Chironomidae sp. 4	4	34	9	3	26	0	28
<i>Simulium</i> sp.	61	30	14	8	11	0	37
Diptera sp. 1	1	39	14	6	20	0	21
<b>Coleoptera</b>							
Coleoptera sp. 1	15	27	14	9	27	0	23
Coleoptera sp. 2	37	29	21	12	12	0	26
<b>Neuroptera</b>							
Neuroptera sp.	3	44	13	17	0	0	26

## Appendix 1 (Continued)

	<i>n</i>	FPOM	CPOM	VPT	ALG	AT	MM
<b>Group II: generalist shredders, generalist predators</b>							
Ephemeroptera							
<i>Atalophlebia</i> sp.	47	18	14	46	8	0	14
Caenidae sp. 1	28	23	14	26	22	0	15
<i>Mirawarra</i> sp.	15	14	16	22	14	20	14
Trichoptera							
<i>Ecnomus</i> sp.	9	19	11	28	20	12	10
<i>Notalina</i> sp. 1	34	12	12	26	15	28	7
<i>Notalina</i> sp. 2	7	10	8	45	2	32	3
Leptoceridae sp. 2	2	0	20	2	27	49	2
Odontoceridae sp.	2	9	23	59	0	0	9
Calocidae sp.	2	24	27	42	5	0	2
Diptera							
Diptera sp. 2	1	18	6	25	19	28	4
Chironomidae sp. 3	88	14	8	17	9	45	7
Chironomidae sp. 5	4	14	21	11	0	46	8
Coleoptera							
Coleoptera sp. 3	15	26	4	16	4	35	15
Lepidoptera							
Pyralidae sp.	5	6	8	15	18	47	6
<b>Group III: generalist scrapers</b>							
Ephemeroptera							
Leptophlebiidae sp.	1	19	9	37	28	0	7
Plecoptera							
Gripopterygidae sp. 1	44	28	15	14	32	0	11
Trichoptera							
Glossosomatidae sp.	13	22	18	17	29	0	14
Antipodoecidae sp.	2	36	9	9	36	0	10
<i>Oxyethira</i> sp.	13	35	13	8	32	5	7
<i>Orthotrichia</i> sp.	1	72	2	2	22	0	2
<i>Hellyethira</i> sp.	1	70	25	0	5	0	0
<i>Ecnomina</i> sp. 1	2	28	7	26	33	0	6
Diptera							
Ceratopogonidae sp.	27	72	2	1	25	0	0
Diptera sp. 3	7	54	11	6	21	0	8
Tipulidae sp.	7	38	8	20	21	5	8
Coleoptera							
Elmidae sp.	78	28	13	11	35	0	13
<i>Sclerocyphon</i> sp.	13	25	8	9	47	1	10
<b>Group IV: specialist shredders</b>							
Trichoptera							
<i>Anisocentropus kirramus</i>	48	1	1	94	4	0	0
<i>Lectrides varians</i>	14	1	3	93	3	0	0
<i>Triplectides</i> sp. 1	2	0	3	97	0	0	0
<i>Triplectides</i> sp. 2	23	3	2	70	17	0	8
<i>Triplectides</i> sp. 3	8	0	0	77	22	0	1
<i>Triplectides</i> sp. 4	5	0	2	85	12	0	1
<i>Triplectides</i> sp. 5	2	9	4	76	9	0	2
Leptoceridae sp. 1	18	1	4	82	13	0	0
Diptera							
Chironomidae sp. 2	88	0	1	93	5	0	1
Coleoptera							
Coleoptera sp. 4	1	10	0	90	0	0	0
<b>Group V: specialist predators</b>							
Plecoptera							
Gripopterygidae sp. 2	5	0	0	0	0	100	0

## Appendix 1 (Continued)

	<i>n</i>	FPOM	CPOM	VPT	ALG	AT	MM
Trichoptera							
Cheumatopsyche sp.	9	0	0	0	0	100	0
Hydrobiosidae sp.	7	0	0	0	0	100	0
Philorheithridae sp.	8	0	0	0	0	100	0
Polycentropodidae sp.	63	0	1	0	0	99	0
<i>Taschorema</i> sp.	1	0	0	0	0	100	0
<i>Apsilochorema</i> sp.	4	13	0	2	2	78	5
<i>Ecnomina</i> sp. 2	51	5	1	2	1	90	1
<i>Oecetis</i> sp.	16	3	1	4	6	86	0
<i>Plectrocnemia</i> sp.	1	5	0	5	0	90	0
Odonata							
Aeshnidae sp.	9	0	0	0	0	100	0
Cordulidae sp.	38	0	0	0	0	100	0
<i>Diphlebia</i> sp.	45	0	0	0	0	100	0
Gomphidae sp.	28	0	0	0	0	100	0
Petaluridae sp.	12	0	0	0	0	100	0
<i>Synlestes tropicus</i>	49	0	0	0	0	100	0

