Omnivory and opportunism characterize food webs in a large dry-tropics river system

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Abstract: We analyzed basal sources, trophic levels, and connectance in dry-season food webs on 4 rivers in the upper Burdekin catchment in the dry tropics of northeastern Australia. The region is characterized by episodic summer rainfall, and most of the annual river flow occurs in a short period. In the dry season, rivers typically contract into a series of water holes of varying permanence and hydrologic connectivity. We used stable-isotope and stomach-content analyses to identify trophic levels of macroinvertebrates and fish, and we used a mixing model (SIAR) to identify foodweb basal sources at each site. We found substantial variability among sites in basal-source contributions, trophic position of individual taxa, and foodweb structure, and sites from the same river often were as different as sites from different rivers. Important basal sources at different sites included allochthonous tree litter, autochthonous algae and macrophytes, and Fe-fixing bacteria. Many relationships between consumers and basal sources were not resolved in the mixing model, mainly because of extensive omnivory or isotopic overlap among sources. Nevertheless, our results show high variability of dry-tropics river communities that extends beyond previously described macroinvertebrate assemblages to the broader food web. However, the main components of the upper trophic levels were similar across sites, such that different lower trophic levels supported similar assemblages of top consumers. These tropical rivers were defined by omnivory and ecological opportunism, which may be adaptations to seasonal hydrological variability.

Key words: tropical rivers, food webs, omnivory, stable isotopes, macroinvertebrates, fish, connectance, Burdekin

Food webs in tropical rivers are characterized by widespread omnivory and tend to be short, diffuse, and highly interconnected (Winemiller 2004, Douglas et al. 2005, Pusey et al. 2010). For example, large predatory fish can occupy trophic positions similar to those of smaller fish (Layman et al. 2005a) and, even within the same species, significant size-related shifts in trophic position can occur (Werner and Gilliam 1984, Davis et al. 2011). This trophic flexibility can extend to the broader food web, with tropical fishes filling ecological roles that normally are occupied by aquatic insects in temperate rivers (Winemiller 2004). Recent research has advanced our understanding of how river ecosystems of the seasonal tropics function, but significant gaps in this knowledge still exist (Pettit et al. 2011, Warfe et al. 2013).

Identifying sources of organic matter is fundamental to understanding the dynamics of food webs (Finlay 2001). Various models of the C pathways in rivers have been proposed, each reflecting the type of river for which they were developed (e.g., Vannote et al. 1980, Junk et al. 1989, Thorp and Delong 1994, Thorp et al. 2006). Typically, allochthonous material is the main C source for food webs in small forested streams (e.g., Anderson and Sedell 1979, Benfield and Webster 1985, Cheshire et al. 2005), whereas in larger systems, autochthonous sources of C are major drivers of food webs, especially in rivers with seasonal warm-weather floods (Thorp et al. 2006). Even in rivers with large amounts of riparian-derived leaf litter, autochthonous production can still be the main source of C (McCutchan and Lewis 2002), possibly because of its palatability to metazoans (Thorp and Delong 2002). In Australian rivers of the arid zone and the seasonal (wet–dry) tropics, autochthonous production has been described as the dominant source of C for benthic metabolism and food webs (Bunn et al. 2003, Douglas et al. 2005, Fellows et al. 2007, Jardine et al. 2013). However, recognition of the variability of food webs and basal-source contributions in these rivers is growing (Leigh et al. 2010). Allochthonous C derived from

terrestrial or floodplain sources may be important in food webs of large wet–dry tropical rivers with variable hydrological regimes (Zeug and Winemiller 2008, Leigh et al. 2010, Hunt et al. 2012), with overall importance varying according to season and consumer taxa (Hunt et al. 2012).

Assessments of consumer diets and foodweb structure generally have been achieved via stomach-content analysis (SCA). However, this approach can be limited because it provides only a snapshot of trophic interactions (Hyslop 1980), and little information on the assimilation of ingested material (Parkyn et al. 2001). This limitation has led to the increasing use of stable-isotope analysis (SIA), which provides longer-term dietary information and allows quantification of prey assimilation by consumers (Vander Zanden et al. 1997, Post 2002). Despite its constraints, SCA has the advantage of providing the identity and size of food items, which cannot be detected from SIA (Layman et al. 2005b, Winemiller et al. 2007). Therefore, SCA and SIA are often used together to provide complementary estimates of trophic position (Mantel et al. 2004, Layman et al. 2005b, Winemiller et al. 2007, Davis et al. 2012a).

Blanchette and Pearson (2012, 2013) showed that biophysical variables and macroinvertebrate assemblages are highly spatially and temporally variable in 4 rivers of the Burdekin catchment in northeastern Australia, and that local factors were as important as the regional setting in determining assemblage composition and temporal trajectories in these seasonal river systems (cf. Warfe et al. 2013). Here we investigated food webs and their basal sources in the same 4 rivers during the late dry season, when habitats would be most stable in terms of hydrology and other biophysical variables (Blanchette and Pearson 2013). Riparian condition and associated in-stream habitat metrics (e.g., variation in canopy cover, benthic leaf-litter cover, bank overhanging vegetation) strongly influenced macroinvertebrate assemblages in

rivers of the Burdekin catchment on a local scale, with biophysical variables and assemblages from sites within the same river often as different as those between rivers (Blanchette and Pearson 2012, 2013). Therefore, the presence or absence of allochthonous material was a major ecological driver, and its influence on macroinvertebrate assemblages varied across the catchment. We hypothesized that broad foodweb structure would be similarly variable within and among rivers, with the relative importance of allochthonous and autochthonous materials driving this variability (at least at the lower levels of the food web). Hydrologically variable rivers engender omnivory and trophic simplicity as adaptive strategies to seasonal resource variability, particularly for longer-lived fauna, such as fish (Poff and Allan 1995, Douglas et al. 2005, Pusey et al. 2010). Therefore, we predicted that Burdekin catchment food webs would be characterized by omnivory, particularly among fishes, and that links between trophic levels would be short. To test our hypotheses, we used SCA, SIA with a mixing model (stable-isotope analysis for R [SIAR]), and constructed food webs with measures of connectivity across all sampled sites.

METHODS

Study area and sites

The Burdekin catchment (133,432 km^2) (Fig. 1) is an important contributor of run-off to the Great Barrier Reef lagoon. Our study sites were in the middle reaches of the catchment, which consists of wooded savanna landscape used mainly for cattle grazing. The regional climate is wet–dry tropical, with a summer wet season (November–March), during which flows are driven by monsoonal and cyclonic weather patterns, followed by a long dry season (May–October), during which flows diminish, often leaving hydrologically isolated waterholes along

111 dry river beds (Kennard et al. 2010, Blanchette and Pearson 2012). Substantial variation in
112 biophysical characteristics among rivers is caused by differences in weather pattern, lithology,
113 and local factors (see Blanchette and Pearson 2012 for detailed site descriptions).
114 We sampled 12 sites in the Burdekin catchment: 4 on the Burdekin River and 8 on 3
115 tributaries (2 sites each on the Cape-Campaspe and Basalt Rivers and 4 sites on Keelbottom
116 Creek) (Fig. 1). We selected sites for their hydrological permanence (information from
117 landholders and gauging-station data), unimpounded location well upstream of the Burdekin
118 Falls Dam, accessibility under most weather conditions, and representativeness of each river
119 (assessed by preliminary site visits). However, sites within rivers were variable (Table 1; also see
120 Blanchette and Pearson 2012). Spatial autocorrelation was unlikely to be a significant driving
121 factor in our study because previous work demonstrated no effect of geographical distance
122 between sites on macroinvertebrate assemblage composition (Blanchette and Pearson 2012). We
123 sampled in the late dry season between September and December 2009 when rivers were most
124 likely to be at their driest and, therefore, unlikely to be disturbed by floods. Each river had its
125 own hydrological characteristics. Keelbottom Creek and the Cape-Campaspe River contracted
126 longitudinally during the dry season, leaving a series of isolated water holes separated by dry
127 river bed. The Basalt River also contracted substantially during the dry season, but was
128 groundwater-fed and water holes were variously connected (although most connecting flows
129 were insufficient to allow passage of larger fish). The Burdekin River was fed by ground water,
130 and flowed throughout the dry season, with flows between sites generally sufficient to allow
131 passage of larger fish.
132 We measured major physicochemical variables with a Hydrolab Quantum multiprobe
133 meter (Hach/Hydrolab, Loveland, Colorado) and collected water samples for analysis at the

Australian Centre for Tropical Freshwater Research at James Cook University (see Bainbridge et al. 2009). We assessed riparian-zone condition at each study site with the tropical rapid appraisal of riparian condition (TRARC) method, a multimetric index of pressure, condition, and vegetation cover developed for tropical Australian rivers (Dixon et al. 2006).

Collection of samples for stable-isotope analysis

We collected fish and large crustaceans with a boat-mounted electrofisher (Model 2.5 GPP; Smith–Root, Vancouver, Washington USA) and gill nets in deep water (present at most sites) and a backpack electrofisher (Smith-Root Model 12B) in shallows with the aim of collecting the full range of size classes (following Pusey et al. 2010) for each species. Where possible, we conducted eight 5-min passes with each electrofishing method in the sampled reach. We collected macroinvertebrates from all major in-stream habitats (edge, bed, macrophytes, riffle, run) with a dip net with 250-µm mesh, picked them while they were alive, and placed them in distilled water for ≥3 h to facilitate purging of gut contents. We then rinsed animals with distilled water and stored them in plastic bags on ice for transport after pooling samples from different habitats at the site level. We froze all samples upon return to the laboratory. We collected zooplankton samples with 20 vertical hauls of a 63-µm net through the water column, stored them in river water on ice for transport, and processed them on return to the laboratory.

