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## Organic matter sources and size structuring in stream invertebrate food webs across a tropical to temperate gradient

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Review

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4 1 Organic matter sources and size structuring in stream invertebrate food  
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7 2 webs across a tropical to temperate gradient  
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29 11 Short title : Stream invertebrate food webs  
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38 15 **Summary**  
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40 16 1. Given large differences in species diversity across latitudinal gradients, it has been suggested  
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42 17 that certain structural and functional attributes of freshwaters may differ over a latitudinal range,  
43  
44 18 an important consideration for knowledge-poor tropical systems that are undergoing major  
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46 19 human-induced changes.  
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48  
49 20 2. Two key features of aquatic ecosystems, the contribution of *in situ* production (periphyton) to  
50  
51 21 consumer biomass and size structuring (body size versus trophic level), were measured in stream  
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53 22 invertebrate food webs across a gradient of 15 degrees of latitude in Australia from the wet  
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55 23 tropics to a temperate island.  
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3 24 3. Consistent with earlier work, crustaceans (Atyidae and Palaemonidae) were responsible for a  
4  
5 25 large fraction of the community biomass at tropical and subtropical sites. The periphyton food  
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7  
8 26 source pathway accounted for a large proportion of the biomass at intermediate latitudes (79% in  
9  
10 27 the subtropics and 95% at temperate mainland sites), with lower contributions in the most distal  
11  
12 28 regions (51% in the tropics and 31% in temperate island sites). These lower contributions were  
13  
14 29 driven by the biomass dominance of large crustaceans in the tropical region and by shredding  
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16 30 and filtering insects in the temperate island region.  
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19

20 31 4. Though these differences in taxonomic composition did not translate into a latitudinal gradient  
21  
22 32 in size-structuring, the larger individual body size of crustaceans compared to insects for a given  
23  
24 33 trophic level suggests that food webs dominated by the former, as is expected in tropical river  
25  
26 34 food webs, are likely to exhibit altered biomass distributions with implications for higher  
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28 35 predators.  
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32 36 5. These results suggest that stream food webs can share common features despite differences in  
33  
34 37 species composition, and that local factors are likely as important as broad-scale biogeography  
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36 38 and climate in driving food web patterns.  
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## 47 **Introduction**

48 Early ecologists recognized strong latitudinal gradients in productivity and diversity  
49 (Hawkins 2001). Tropical systems with their higher temperatures and greater insolation  
50 supported greater species diversity than temperate and arctic systems, leading to decades of  
51 research on the possible links between these factors (Pianca 1966; Huston 1979; Partel, Laanisto  
52 & Zobel 2007). Less studied are patterns of ecological structure and function across the gradient  
53 (Mullholland *et al.* 2001; Olesen & Jordano 2002; Liski *et al.* 2003), most notably those for  
54 aquatic food webs (Paine 1966; Hecky & Hesslein 1995; Boyero *et al.* 2011). The same  
55 environmental factors that may be responsible for the diversity gradient could influence the  
56 relative importance of different primary food sources (leaf litter, periphyton) to overall  
57 secondary production in rivers and streams and the predator-prey relationships that occur therein.  
58 If ecological organization differs in the tropics and certain ecological processes are unique, there  
59 are potential management implications for systems that are likely to be placed under greater  
60 human-induced pressures in the 21<sup>st</sup> century (Dudgeon 2000). This has led to a call for greater  
61 study of tropical freshwaters, and a particular need for direct comparisons between the tropics  
62 and other biomes (Boulton *et al.* 2008; Boyero *et al.* 2009).