**Appendix 2** Food web descriptive statistics. *S* is number of elements in the web (invertebrate species plus food categories); maximum number of links in web is  $S(S-1)/2$ ; chain length assumes three levels of predator; connectance is number of links/maximum number of links; linkage density is number of links/*S*; linkage complexity is  $S/\text{connectance}$ ; proportion of top species includes rare large predators; proportion of top invertebrate predators includes odonates only

Statistic	Pools		Riffles	
	Wet season	Dry season	Wet season	Dry season
<i>S</i>	27.75 ± 0.63	32.50 ± 1.55	38.75 ± 1.03	40.50 ± 2.02
No. links	95.50 ± 4.01	114.00 ± 6.20	142.25 ± 6.05	149.00 ± 11.73
Max. no. links	371.80 ± 16.90	515.50 ± 51.69	733.00 ± 39.53	806.00 ± 83.09
Max. chain length*	5	5	5	5
Connectance	0.26 ± 0.00	0.22 ± 0.01	0.19 ± 0.00	0.19 ± 0.01
Linkage density	3.44 ± 0.08	3.51 ± 0.09	3.67 ± 0.07	3.66 ± 0.10
Linkage complexity	7.14 ± 0.15	7.23 ± 0.19	7.54 ± 0.13	7.52 ± 0.21
% Top spp.	0.11 ± 0.00	.09 ± 0.00	0.08 ± 0.00	0.07 ± 0.00
% Top invert predator spp.	0.15 ± 0.01	0.13 ± 0.01	0.16 ± 0.01	0.14 ± 0.01

**Appendix 3** Biomass (mg) of invertebrates per sampling site from Birthday Creek and Camp Creek. Means and standard errors of every habitat type × season combination are shown.

	Wet season				Dry season			
	Pool		Riffle		Pool		Riffle	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Ephemeroptera								
<i>Atalophlebia</i> sp.	115.00	49.58	28.53	11.37	114.00	32.01	8.05	7.98
<i>Austrophlebioides</i> sp.	17.13	8.86	4.63	3.25	1.08	0.98	23.25	12.81
Caenidae sp. 1	0.13	0.13	6.80	5.20	–	–	2.03	1.99
Caenidae sp. 2	–	–	1.38	1.21	–	–	0.05	0.03
<i>Jappa</i> sp.	8.00	8.00	–	–	–	–	1.75	1.75
<i>Koornoonga</i> sp.	4.25	4.25	3.50	3.50	8.50	3.77	7.25	4.17
Leptophlebiidae sp.	1.50	1.50	0.00	0.00	0.00	0.00	0.00	0.00
<i>Mirawarra</i> sp.	–	–	0.05	0.03	4.53	4.49	9.25	5.47
<i>Neboissophlebia</i> sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.75	0.75
<i>Nousia</i> sp.	30.50	14.98	95.78	40.99	16.50	5.04	68.50	39.15