We collected potential basal food sources (dominant terrestrial and aquatic vascular plants, submerged leaf litter, filamentous algae, seston) as follows. We clipped leaves of the dominant terrestrial and aquatic vascular plants at each site directly from the plant, rinsed them with distilled water, and stored them in plastic bags for transport. We collected submerged terrestrial leaf litter and filamentous algae from the substratum at each site. We collected seston

(phytoplankton plus traces of particulate matter) by vertical hauls of a plankton net with 20-µm mesh. Fine particulate organic matter (FPOM; 250 µm to < 1 mm) and coarse particulate organic matter (CPOM; > 1 mm) were collected by elutriating sediments on site. We then passed the organic matter through sieves (1 mm for CPOM, 250 µm for FPOM) and rinsed it in distilled water. We collected epilithic biofilm by scrubbing 3 stones/site with a toothbrush and washed collected material through sieves (800- and 250-µm mesh sizes) to remove coarse detritus and macroinvertebrates. We placed the resultant slurry from each stone in individual tubes and stored them in the dark. We collected samples of the benthic Fe-fixing bacteria matrix (red flocculent; see Crerar et al. 1981) by hand at 3 points at the only site where they were present. We processed plankton samples immediately on return to the laboratory and then froze them. Other samples were stored on ice in the field and frozen on return to the laboratory.

Laboratory processing and stable-isotope analysis

We identified fish to species, measured (standard length) and weighed them, and conducted SCA per Davis et al. (2012a). We excised samples of abdominal muscle from larger decapod crustaceans and obtained tissue samples from snails and bivalves by crushing shells and excising muscles. We pooled all other macroinvertebrates by taxonomic or functional group (after Merritt and Cummins 1984, Cheshire et al. 2005; Table S1), and processed each group as a composite sample to attain adequate mass for isotope analysis. We oven-dried samples at 60°C for 96 h, ground them to a fine powder with a mortar and pestle, and stored them at room temperature.

We rinsed aquatic and terrestrial vascular plants, CPOM, FPOM, Fe-fixing bacteria, and filamentous algae with distilled water and inspected material under a microscope to remove any

contaminants (e.g., invertebrates) before oven-drying. We classified aquatic macrophytes as true aquatics or semiterrestrial following Sainty and Jacobs (1994) and Cowie et al. (2000). We processed zooplankton and seston samples before freezing. We poured each zooplankton sample through sieves (250 and 60 µm), rinsed them with distilled water, and retained the 60-µm size fraction for analysis. We poured each seston sample through sieves (60 and 20 µm) to remove contaminants >60 µm, rinsed them with distilled water, and retained the 20-µm size fraction. We oven-dried these samples (as above) in Petri dishes. We centrifuged biofilm samples collected at each site at ~1000 rpm for 10 min and collected the chlorophyll-rich top fraction from each tube. We filtered this material through precombusted glass-fiber filter papers (0.7 µm) and stored it frozen in aluminum foil until we oven-dried it. With the exception of the biofilm and plankton samples, we dried, finely ground, and stored plant material at room temperature.

Analysis for $\delta^{15}N$, $\delta^{13}C$, %C, %N, and C:N was done by personnel at the Colorado Plateau Stable Isotope Laboratory (CPSIL) at Northern Arizona University. Samples were analyzed on a Thermo-Finnigan Deltaplus Advantage gas isotope-ratio mass spectrometer (see Davis et al. 2012a).

An emerging issue in SIA studies is the confounding effect of lipids, especially in fish tissues (Post et al. 2007, Logan et al. 2008). Therefore, isotopic analysis of duplicate samples (1 lipid-extracted, 1 bulk tissue) were conducted on 15% of samples from each size class of each fish species to develop a lipid-correction equation (Logan et al. 2008). Lipid extraction was performed by the CPSIL following a modified Folch et al. (1957) technique (Davis et al. 2012a).

Data analyses

In one family of fish (grunters [Terapontidae]), C:N ratios were >4, indicating high lipid

concentrations and necessitating lipid correction of $\delta^{13}C$ using a family-specific equation:

$$\delta^{13}C_{normalized} = \delta^{13}C_{untreated} + 3.33 \log(C{:}\,N_{bulk}) - 3.6219 \quad \text{(Eq. 1)}$$

(r^2 = 0.635). Other fish had C:N ratios <4, so corrections were not required. Corrections were unnecessary for macroinvertebrates (Logan et al. 2008).

We used Stable Isotope Analysis in R (SIAR; Parnell et al. 2010), a Bayesian mixing model that runs on the R platform (R Project for Statistical Computing, Vienna, Austria) to estimate the contributions of different basal sources to consumer diets for each site. The advantage of using SIAR rather than other mixing models (e.g., IsoSource; Phillips and Greg 2003) is that it incorporates the inconsistencies and uncertainties associated with the data into the model and accurately represents the variability inherent in the natural system (Parnell et al. 2010). The SIAR model is fit via the Markov Chain Monte Carlo method to produce simulations of plausible values of dietary proportions of sources consistent with the data using a Dirichlet prior distribution (Jackson et al. 2009, Parnell et al. 2010). Each model was the product of 500,000 iterations, with the first 50,000 discarded. We report results as the 95% confidence intervals (CIs; Phillips and Gregg 2003, Jackson et al. 2009, Parnell et al. 2010). Prior to analyses, we plotted consumer and source data with standard deviations to ensure that consumers were within the isotopic mixing space. We removed consumers that were outside the isotopic mixing space (after application of trophic enrichment values; see below) from further analyses.

We report SIAR results for consumers present at ≥50% of sites, which is a useful threshold for between-site comparison. We calculated standard deviations of source values for input into SIAR mainly from samples collected from the same site. However, not all sources were present at all sites, and only 1 sample each of filamentous algae and biofilm was analyzed per site. We calculated standard deviations in these cases with river- and then catchment-scale

data (Table S2). Examination of data for each site indicated that some basal sources (e.g., CPOM and terrestrial C3 vegetation) could be combined (Bunn et al. 1999, Winemiller et al. 2007) using a conservative threshold of 2.0‰ between taxa. Conversely, 2 macrophyte species (*Myriophyllum* sp. and *Potamogeton* sp.) at site BA1 could not be combined with the aquatic macrophyte group and were treated individually.

Isotopes, especially of N, exhibit a predictable trophic enrichment factor (TEF) between prey and consumer tissues, and the highest-level consumers generally have the most enriched tissue (DeNiro and Epstein 1981, Peterson and Fry 1987, Vander Zanden and Rasmussen 1999). SIAR includes TEF data to correct for the N-enriched status of consumers and places them within the N-depleted source-mixing geometry. We used TEF values for consumers and their putative diets calculated from Australian dryland/dry-tropics rivers (Bunn et al. 2013) to back-calculate basal-source mixtures. TEFs were as follows: herbivorous fish, 3.9 ± 1.3 (SD); predatory fish, 7.0 ± 1.7; herbivorous macroinvertebrates, 0.6 ± 2.2; predatory macroinvertebrates 1.8 ± 1.9. We excluded omnivores from analysis because of their highly variable TEF values. The $\Delta\delta^{15}N$ values of 0.6 and 1.8 are lower than the 2.3 to 3.4‰ commonly reported in the literature across multiple taxa and trophic levels (e.g., DeNiro and Epstein 1981, Minagawa and Wada 1984, McCutchan et al. 2003). However, Kilham et al. (2009) reported $\Delta\delta^{15}N$ values between 0.8 and 3.4 across food webs in tropical and temperate aquatic ecosystems, and McCutchan et al. (2003) found that $\delta^{15}N$ in consumers can vary depending on diet: 1.4 ± 0.20‰ on macroinvertebrate and 3.3 ± 0.26‰ on high-protein diets. Assigning discrete TEF values to herbivorous and predatory macroinvertebrates was straightforward because of their conservative dietary preferences, whereas fish were assigned to feeding groups on the basis of stomach-content analysis (see Davis et al. 2011) and previous studies (Jepsen and

Winemiller 2002, Douglas et al. 2005, Pusey et al. 2010) because of their widespread omnivory in tropical rivers. Some species had large $\delta^{15}N$ values that placed them outside source-mixing polygons even after TEF correction, so we used alternative (nontrophic aligned) TEF values to place fishes within the source-mixing polygon (site-specific predator TEF used first, then *H. fuliginosus* size class 4 TEF – 8.06 ± 0.47, which was the largest calculated TEF in our study). We assumed that if source contribution was influential enough in the mixing model, SIAR could account for the inconsistencies associated with the data, such as TEF variability and uncertainty (Parnell et al. 2010). We documented the TEF values and mixing-model results for all consumers to facilitate comparison across sites and taxa. C is relatively conserved across trophic levels, so we assumed a $\delta^{13}C$ fractionation rate of 0.4 ± 1.3‰ per trophic level, as did Post (2002) and Davis et al. (2012a). When analyzing outputs, we considered a source to be a likely contributor if its minimum contribution was ≥20% and a possible contributor if its minimum contribution was >0% and its maximum was ≥50%.