63 Recent investigations using stable isotope analysis of carbon ( $^{13}\text{C}/^{12}\text{C}$ ) have found a  
64 disproportionately large importance of periphyton in supporting food webs in tropical and  
65 subtropical rivers. Traditional views of organic matter processing in temperate systems,  
66 particularly small heterotrophic streams, held that food webs were supported almost exclusively  
67 by inputs of terrestrial leaf litter (Fisher & Likens 1973; Vannote *et al.* 1980). While these  
68 predictions have been reasonably well-supported by isotopic evidence in temperate systems (*e.g.*  
69 Doucett *et al.* 1996; Reid *et al.* 2008), early isotope work in the Neotropics suggested a strong

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3 70 role for algae (Hamilton, Lewis & Sippel 1992), and more recent investigations in the northern  
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5 71 half of Australia (Bunn, Davies & Kellaway 1997; Bunn, Davies & Mosisch 1999; Hadwen,  
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7 72 Spears & Kennard 2010), Puerto Rico (March & Pringle 2003), Hong Kong (Lau, Leung &  
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9 73 Dudgeon 2009) and Brazil (Brito *et al.* 2006) have shown a dominance of aquatic sources,  
10  
11 74 largely periphyton, in supporting these food webs. Some of these latter studies were conducted  
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13 75 in small, canopied streams (Lau *et al.* 2009), suggesting that climatic or biogeographic factors  
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15 76 unique to warm regions may override the importance of local factors such as shade and nutrients  
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17 77 on energy pathways for food webs. Thus, separate food web models for the tropics have been  
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19 78 proposed that include a reduced emphasis on the importance of detritus and a greater role for  
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21 79 autochthonous or in-stream sources (Dudgeon, Cheung & Mantel 2010).  
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27 80 Size-structuring, a key attribute of food webs that dictates metabolism and energy  
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29 81 requirements (Peters 1986) and predator-prey interactions (Cohen *et al.* 1993) may also vary  
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31 82 across climatic gradients. Gape limitation in many aquatic communities leads to predators  
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33 83 necessarily being larger than their prey (Brose *et al.* 2006), resulting in a progressive increase in  
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35 84 body size with each increase in trophic level with some exceptions (Riede *et al.* 2011). For  
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37 85 example, fish food webs in tropical freshwaters are only weakly size-structured because of the  
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39 86 presence of large-bodied herbivores (Layman *et al.* 2005). In addition, large-bodied crustaceans  
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41 87 such as prawns (*Macrobrachium* spp.), shrimps (Atyidae) and crayfish (*Cherax* spp.) often  
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43 88 dominate invertebrate biomass in the tropics (Jacobsen, Schultz & Encalada 2008) and therefore  
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45 89 play a central role in organic matter cycling. These taxa are unlikely to be preyed upon by other  
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47 90 invertebrates, particularly insects, which may weaken overall body size-trophic level  
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49 91 relationships if the crustaceans occupy low trophic levels (Burns & Walker 2000). Given these  
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3 92 observations, invertebrate food webs in the tropics, like fish food webs, may also be less size-  
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5 93 structured than those in temperate systems.  
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8 94 Much of the difficulty in comparing the structure and function of tropical and temperate  
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10 95 streams comes from synthesizing data across studies that vary widely in local factors such as  
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12 96 stream size (Finlay 2001; Sabo *et al.* 2010; Kobayashi *et al.* 2011). In this study, invertebrate  
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14 97 food webs were sampled in similar-sized streams and rivers from tropical North Queensland to  
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16 98 temperate Tasmania, Australia. Sources (periphyton and leaf litter) and consumers were  
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18 99 analysed for stable C isotopes that are known to vary from site to site, and the gradient approach  
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20 100 was used to calculate the contribution to the food web from periphyton (Rasmussen 2010). Body  
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22 101 mass of all organisms was measured and compared to trophic level (calculated from stable N  
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24 102 isotopes) to assess size-structuring. I hypothesized that invertebrates from tropical streams  
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26 103 would exhibit stronger links to periphyton and show weaker size-structuring than those from  
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28 104 temperate streams.  
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### 36 106 **Methods**