## Appendix 3 (Continued)

	Wet season				Dry season			
	Pool		Riffle		Pool		Riffle	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
<i>Ulmerophlebia</i> sp.	34.50	10.41	–	–	16.53	5.71	–	–
Plecoptera								
<i>Gripopterygidae</i> sp. 1	1.00	0.71	17.75	5.88	0.00	0.00	49.50	15.19
<i>Gripopterygidae</i> sp. 2	0.00	0.00	0.25	0.25	0.00	0.00	4.00	2.83
Trichoptera								
<i>Anicentropus kirramus</i>	2.63	2.46	10.80	10.73	7.03	3.01	9.28	7.66
Antipodecidae sp.	–	–	0.03	0.03	–	–	–	–
<i>Apsilochorema</i> sp.	–	–	0.13	0.13	–	–	–	–
Calocidae sp.	–	–	0.13	0.13	–	–	1.03	0.99
<i>Cheumatopsyche</i> sp.	–	–	0.03	0.03	–	–	3.30	3.23
<i>Chimarra</i> sp.	–	–	64.50	53.93	–	–	38.03	22.02
<i>Ecnomina</i> sp. 1	1.25	1.25	0.50	0.50	0.00	0.00	0.03	0.03
<i>Ecnomina</i> sp. 2	6.25	1.49	0.18	0.11	4.03	1.56	0.80	0.73
<i>Ecnomus</i> sp.	1.25	1.25	0.15	0.12	1.58	1.48	0.03	0.03
Glossosomatidae sp.	–	–	4.25	4.25	–	–	0.05	0.03
Helicopsychidae sp.	–	–	0.08	0.03	0.03	0.03	14.75	5.02
<i>Hellyethira</i> sp.	–	–	–	–	0.08	0.03	–	–
<i>Hydrobiosella</i> sp.	–	–	–	–	0.05	0.03	5.30	5.23
Hydrobiosidae sp.	–	–	–	–	–	–	–	–
<i>Lectrides varians</i>	4.00	4.00	9.50	9.50	21.50	11.32	4.53	4.49
Leptoceridae sp. 1	12.38	6.57	–	–	33.50	17.64	0.50	0.50
Leptoceridae sp. 2	–	–	–	–	1.00	1.00	0.03	0.03
<i>Notalina</i> sp. 1	4.00	2.11	0.78	0.47	0.55	0.48	0.25	0.25
<i>Notalina</i> sp. 2	–	–	–	–	3.00	1.78	1.00	1.00
Odontoceridae sp.	–	–	–	–	0.03	0.03	2.00	2.00
<i>Oecetis</i> sp.	0.15	0.12	0.05	0.03	2.55	1.63	0.10	0.00
<i>Orthotrichia</i> sp.	–	–	0.08	0.03	–	–	0.03	0.03
<i>Oxyethira</i> sp.	–	–	0.10	0.00	–	–	0.03	0.03
Philorheithridae sp.	–	–	6.00	6.00	–	–	3.03	2.99
<i>Plectrocnemia</i> sp.	–	–	5.00	5.00	0.05	0.03	0.03	0.03
Polycentropodidae sp.	31.75	21.93	2.50	2.50	5.00	3.61	21.00	5.03
<i>Taschorema</i> sp.	–	–	6.00	3.83	–	–	–	–
<i>Triplectides</i> sp. 1	–	–	0.03	0.03	0.03	0.03	0.03	0.03
<i>Triplectides</i> sp. 2	14.50	8.53	14.00	14.00	2.75	2.75	0.03	0.03
<i>Triplectides</i> sp. 3	0.75	0.75	3.75	3.75	–	–	–	–
<i>Triplectides</i> sp. 4	2.00	2.00	–	–	1.28	1.24	–	–
<i>Triplectides</i> sp. 5	5.25	4.92	–	–	10.28	6.32	113.50	113.50
Diptera								
Ceratopogonidae sp.	0.38	0.13	0.30	0.12	0.08	0.03	0.05	0.03
Chironomidae sp. 1	8.00	4.02	7.78	3.73	8.53	3.84	48.25	9.20
Chironomidae sp. 2	17.65	14.01	1.93	1.69	3.78	1.47	0.80	0.73
Chironomidae sp. 3	22.25	10.58	4.83	4.73	24.53	8.70	4.30	2.43
Chironomidae sp. 4	4.75	4.75	0.05	0.03	0.03	0.03	–	–
Chironomidae sp. 5	–	–	–	–	1.00	1.00	–	–
Diptera sp. 1	–	–	1.00	1.00	–	–	–	–
Diptera sp. 2	0.13	0.13	0.75	0.75	4.78	4.74	9.75	5.36
Diptera sp. 3	–	–	0.75	0.75	–	–	13.00	4.88
<i>Simulium</i> sp.	0.28	0.13	83.75	50.03	0.80	0.73	340.75	169.76
Tipulidae sp.	1.65	1.45	–	–	–	–	10.33	10.23
Coleoptera								
Elmidae sp.	0.40	0.10	6.00	0.82	0.05	0.03	4.28	3.91
Coleoptera sp. 1	–	–	3.50	1.26	–	–	4.03	3.99

## Appendix 3 (Continued)

	Wet season				Dry season			
	Pool		Riffle		Pool		Riffle	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Coleoptera sp. 2	0.13	0.13	9.15	6.06	0.03	0.03	3.58	3.48
Coleoptera sp. 3	–	–	0.78	0.74	–	–	75.03	61.21
Coleoptera sp. 4	–	–	–	–	–	–	1.78	1.74
<i>Sclerocyphon</i> sp.	3.25	3.25	13.25	7.40	1.00	1.00	5.03	3.78
Odonata								
Aeshnidae sp.	–	–	284.25	68.30	–	–	211.00	116.17
Cordulidae sp.	49.75	28.11	2.63	1.60	26.78	22.46	7.83	7.73
<i>Diphlebia</i>	46.50	27.73	116.28	58.79	0.08	0.03	159.75	75.13
Gomphidae sp.	27.00	15.02	47.25	44.95	25.00	17.02	117.00	52.81
Petaluridae sp.	–	–	22.00	6.94	–	–	1.78	1.02
<i>Synlestes tropicus</i>	58.88	39.07	8.00	2.48	38.55	24.61	0.03	0.03
Lepidoptera								
Pyralidae sp.	–	–	–	–	–	–	0.80	0.73
Neuroptera								
Neuroptera sp.	0.00	0.00	0.00	0.00	0.00	0.00	6.50	6.50