We standardized $\delta^{15}N$ for basal-source variability to calculate isotopic trophic position (ITP) for macroinvertebrates and fish. Plotting the values of primary consumers establishes a baseline relationship between these isotopic values for a given system that can then be used to calculate ITP for each individual based on its $\delta^{13}C$ and $\delta^{15}N$ (Vander Zanden and Rasmussen 1999, Jardine et al. 2013). It is necessary to account for this relationship to determine ITP of higher consumers because many individuals consume a variety of sources that differ in baseline $\delta^{15}N$ (Vander Zanden and Rasmussen 1999). $\delta^{15}N_{base}$ for a consumer was calculated from its corresponding raw $\delta^{13}C$ value as

$$\delta^{13}N_{base} = -1.850 - 0.196(\delta^{13}C) \quad \text{(Eq. 2)}$$

derived from primary-consumer baseline relationships ($r^2 = 0.177$, $p < 0.001$). Primary

consumers in our study were: zooplankton, Ephemeroptera (Baetidae, Caenidae, Leptophlebiidae), Coleoptera (Psephenidae, Hydrophilidae, Hydrochidae, Circulionidae, Elmidae, Hydraenidae), nonpredatory Trichoptera (Calamoceratidae, Leptoceridae:*Triplectides*), Lepidoptera, Decapoda (Atyidae), Gastropoda (Thiaridae, Corbiculidae, Hyriidae), and Diptera (Simuliidae, Culicidae). We calculated the isotopic trophic positions of macroinvertebrates and fish with the equation used by Winemiller et al. (2007):

$$\mathrm{ITP} = \left(\frac{\left[\delta^{15}\mathrm{N}_{\mathrm{consumer}} - \delta^{15}\mathrm{N}_{\mathrm{base}}\right]}{\Delta^{15}\mathrm{N}}\right) + 2 \qquad \text{(Eq. 3)}$$

where Δ^{15}N is the average change in δ^{15}N per trophic level based on the trophotaxon-specific diet–tissue fractionation values published by Bunn et al. (2013). We used 1-way analysis of variance (ANOVA) with Tukey's post hoc test (SigmaPlot 11, Systat Software Inc., San Jose, California) to identify differences in ITPs of herbivorous, predatory, and omnivorous fishes (classified by stomach-content analysis and Pusey et al. 2004, 2010) across all sites.

We estimated trophic position of fishes from stomach-content data (STP) with the equation published by Winemiller et al. (2007):

$$\mathrm{STP}_i = \sum_{j=1}^{n} \mathrm{TL}_j\left(\mathrm{p}_j\right) + 1 \qquad \text{(Eq. 4)}$$

where STP_i is the trophic position of target consumer *i*, TL_j is the trophic level of prey taxon *j*, and p_j is the volumetric contribution of prey species *j*. We based trophic levels of prey items on the dominant functional group of most of the members of a taxon (macroinvertebrates: Merritt and Cummins 1984, Cheshire et al. 2005; fishes: Pusey et al. 2010, our study). We coded primary producers (algae, vegetation, detritus, sediment) as TL = 1 and primary consumers (Ephemeroptera, Hydrophilidae, Elmidae, Lepidoptera, Orthoptera, Cladocera, Mollusca, and the fishes *Nematalosa erebi* and *Oreochromis mossambicus*) as TL = 2. We coded secondary consumers (Odonata, Ceratopogonidae, Tabanidae, Naucoridae, Gerridae, Veliidae, Dytiscidae,

295 Acarina, and the fishes *Craterocephalus stercusmuscarum*, *Oxyeleotris lineolatus*, and *Ambassis*
296 spp.) as TL = 3. We coded omnivores (Chironomidae, Simuliidae, Corixidae, Formicidae,
297 macrocrustacea, Copepoda, Ostracoda, the fish *Melanotaenia splendida*, unidentified fish, and
298 fish eggs) as TL = 2.5, while recognizing that the ratio of plant to animal consumption is unlikely
299 to be strictly 1:1 (and that not all members may feed in the same trophic group). We explored the
300 relationship between STP and ITP by linear regression.
301
302 **Food webs**
303 We constructed food webs for each site based on major links between foodweb
304 components (nodes). We considered a basal-source node present if components were available in
305 sufficient quantities for SIA (applies mainly to autochthonous material). A consumer was
306 'present' if ≥1 individual was collected from a site. We placed consumers in 1 of 10 categories:
307 zooplankton, detritus shredders, live-plant shredders/scrapers, benthic scrapers, benthic
308 gatherers/filter collectors, predatory macroinvertebrates, terrestrial/semiterrestrial
309 macroinvertebrates, herbivorous fishes, omnivorous fishes, or predatory fishes. We added links
310 according to SCA (fish only) and review of the literature. We did not use consumer ITPs to add
311 links. We designated macroinvertebrates (and their links) according to the feeding groups of
312 Merritt and Cummins (1984), Chessman (1986), and Gooderham and Tsyrlin (2002), and we
313 grouped fishes as herbivores, predators, or omnivores according to SCA (Pusey et al. 2010, our
314 study). We did not include other top predators (e.g., water birds and turtles) in these food webs.
315 We estimated the relative complexity of each food web by calculating the connectance of the
316 webs and their component groups as a proportion of the maximum possible connectance (Pimm
317 1984, Pimm et al. 1991). Following Chesire et al. (2005), we calculated link number as the actual

number of links, *S* as the number of elements in the food web (consumers + basal sources), maximum link as the maximum number of links possible in the food web (*S*[*S* – 1]/2), and connectance as the number of links/maximum number of links.

RESULTS

Across all sites, basal sources were the most N-depleted, fish were the most N-enriched, and macroinvertebrates were intermediate (Fig. 2). Basal sources were separated according to C value. The C4 grass *Cynodon dactylon* (Poaceae) had a $\delta^{13}C \approx -13‰$, and the rest of the sources (mostly C3 vegetation) had $\delta^{13}C$ values between –20 and –35‰ (Fig. S1A). With the exception of *C. dactylon*, different sources tended to overlap, especially filamentous algae with semiaquatic macrophytes and filamentous algae with FPOM/seston. Tree species within genera (e.g., *Melaleuca* and *Eucalyptus*) did not always have similar $\delta^{13}C$ values, and values for filamentous algae varied greatly. $\delta^{13}C$ values of macrophyte species tended to group according to habit (true aquatic, e.g., *Potamogeton* spp. or semiterrestrial, e.g., *Persicaria decipiens*) (Fig. S1B).

Among the consumers, herbivorous macroinvertebrates (e.g., Ephemeroptera) were N-depleted, and predators (e.g., Acarina, Odonata, some Hemiptera and Coleoptera) were N-enriched (Fig. S2A). Detritivores, scavengers, filter feeders, and omnivores (notably the Bivalvia [Fig. S2A] and Decapoda [Fig. S2B]) also were N-enriched. This pattern was repeated in the fishes. Herbivores (*Nematalosa erebi* and *Oreochromis mossambicus*) usually were N- and C-depleted (Fig. S3), but 3 omnivorous/herbivorous terapontids (*Hephaestus fuliginosus*, *Scortum parviceps*, *Leiopotherapon unicolor*) were the most C- and N-enriched. Falling between these 2 groups were the predators, which had the greatest range of $\delta^{13}C$ and $\delta^{13}N$ values.

The SIAR mixing calculations were notable for the high level of source fidelity within

individual sites by different consumer taxa (Tables 2, 3). For both macroinvertebrates and fish, 7 of the 9 sites with multiple significant results had only 1 type of likely or possible basal source per site, despite the presence of a wide range of taxa and potential sources. Sites varied in their dominant basal sources even within a river: for example, the main source at sites BU1, BU1a, and BU2 was terrestrial C3 vegetation, but at site BU3 it was filamentous algae. Semiaquatic macrophytes were an important source for fish at site C1 and for macroinvertebrates and fishes at site BA4. At site BA1, macroinvertebrates were strongly aligned with filamentous algae, as was the herbivorous fish *Nematalosa erebi*. However, the diet of *Amniataba percoides*, also at site BA1, appeared to be based on terrestrial C3 vegetation. At site K2, macroinvertebrates and the fish *Mogurnda adspersa* were aligned with Fe-fixing bacteria. Sources at site K4 were consistent within but not between consumer groups (macroinvertebrates: terrestrial C3 vegetation and semiaquatic macrophytes, fish: C4 grasses).

High proportions of macroinvertebrates (72%) and fish (87%) had unresolved mixing models (Tables 2, 3). Only 10% of the unresolved models for macroinvertebrates were the result of consumers being outside the source-mixing polygon, a result indicating that most unresolved models resulted from omnivory or lack of source differentiation (even between autochthonous and allochthonous sources). For example, at site BA1, filamentous algae and submerged terrestrial leaves (dominant species *Eucalyptus camaldulensis*) were not well differentiated ($\delta^{13}C$ = –31.37 and –29.87, respectively). At site K3, filamentous algae and submerged *Melaleuca leucadendra* leaves were not well differentiated ($\delta^{13}C$ = –31.89 and –32.45, respectively). Only 7% of the unresolved models for fishes were outside the source-mixing polygons after application of alternative TEFs. The remaining unresolved fish models were within the source-mixing polygons with (19%) or without (74%) alternative TEFs.

ITP of macroinvertebrates varied among sites, even within a taxon (Table S3; also shows site-specific taxonomic groups). Decapods (particularly Palaemonidae) generally had the highest ITP (3.18–5.06). Little consistency was observed at the lower and middle trophic positions, although the Odonata (Hemicorduliidae, Urothemistidae, Libellulidae) had the lowest ITP at 4 sites (ITP = 1.25–3.23).

ITP of fish also varied among sites and within species (Table S4). However, one trophotaxon (*Hephaestus fuliginosus* size class 4) had the highest ITP (3.53–4.81) at 6 of 8 sites. ITP differed significantly among herbivores, omnivores, and carnivores across all sites (F_{407} = 26.35, $p < 0.001$). The differences were associated with herbivorous fishes. ITPs of omnivores and carnivores did not differ (Tukey's post hoc test $p = 0.205$), but herbivores differed significantly from both ($p < 0.001$) and generally had lower ITPs (mean herbivore ITP = 3.00 ± 0.591, omnivore ITP = 3.60 ± 0.47, carnivore ITP 3.36 ± 0.43). Little consistency in ITP values was found at the lower and middle trophic positions for fish.

STP of fish varied among sites, even within the same species (Table S5). STP differed significantly among herbivores, omnivores, and carnivores ($F_{317} = 62.91$, $p < 0.001$), with all groups significantly different from each other (Tukey's post hoc test, $p < 0.003$). STP and ITP were not correlated within species, and they were correlated at only 2 sites: BA4 ($p = 0.011$, r^2 = 0.179), and K4 ($p = 0.024$, $r^2 = 0.266$).