37  
38 107 A total of 43 sites were sampled from four regions along the east coast of Australia  
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40 108 (Table 1). The Great Dividing Range runs in a north-south direction along this coast, limiting  
41  
42 109 the size of east-flowing coastal streams and rivers that drain to the Coral Sea in the north and the  
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44 110 Tasman Sea in the south and thus constraining stream size as a contributing variable in dictating  
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46 111 food web structure (Finlay 2001; Sabo *et al.* 2010; Kobayashi *et al.* 2011). The four regions  
47  
48 112 were chosen to make latitudinal comparisons, and sites were largely upstream of road crossings  
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50 113 to facilitate access. The most northerly region was tropical north Queensland, where nine sites  
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52 114 were located north of the city of Cairns, ranging in latitude from 15.4° S to 16.9° S. Southeast  
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3 115 Queensland served as the subtropical region, with six sites sampled south of Brisbane from 27.8°  
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5 116 S to 28.1° S. There were two regions sampled in the temperate zone. The first was in the state  
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8 117 of Victoria, east of the city of Melbourne in the Gippsland Lakes region. These 16 sites had a  
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10 118 narrow latitudinal range from 37.7° S to 38.0° S and are hereafter referred to as “temperate  
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12 119 mainland”. The second temperate region was the island of Tasmania. East-flowing streams and  
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15 120 rivers were sampled and ranged in latitude from 40.9° S to 42.3° S. These 12 sites are hereafter  
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17 121 referred to as “temperate island”.

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20 122 Sites in all regions were wadeable streams and rivers that typically had gravel/cobble  
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22 123 bottoms. Stream order ranged from 2 to 5, and upstream drainage area ranged from 9 to 2112  
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24 124 km<sup>2</sup> (Table 1). Overall, sites were typically circumneutral and well-oxygenated with low  
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27 125 nutrient concentrations and benthic algal biomass, indicative of oligotrophic conditions (Smith,  
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29 126 Tilman & Nekola 1999) (Table 1). Riparian disturbance was generally minimal with the  
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31  
32 127 exception of some sites in the temperate mainland region where the dominant land use was  
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34 128 pasture for dairy production, leading to slightly elevated turbidity (Table 1). While mean canopy  
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36 129 cover at sites (estimated from satellite imagery) was similar among regions ( $F_{3,39} = 1.278$ ,  $p =$   
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39 130  $0.295$ ), mean site elevations did differ ( $F_{3,39} = 6.655$ ,  $p = 0.001$ ), with subtropical sites  
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41 131 significantly higher in elevation than temperate island or tropical sites (Table 1). Combining all  
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43 132 environmental variables into a principal component analysis following log-transformation and  
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46 133 normalization (subtracting the mean and dividing by the standard deviation) separated regions  
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48 134 but with low explanatory power (Figure S1). Only 46.3% of total variation was explained by  
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50 135 PC1 (25.2%) and PC2 (21.1%). Temperate mainland sites separated from other regions based on  
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53 136 larger stream order and catchment areas (PC1), and tropical sites separated from other regions  
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55 137 based on lower total phosphorus, pH and turbidity (PC2) (Figure S1).  
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3 138 At each site, three replicate samples of benthic invertebrates were collected with a 676  
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5 139 cm<sup>2</sup> surber sampler with 500 µm mesh in representative habitats (pools, rifles and runs).  
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8 140 Sampling methods were not optimized to capture crustaceans; thus, their absolute contribution to  
9  
10 141 community biomass is likely an underestimate. However, the same individual (TDJ) was  
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12 142 responsible for all collections so their relative contribution across sites and regions is likely  
13  
14 143 comparable. Samples were stored on ice and frozen for transport to the laboratory. To  
15  
16 144 characterize isotope ratios of food sources, three composite samples of biofilm were scrubbed  
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18 145 from submerged surfaces (almost exclusively rocks) and stored frozen in ziplock bags. A single  
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20 146 pooled sample of leaf litter was also collected at each site to verify that isotopic variation across  
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22 147 sites was minimal (Finlay 2001).  
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27 148 In the laboratory, the biomass of invertebrates was quantified while preparing samples for  
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29 149 isotope analysis. Samples were thawed, identified to family level, counted, tamped dry on a  
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31 150 paper towel (kimwipe), and individuals from a given family placed together in a pre-weighed  
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33 151 plastic vial. The total wet mass of each sample was then determined before being dried.  
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35 152 Because the number of individuals in a sample was counted, wet mass per individual could also  
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37 153 be estimated by division. After drying (60° C for 48 hr), samples were re-weighed to estimate  
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39 154 dry mass then ground into a powder and a sub-sample weighed out at approximately 0.8 mg for  
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41 155 C&N isotope analysis.  
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46 156 Samples of biofilm were thawed, allowed to settle and the top layer and overlying water  
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48 157 pipetted into a plastic tube. The bottom (heavy), inorganic/detrital-dominated layer was  
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50 158 discarded. Algal-dominated top layer samples were dried for 48 hr at 60° C, ground to a powder  
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52 159 and weighed at approximately 3 mg for C&N isotopes. Leaf litter samples were dried under the  
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54 160 same conditions, ground to a powder and weighed at approximately 4 mg for C&N isotopes.  
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3 161 Samples were analysed for stable isotope ratios at two laboratories. The majority of the  
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6 162 samples were analysed by combustion in a PDZ Europa ANCA-GSL elemental analyser  
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8 163 followed by delivery of gases to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon,  
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10 164 Ltd., Cheshire, UK). Duplicate samples yielded a mean absolute difference of 0.3‰ for  $\delta^{13}\text{C}$   
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13 165 and 0.5‰ for  $\delta^{15}\text{N}$  (n = 20), while five working standards analysed alongside samples had 1 S.D.  
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15 166 that ranged from 0.1‰ to 0.3‰ for sample sizes ranging from 12 to 119. A small number of  
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18 167 samples was analyzed by combustion in a Eurovector EA 3000 followed by delivery of gases to  
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20 168 an Isoprime mass spectrometer (GV Instruments, Manchester, UK). Duplicate samples yielded a  
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23 169 mean absolute difference of 0.1‰ for  $\delta^{13}\text{C}$  and 0.2‰ for  $\delta^{15}\text{N}$  (n = 7), while five working  
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25 170 standards analysed alongside samples had 1 S.D. that ranged from 0.1‰ to 0.2‰ for sample  
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28 171 sizes ranging from 4 to 9. To ensure comparability among labs, two samples that had been  
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30 172 analysed at the first lab ( $\delta^{13}\text{C} = -19.3 \pm 0.1\%$  S.D.,  $\delta^{15}\text{N} = 9.1 \pm 0.2\%$  S.D. and  $\delta^{13}\text{C} = -25.7\%$ ,  
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32 173  $\delta^{15}\text{N} = 0.0\%$ ) were also analysed once at the second lab, yielding comparable values ( $\delta^{13}\text{C} = -$   
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35 174  $19.3\%$ ,  $\delta^{15}\text{N} = 8.3\%$  and  $\delta^{13}\text{C} = -25.9\%$ ,  $\delta^{15}\text{N} = 0.5\%$ ).