Omnivory occurred throughout the food web and was most prevalent at the top, where omnivorous fishes were numerous and fed at all trophic levels. Relative to other taxonomic groups, omnivorous fishes also had the most potential connectivity (Fig. 3). Feeding across multiple trophic levels also was characteristic of many of the macroinvertebrate taxa collected, particularly the aquatic predators and semiterrestrial spiders, which varied among sites (Fig. 4).

Within invertebrate feeding groups (especially the live-plant shredders/scrapers and benthic gatherers/filter collectors), taxa were able to exploit multiple basal sources at different sites (Fig. 4). Overall, foodweb structure differed among sites mainly because of the presence or absence of 2 basal sources (filamentous algae and Fe-fixing bacteria) and particular primary consumers (zooplankton, shredders, aquatic macrophyte consumers) (Table S6, Fig. 4). The higher consumer levels were represented at all sites.

The average connectance across sites was 0.320 ± 0.04, with BU1a having the lowest connectance (0.231) and K3 having the highest connectance (0.385) (Table 4, Fig. 4).

DISCUSSION

Omnivory was a major feature of the food webs in the seasonal rivers of the Burdekin catchment, and connections between consumers and prey items were short. We hypothesized that, particularly for fish, omnivory would be widespread. We found that the use of stable isotopes in this variable system resulted in many unresolved mixing models (for fish and invertebrates), and occasionally poor differentiation among basal sources. Therefore, we support the use of complementary techniques (such as SCA) to enhance the outcomes of stable isotope studies (e.g., Beaudoin et al. 1999, Mantel et al. 2004, Davis et al. 2012a). Complementary techniques can provide useful comparisons, even if a potential mismatch exists between STP and ITP because of seasonal opportunism in feeding (Beaudoin et al. 1999).

Omnivory in dry-tropics rivers may be an adaptation to seasonally variable hydrological conditions (Winemiller 2004, Douglas et al. 2005, Leigh et al. 2010, Pusey et al. 2010) because dietary specialization is more prevalent when food sources are predictable (Pusey et al. 2010). Widespread omnivory among fishes of the Burdekin River has been recorded previously,

410 although spatial variability in diets was low (Pusey et al. 2010). STP of fish in our study
411 indicated that diets varied within some fish trophospecies across sites, as did foodweb structure
412 and connectance. The results obtained by Pusey et al. (2010) differ from ours and those of other
413 studies in which diets of fishes differed spatially according to habitat structure and prey
414 availability (Pusey et al. 1995, Romanuk et al. 2006), even within reaches (Rayner et al. 2009).
415 Pusey et al. (2010) attributed this disparity in the Burdekin River to a lack of in-stream habitat
416 structure (floodplains, backwaters, riffles, rapids), but we found diverse habitats and varying
417 hydrological conditions among sites. These contrasting results may reflect different temporal
418 conditions, or simply methodological and fine-scale habitat variability. Despite these incongruent
419 findings, omnivory, especially in fish, clearly is characteristic of dry-tropics river assemblages.
420 Foodweb structure differed mainly in the presence or absence of particular primary
421 consumers and basal sources, with some food webs driven by allochthonous C and others by
422 autochthonous sources, such as filamentous algae, even among sites within the same river. We
423 hypothesized that basal-source importance would be patchy within and among rivers as a
424 function of local-scale biophysical variability (especially riparian condition). It is tempting to
425 equate availability of basal sources with their relative importance in the food web (e.g., Vannote
426 et al. 1980), but this relationship was inconsistent across sites. For example, Keelbottom Creek
427 had extensive canopy cover and large accumulations of terrestrial leaf litter in the stream, but
428 mixing-model analysis identified a variety of sources, with C3 vegetation only weakly important
429 for macroinvertebrates at 1 site. In contrast, C3 vegetation was consistently important at the
430 Burdekin River sites, despite varying canopy cover and leaf-litter input. In a subalpine Colorado
431 stream, C assimilated by consumers did not reflect its availability because terrestrial C3
432 vegetation was important in the food webs despite little canopy cover (McCutchan and Lewis

433 2002). At lower elevations in this Colorado stream, where allochthonous litter was abundant,
434 benthic algae were more important sources of C (McCutchan and Lewis 2002). In a forested
435 stream in tropical Queensland, stable-isotope data indicated that consumers were more dependent
436 on epilithic algae than terrestrial vegetation and that filamentous algae and aquatic macrophytes
437 did not contribute to the broader food web (Bunn et al. 1999). This tropical Queensland study
438 assumed that sites from 3 streams in the same catchment ('biome') were sufficiently similar to be
439 replicates. Streams from a small catchment might possibly be less spatially diverse than large
440 dry-tropics rivers, but our data and those of others (e.g., McCutchan and Lewis 2002) show that
441 we cannot assume that conditions at individual sites can be extrapolated to larger scales or that
442 data can be reliably compared to reference sites to determine baseline ecological function
443 (Sheldon 2005, Blanchette and Pearson 2012, 2013). In the case of stable-isotope studies, we
444 cannot rely on basal-source availability as a proxy for basal-source importance.

445 The importance of terrestrial C3 vegetation at some sites and the basal-source variability
446 throughout the catchment, contrasts with the findings from some other dryland and dry-tropics
447 river foodweb studies that identify autochthonous material as the most important dry-season C
448 source (Bunn et al. 2003, Douglas et al. 2005, Fellows et al. 2007, Jardine et al. 2013). This view
449 differs from the notion of floodplain connectivity, whereby floodplain-derived terrestrial
450 vegetation supports food webs for at least part of the year (Junk et al. 1989, Junk and Wantzen
451 2004). In a hydrologically variable Texas river, terrestrial C3 vegetation supported most
452 consumers, but important C sources varied with flow regime (Zeug and Winemiller 2008). These
453 results concur with other Australian wet–dry tropics studies (Leigh et al. 2010, Hunt et al. 2012)
454 where terrestrial or floodplain sources can be important in riverine food webs, and the
455 importance of different basal sources can be spatially and temporally variable.

In addition to predicted basal sources (e.g., leaf litter and filamentous algae), isotopic mixing models identified some surprising C sources, such as Fe-fixing bacteria at site K2 and aquatic macrophytes at sites C1, BA4, and K4. Site K2 was blanketed with a thick layer of bacteria at the time of sampling, and basal sources could have been contaminated by the bacteria, which were inadvertently ingested by consumers. However, previous investigators using SIA (e.g., Sarbu et al. 1996, Opsahl and Chanton 2006, Roach et al. 2011) have described the importance of microbes to freshwater metazoans, although their research mainly occurred in light-limited subterranean caves. Clearly, more research is needed to describe the influence of microbes on freshwater food webs. We found that, consistent with gut contents, aquatic macrophytes were important sources for macroinvertebrates and fish at some sites (cf. Watson and Barmuta 2011). However, others have reported that macroinvertebrates do not assimilate aquatic macrophytes (e.g., Hamilton et al. 1992, Bunn and Boon 1993). We suggest that macrophytes be considered as potential sources when collecting data for foodweb studies, and field sampling regimes should be flexible enough to take advantage of unanticipated C sources.

We did not find good agreement between ITP and STP, a result that probably was a reflection of the contrasting temporal and physiological attributes characteristic of both methods. Stable isotope analysis provides a direct measure of tissue assimilation and is a longer-term indication of diet than gut content analysis (Winemiller et al. 2007) because of lags in material assimilation (Fry and Arnold 1982, Herzka and Holt 2000, McIntyre and Flecker 2006). For longer-lived animals, especially those that are migratory, isotopic composition may reflect their feeding in environments other than where they were collected (Jackson and Harkness 1987, Herzka 2005) and hydrological connectivity between sites (Jardine et al. 2012). This consideration is important when using mixing models to estimate the contribution of food

479 sources because models assume that consumer tissues are in isotopic equilibrium with the
480 sources present at time of collection (Martinez del Rio et al. 2009, Codron et al. 2012).
481 Moreover, many fishes display size-related dietary shifts, e.g., juveniles of most terapontid
482 species are invertivorous, but become carnivorous, omnivorous, herbivorous, or detritivorous as
483 they grow (Davis et al. 2011). These transitions also are affected by habitat and environmental
484 variability (Davis et al. 2012b). The temporal effects of assimilation on such species are unclear,
485 but a significant lag time coupled with migration probably would affect source–consumer
486 equilibrium (e.g., Jardine et al. 2012) and, hence, calculation of ITP. Feeding experiments are
487 needed to correct for differential assimilation between taxa and among tissue types (Gannes et al.
488 1997, Martinez del Rio et al. 2009) and to allow for more robust comparisons between stomach-
489 content and SAI approaches.

490 Temporal variability in basal-source use is likely to be more apparent lower in the food
491 web where organisms are shorter-lived. Food webs at all sites had representatives of the higher-
492 level consumers (omnivores and predators), but differed mainly in connectance because of the
493 presence (or absence) of particular taxa at some sites. Therefore, despite variation in basal
494 sources among sites, food webs were similar at the top. Dryland-river fish are hardy but
495 assemblages are species-poor, compared to nearby wet-tropical assemblages (e.g., Pusey and
496 Kennard 1996), and consumer persistence and mobility could have affected the relative
497 importance of basal sources. For example, in another Australian tropical river, within-channel
498 benthic algae supported macroinvertebrates during the dry season, whereas higher consumers
499 may have assimilated a floodplain C source (Hunt et al. 2012). Therefore, the relatively long-
500 lived fishes may reflect interannual processes (including hydrological connectivity) and spatial
501 variability of C sources, whereas macroinvertebrates, with shorter generation times, reflect more

recent, local conditions and basal sources (Jardine et al. 2012). Thus, generation time and prevailing environmental conditions may partly explain variability among sites at the base of the food webs.

Despite this variability, herbivores were generally N-depleted, predators were generally N-enriched, and omnivores varied, as expected (e.g., Minagawa and Wada 1984, Fry 1988). Notably, the omnivorous macroinvertebrates and the omnivorous–herbivorous terapontid *H. fuliginosus* were highly N-enriched, even in comparison with the top predators. It is not uncommon for isotopic values to overestimate trophic position in herbivores and omnivores (Carseldine and Tibbetts 2005, Layman et al. 2005a, Mill et al. 2007, Winemiller et al. 2011). Given that our SCAs concurred with those of Pusey et al. (2010), this result may have been partly caused by assimilation by animals of invertebrate biomass and voiding of refractory detritus (Winemiller et al. 2007).

Despite our care in separating sources and consumers, the characteristics of the system under study (high spatial and temporal ecological variability, basal-source similarity) precluded definitive answers to some stable-isotope questions, at least at some sites. In addition, the use of isotopic mixing models has its own challenges. In the absence of feeding trials, assumed TEF values are widely applied in most ecological studies, despite the fact that this assumption has been cited as a potential source of error in modeling (Caut et al. 2009, Bond and Diamond 2011). We used the trophic-level-specific TEF values published by Bunn et al. (2013) (and, in some cases, nontrophic-aligned TEF values derived from our study) rather than the same average value for every consumer, but our values were still assumed and, therefore, were potential sources of error. One of the advantages of SIAR is that it operates under Bayesian assumptions and can readily account for variation in trophic fractionation (Parnell et al. 2010). However, SIAR is not

525 insensitive to variability in fractionation (Bond and Diamond 2011). One strategy is to exclude N
526 from isotope mixing models in favor of other elements, such as C and S (e.g., Melville and
527 Connolly 2005, Benstead et al. 2006, Leigh et al. 2010), which have smaller trophic fractionation
528 values (McCutchan et al. 2003).

529 Comparison of foodweb structure among different ecosystems or studies is hampered by
530 an unequal distribution of variables (Pimm et al. 1991, Vermaat et al. 2009) and different levels
531 of taxonomic resolution (Mantel et al. 2004, Cheshire et al. 2005). In our study, connectance
532 varied among sites, even within the same river. Cheshire et al. (2005) found that in upland
533 rainforest tributaries of the Burdekin catchment, overall connectance of the invertebrate food
534 web varied between 0.19 and 0.26 (cf. 0.23–0.39 in our study). Lowland tributaries of the
535 Burdekin may appear to be more highly connected than the rainforest reaches, but whether these
536 data are directly comparable in unclear because different methods were used in the 2 studies
537 (e.g., animal collection, taxonomic resolution). We used binary trophic links (i.e., a link is either
538 present or absent) to construct food webs. However, binary methods may be hampered by an
539 absence of direct quantitative measurements of energy flow (e.g., biomass, productivity) and,
540 therefore, the relative importance of each link. On the other hand, the difficulty of quantifying
541 every energetic relationship in a food web can obfuscate the broader measurement of energy
542 transfer. Ideal foodweb studies should incorporate both flow- and binary-based data to test the
543 influence of multiple variables on foodweb metrics (Cheshire et al. 2005).

544 Ecosystem robustness, or the ability of a food web to withstand random extinctions, is
545 thought to increase as overall foodweb connectivity increases (Dunne et al. 2002). In highly
546 omnivorous food webs, removal of one well-connected taxon may have little overall effect on
547 the food web, whereas removal of many of these taxa may cause further extinctions (Mantel et

548 al. 2004). In our study, the absence of a few key taxa (e.g., zooplankton and semiterrestrial
549 fishing spiders) appeared to affect connectance strongly at the site level, consistent with
550 theoretical expectations of their strong leverage in food webs (Dunne et al. 2002). Zooplankters
551 provide a critical link between seston and the broader food web, and semiterrestrial spiders
552 facilitate aquatic–terrestrial linkage. In contrast, omnivorous fish provided most links in the food
553 web, but the loss of any one of these taxa had little effect because omnivory was common to
554 several species. Species losses of ≥20% often are required before effects are propagated to the
555 broader food web as secondary extinctions (Dunne et al. 2002). These results suggest that dry-
556 tropical river food webs will be able to withstand perturbations provided that complementary,
557 highly connected species are retained.
558
559 **Conclusions**
560 The SIAR model tended to work best at sites where basal-source groupings were
561 isotopically distinct and sources could be grouped confidently according to habitat (e.g.,
562 terrestrial or aquatic) with minimal variability. In our study, the model did not consistently
563 differentiate between autochthonous sources, and at some sites, autochthonous and allochthonous
564 materials had similar $\delta^{13}C$ values. Such are the well-known problems of stable-isotope-based
565 studies of food webs, and our understanding of them is restricted accordingly. Unfortunately,
566 some authors appear not to report such issues. Appropriate conclusions and future improvements
567 in stable-isotope ecology depend on reporting variability and anomalies in the data.
568 Our study has confirmed the inherent variability of dry-tropics rivers (Blanchette and
569 Pearson 2012, 2013). During the dry season, spatial variability occurred in basal-source
570 contribution to food webs, trophic position of individual taxa, and foodweb structure, with sites

from the same river often as different as sites from different rivers. Therefore, our study is unusual because it highlights this variability of sources across sites in the same catchment (cf. Bunn et al. 2003, Douglas et al. 2005, Fellows et al. 2007, Jardine et al. 2013). The high variability in dryland river ecology may be a response to variable flow regimes, with food webs exhibiting dynamic stability (Leigh et al. 2010) that allows species to persist in the face of harsh environmental conditions. Our study supports this idea, especially at the top of the food web, where omnivorous fishes were found consistently at sites with different basal sources and primary consumers.

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844 **FIGURE CAPTIONS**

845 Fig. 1. Map showing the locations of study sites in the Burdekin catchment, Queensland,
846 Australia.

847 Fig. 2. Mean (±1 SD) $\delta^{13}C$ and $\delta^{15}N$ ratios of basal sources, fish (F), and invertebrates (I)
848 collected from all sites. Basal source codes are: FA = filamentous algae, ST =
849 semiterrestrial macrophytes, FS = fine particulate organic matter and seston, C3 =
850 terrestrial C3 vegetation, BF = biofilm, M = true aquatic macrophytes, C4 = C4 terrestrial
851 grasses, BA = Fe-fixing bacteria, FAD =C^{13}-depleted filamentous algae. Each consumer
852 point represents a unique taxon.

853 Fig. 3. Burdekin River foodweb template showing maximum connectivity of major components
854 (consumers and basal source) across all sites. Abbreviations in circles represent consumer
855 feeding groups/trophic levels: Zoop. = zooplankton, Det. shred. = detrital shredders,
856 LS/scrap. = live plant shredders and scrapers, Bent. scrap. = benthic scrapers, Gath/filt. =
857 benthic gathering and filter collectors, Pred. invert = predatory invertebrates, Terr. Invert
858 = terrestrial/semiterrestrial invertebrates, Herb. fish = herbivorous fishes, Omniv. fish =
859 omnivorous fishes, Pred. fish = predatory fishes. Basal source: FPOM = fine particulate
860 organic matter.

861 Fig. 4. Food webs for each site. Numbers in circles represent consumer feeding groups/trophic
862 levels: 1, zooplankton; 2, detrital shredders; 3, live plant shredders and scrapers; 4,
863 benthic scrapers; 5, benthic gathering and filter collectors; 6, predatory invertebrates; 7,
864 terrestrial/semi-terrestrial invertebrates; 8, herbivorous fishes; 9, omnivorous fishes; 10,
865 predatory fishes. Letters at bottom of figure represent basal sources: C3 = C3 detritus/leaf
866 litter, FA = filamentous algae, FS = fine particulate organic matter/seston, BF = biofilm,

867 M, aquatic macrophytes, BA = Fe-fixing bacteria, FAD = ^{13}C-depleted filamentous algae.
868 Underlined basal sources indicates source present at site and analyzed for δ^{13}C and δ^{15}N.
869 Underlined and bold sources indicate source identified as a significant contributor to food
870 web as determined by stable-isotope analysis for R (SIAR) mixing model. Grey basal
871 sources and links indicate component not found at site. * = source present but not
872 collected for analysis. See Table 1 for abbreviations of sites/rivers.
873

Table 1. Habitats and biophysical variables at study sites in the Burdekin catchment, dry season 2009. BA = Basalt River, BU = Burdekin River, C = Cape-Campaspe River, K = Keelbottom Creek, Peri = benthic periphyton, Macro = macrophyte, Leaf = terrestrial leaf litter, Bare = exposed benthic sediment, Rip = riparian condition (Dixon et al. 2006), DO = dissolved O_2, Cond = conductivity, Temp = temperature, ns = no sample.

Site	In-stream	Sampling		% substratum cover[c]						Shade	Secchi	DO	Cond		Temp	Velocity
codes	habitats[a]	depth (m)	Substratum[b]	Peri	Algae	Macro	Leaf	Bare	Rip	(%)	(m)	(mg/L)	(mS/cm)	pH	(°C)	(m/s)
BA1	E, Ri, Mb	0.15–1.50	1, 2, 3, 5	1	1–2	1–3	1	1–2	32.9	10–50	0.50	9.59	1.29	8.35	27.4	0–0.33
BA4	E, Sp, Ri	0.20–1.75	1, 3, 4, 5	1	1	0	0–1	2–4	40.1	0–50	1.8	8.74	0.97	8.65	27.3	0–0.65
BU1	E, Ru	0.25–0.30	2, 3	1	1	1	1	0	ns	0–5	3.0	7.40	0.66	8.50	23.5	0–0.20
BU1a	Sp, Ru	0.50–1.50	1, 2	0–1	1	0–2	1	0–1	ns	10–50	3.0	8.20	0.62	8.40	25.9	0–0.30
BU2	Ru, Me	0.10–1.50	1, 5	1–2	1	0–3	1	1–2	51.3	0	0.6	8.22	0.35	8.22	25.3	0–0.33
BU3	E, Ru, Ri	0.15–0.75	1, 2, 4, 5	1	1	0–1	0–1	2	46.8	0–50	3.0	9.28	0.49	8.78	28.0	0–0.67
C1	E, Sp	0.20–1.00	1, 2, 3	0	0	0	2	2	63.5	10–15	0. 5	7.82	0.16	8.06	24.7	0–0.3
C3	E, Sp	0.20–0.40	1, 2, 3	1	1–2	0	1–4	0–1	47.5	50–60	1.0	8.47	0.17	7.56	26.6	0
K1	E, Rp	0.10–0.50	1, 5	2	0	0–1	1–3	1–2	50.6	0–50	3.0	8.70	0.16	8.54	25.9	0
K2	Sp, Me	0.70–2.75	1, 2, 3	0	0–2	0–3	4	0–1	40.1	60–95	1.5	6.68	0.32	7.32	27.5	0
K3	Sp, Ri, Me	0.05–2.00	1, 5	1–3	1–2	0–3	1–4	0–2	41.8	0–50	1.6	6.36	0.42	7.43	24.3	0–0.33
K4	E	0.30	1	1	0	0	4	0	50.1	50	1.5	6.55	0.40	7.50	25.8	0

[a] E = edge, Sp = sandy pool, Ru = run, Ri = riffle, Rp = rocky pool, Me = macrophyte-edge, Mb = macrophyte-bed

[b] 1 = silt, 2 = sand, 3 = gravel, 4 = bedrock, 5 = complex mix of boulder, cobble, gravel

879 [c] 0 = <10, 1 = 10–35, 2 = 36–65, 3 = 66–90, 4 = >90%

880 Table 2. Results of stable isotope analysis for R (SIAR) mixing model for invertebrates collected from each site. Abbreviations indicate dominant
881 basal source (see Fig. 4 for abbreviations). Bold = ≥20% minimum contribution to mixing model, regular type = <20% minimum contribution
882 and maximum contribution ≥50%, n = not resolved (equal contribution of sources, isotopic source overlap, or consumer outside basal-source
883 polygon. See Table 1 for site abbreviations. – indicates consumer not found at site.

		Site											
Taxon	Family	BU1	BU1a	BU2	BU3	C1	C3	BA1	BA4	K1	K2	K3	K4
Bivalvia	Corbiculiidae	–	n[a]	–	n	–	n	**FA**	–	–	–	–	–
Coleoptera	Dytiscidae	**C3**	C3	–	n	n	n	**FA**	n	n	n	n	n
	Hydrophilidae and Hydrochidae	n	–	n	n	n	n	n	n	–	–	n	n
Ephemeroptera	Baetidae	–	–	n	n	–	–	FA	n	–	–	–	–
	Caenidae	–	–	–	n	n[a]	n	–	n	n	**BA**	–	C3, ST
Gastropoda	Thiaridae	n	C3	–	n	–	–	n	–	n	–	–	–
Hemiptera	Mixed predators	**C3**	–	n	n	n	n	FA	n	n	n	n	n
Lepidoptera		–	–	n[a]	FAD	–	–	n[a]	n	–	n	–	–
Arachnida	Acarina	–	–	–	–	n[a]	n	–	ST	–	BA	–	–

Odonata	Coenagrionidae	C3	C3	n	n	–	n	FA	–	n	–	n	C3, ST
	Gomphidae	C3	–	C3	**FAD**	n[a]	n	n	n	n	**BA**	n	C3, ST
	H, U, L[b]	C3	C3	n	n	n	n	FA	n	n	BA	n	C3
	Leptoceridae	–	C3	n	n	–	n	n	n	n	BA	n	n

884 [a] Consumer outside source geometry

885 [b] Hemicorduliidae, Urothemistidae, Libellulidae

886

887 Table 3. Results of stable isotope analysis for R (SIAR) mixing model for fish collected from each site. Taxon size classes follow Pusey et al.
888 (2010). Abbreviations indicate dominant basal source (see Fig. 4 for abbreviations). Bold = ≥20% minimum contribution to mixing model,
889 regular type = <20% minimum contribution and maximum contribution ≥50%, n = not resolved (equal contribution of sources, isotopic source
890 overlap, or consumer outside basal-source polygon. See Table 1 for site abbreviations. – indicates consumer not found at site.

Taxon (size class)	Site											
	BU1	BU1a	BU2	BU3	C1	C3	BA1	BA4	K1	K2	K3	K4
Ambassis agrammus (2)	–	n	–	–	n[b]	n[b]	n	–	n	n	–	–
Amniataba percoides (2)	–	n	n	–	–	–	**C3**[b]	**ST**	n[3]	n	n	n
Hephaestus fuliginosus (4)	n[a]	n	n	n	n[a]	–	n	–	n	n	–	–
Leiopotherapon unicolor (1)	–	n	n	n	n[a]	n[b]	–	n	n	n	n	n[a]
Leiopotherapon unicolor (3)	n	n	n	n	n[a]	–	n	n	n	n	n[a]	**C4**[b]
Melanotaenia splendida (1)	C3	n	n	–	n[b]	n[b]	n	–	n	–	n	n
Melanotaenia splendida (3)	–	n	n	–	n[b]	–	n	n	n	n	n[a]	**C4**[b]
Mogurnda adspersa (2)	–	–	–	–	n[b]	n[b]	n	–	n	BA	n	**C4**
Nematalosa erebi (3)	–	–	n	–	n[a]	–	**C3**[b]	n	n	–	n	–
Neosilurus ater (4)	–	n	n	n	**ST**[b]	–	–	n	n	n	–	–
Neosilurus hyrtlii (3)	–	n	–	–	**ST**[b]	n[b]	–	–	–	n	n	n
Neosilurus mollespiculum (4)	–	–	–	–	–	–	–	n[b]	–	–	–	–

Oreochromis mossambicus (2)	n	–	–	–	–	n[b]	–	n	–	n	n	n[c]
Oreochromis mossambicus (4)	–	C3	–	FA	n[b]	–	–	–	n	n	n	–
Oxyeleotris lineolatus (2)	–	n	n	n	ST[b]	–	–	n	C3	n	–	n[a]
Oxyeleotris lineolatus (4)	n	n	n	n	n[b]	n[b]	–	–	n	n	n	**C4[b]**
Scortum parviceps (2)	–	n[b]	–	n	–	–	–	–	–	–	–	–
Scortum parviceps (3)	–	n	–	n	–	–	–	–	–	–	–	–
Scortum parviceps (4)	–	–	n[2]	–	ST[b]	–	–	n	–	–	–	–

[a] Consumer outside source geometry

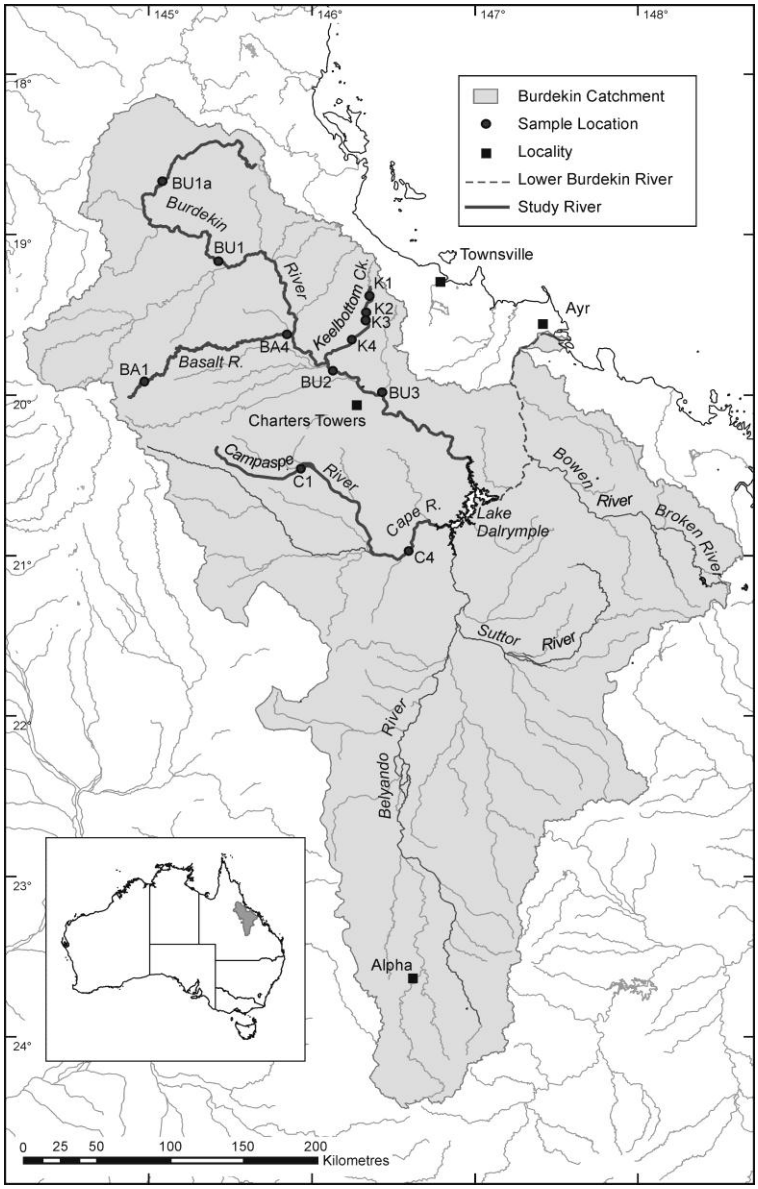
[b] *Hephaestus fuliginosus* (4) trophic enrichment factors used to place consumer within basal-source polygon

[c] Site-specific predator trophic enrichment factors used to place consumer within basal-source polygon

895 Table 4. Foodweb connectance at sites in the Burdekin catchment, organized by connectance
896 (as per Pimm 1984, Pimm et al. 1991, and see Cheshire et al. 2005). Links is actual number of
897 links, S is number of elements in the web (consumers plus basal sources), Max. links is
898 maximum number of links possible in web according to S(S – 1)/2, connectance is number of
899 links/maximum number of links. Also shown is mean connectance (with standard deviation
900 [SD]) across all sites. Sites as per Table 1.

Site	Links	S	Max. links	Connectance
BU1a	18	13	78	0.231
C3	27	15	105	0.257
BU3	32	15	105	0.305
BA4	28	14	91	0.308
K2	43	17	136	0.316
K1	29	14	91	0.319
BU1	25	13	78	0.321
C1	25	13	78	0.321
BU2	32	14	91	0.352
BA1	37	15	105	0.352
K4	29	13	78	0.372
K3	35	14	91	0.385
Mean				0.320
SD				0.044

901


145°
146°
147°
148°
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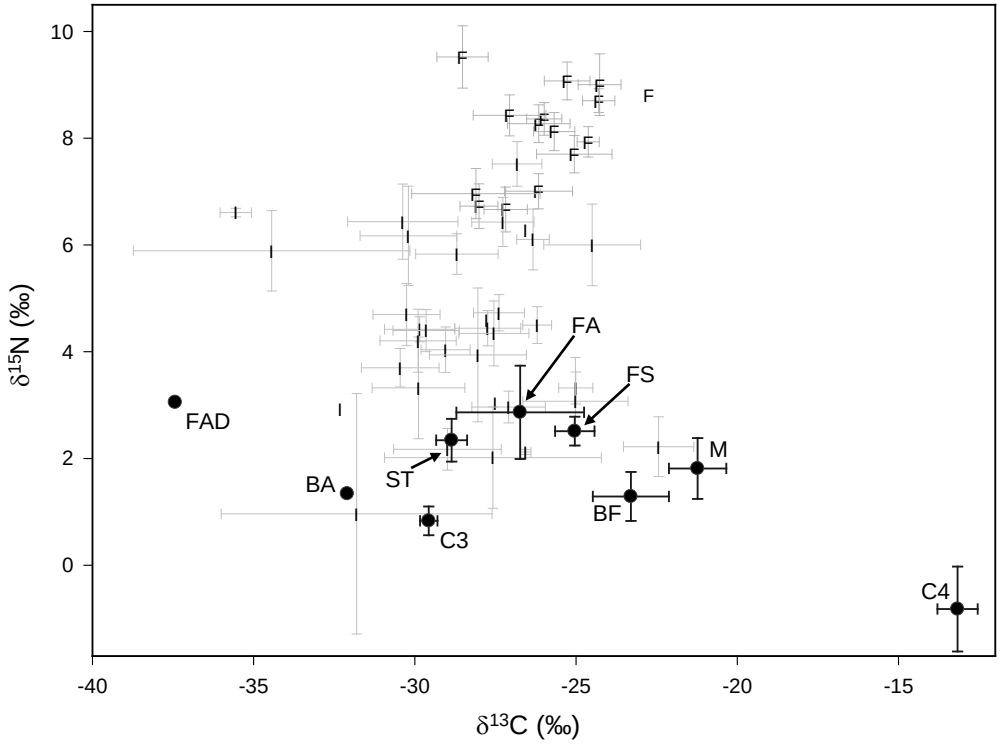
20°
21°
22°
23°
24°
Burdekin Catchment
Sample Location
Locality
Lower Burdekin River
Study River
BU1a
Burdekin
BU1
River
Townsville
K1
Keelbottom Ck.
K2
K3
Ayr
BA4
K4
BA1
Basalt R.
BU2
BU3
Charters Towers
Campaspe
C1
River
Cape R.
Lake
Dalrymple
C4
Bowen River
Broken River
Suttor River
Belyando River
Alpha
0 25 50 100 150 200
Kilometres


10
8
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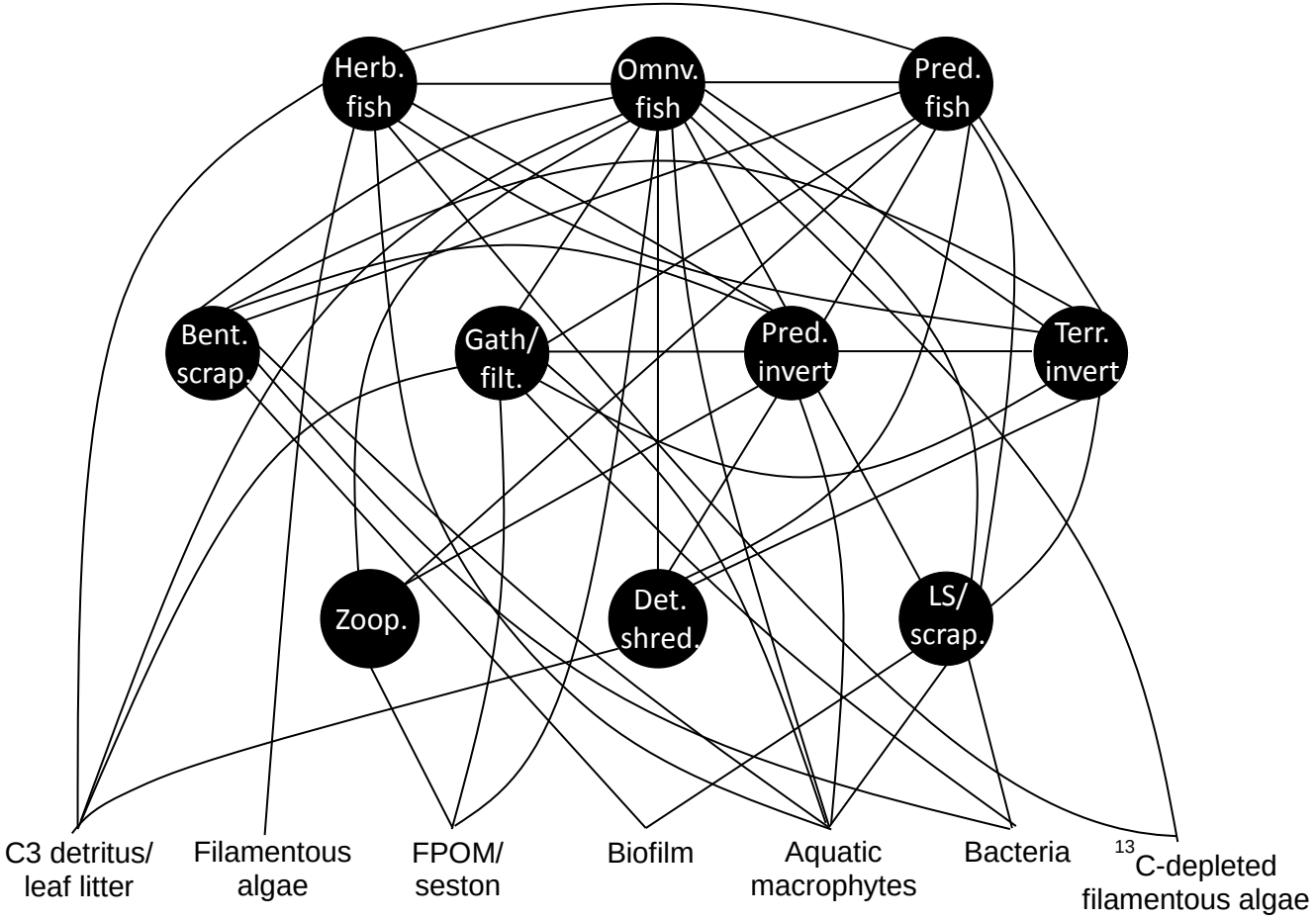
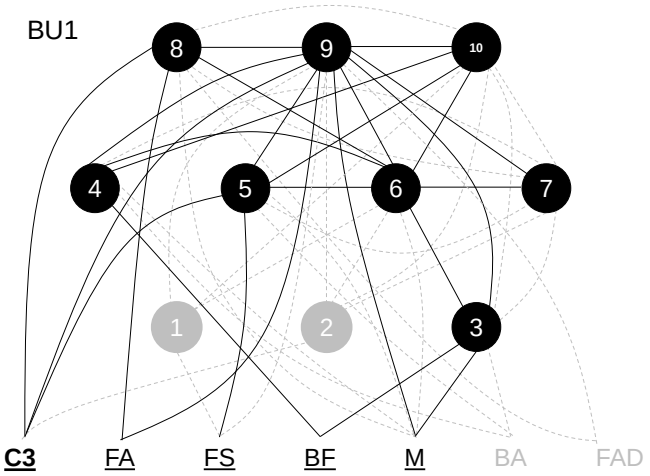
4
2
0
-40
-35
-30
-25
-20
-15
δ15N (‰)
δ13C (‰)
FAD
BA
ST
C3
FA
FS
M
BF
C4


Herb. fish
Omnv. fish
Pred. fish
Bent. scrap.
Gath/ filt.
Pred. invert
Terr. invert
Zoop.
Det. shred.
LS/ scrap.
C3 detritus/ leaf litter
Filamentous algae
FPOM/ seston
Biofilm
Aquatic macrophytes
Bacteria
13C-depleted filamentous algae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C3
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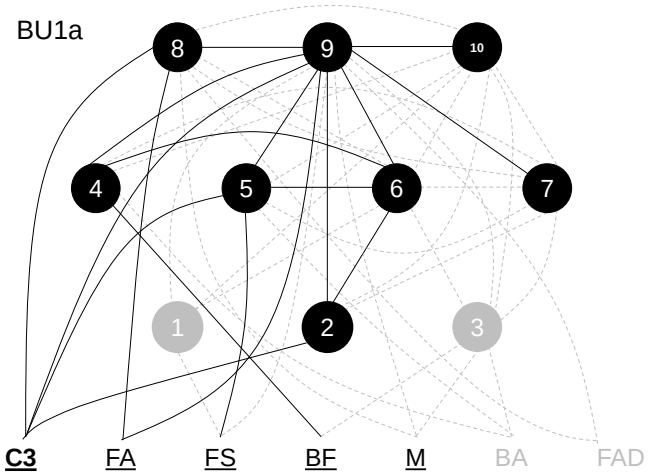
BU1a
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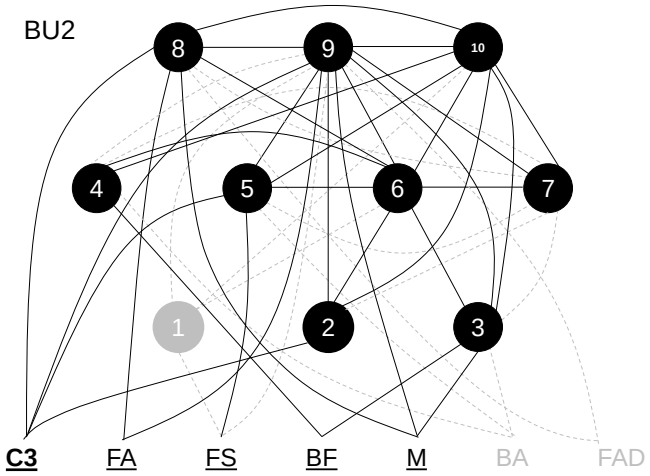
BU2
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C3
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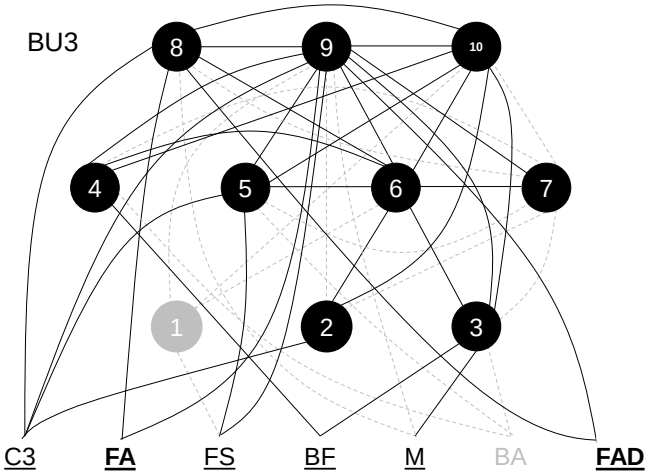
BU3
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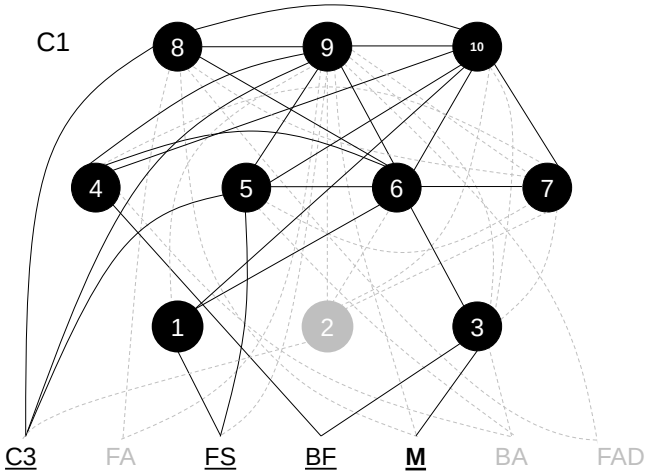
C1
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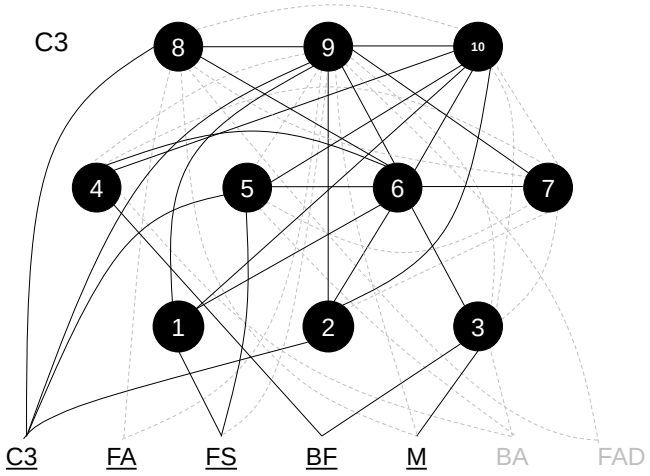
BA
FAD


C3
8
9
10
4
5
6
7
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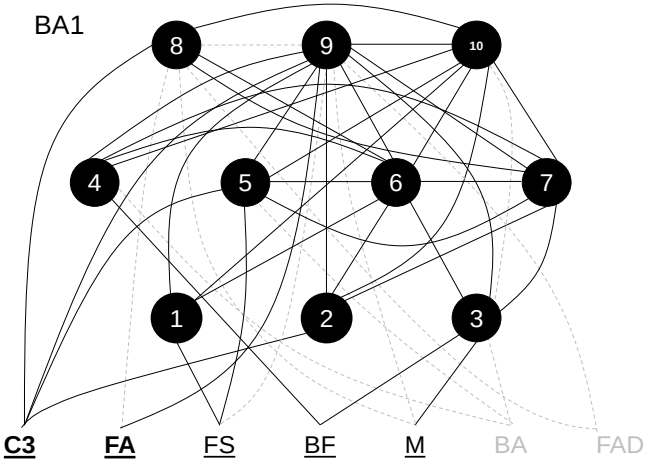
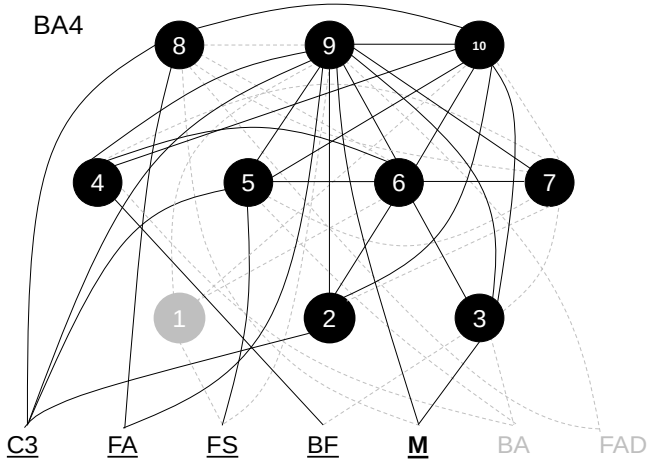
2
3
C3
FA
FS
BF
M
BA
FAD

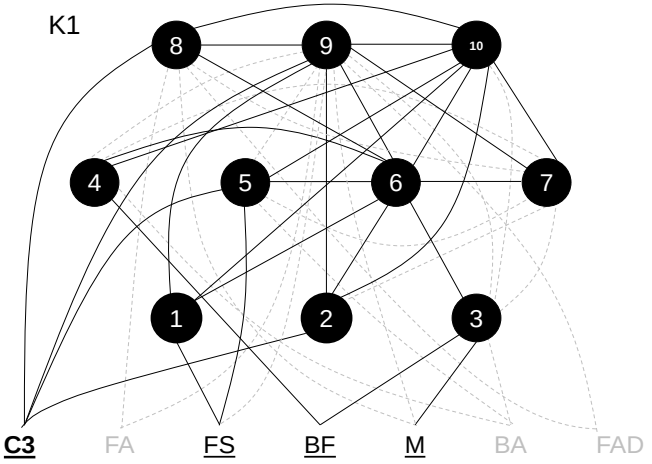
BA1



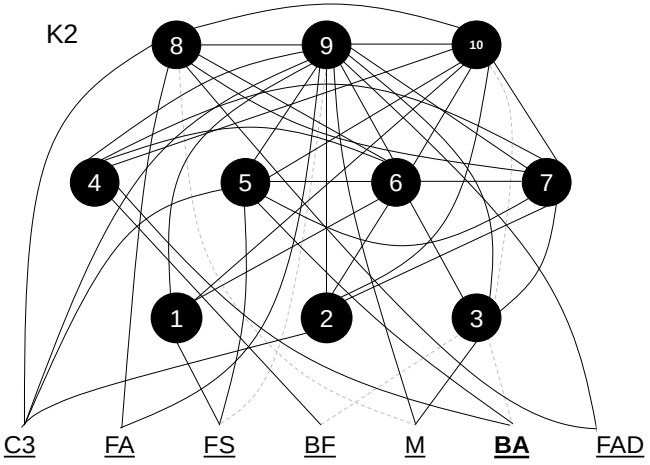
BA4



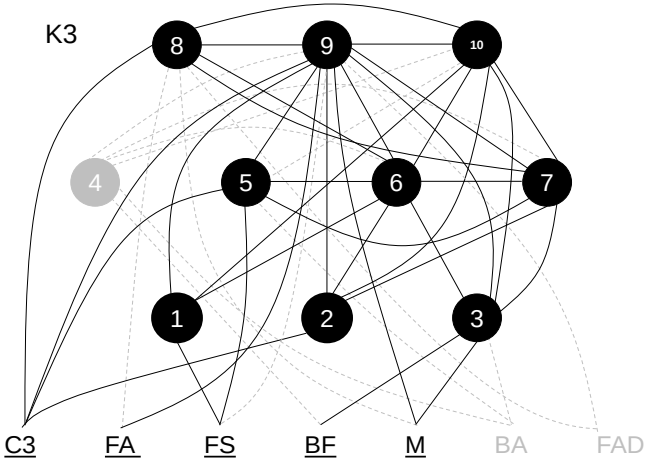
K1



K2



K3



K4