37 175 The taxonomic composition of the biomass and average body sizes were compared  
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39 176 among regions. Taxonomic composition was qualitatively compared by plotting average  
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42 177 percent biomass contribution within sites. The average body size of consumers among regions  
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45 178 was tested using analysis of co-variance (ANCOVA), with  $\log_{10}$  of individual wet mass as the  
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47 179 dependent variable, region as the fixed factor, and  $\log_{10}$  of the proportion of site biomass as the  
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50 180 co-variate. The ANCOVA was used because few large individuals can dominate biomass and  
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52 181 thus bias comparisons among regions if only mean values are used; by having proportion of site  
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54 182 biomass as the co-variate direct comparisons can be made more readily. The interaction term in  
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56 183 this model was first tested, found to be non-significant ( $F_{3,302} = 1.004$ ,  $p = 0.391$ ) and the model  
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3 184 re-run after its removal. For taxon-specific comparisons of individual wet mass, a GLM-  
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5 185 ANOVA was used; the ANCOVA was not necessary because the range of body sizes within taxa  
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8 186 and their contribution to biomass was far less variable.  
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11 187 To quantify the reliance of consumers on periphyton as a food resource in the different  
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13 188 regions, the gradient approach was used (Rasmussen 2010). The site-specific  $\delta^{13}\text{C}$  of a given  
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15 189 taxon (family or functional feeding group) was regressed against the  $\delta^{13}\text{C}$  of biofilm (periphyton-  
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18 190 dominated) at the site. Because the other potential food source pathway begins with terrestrial  
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20 191 leaf litter that exhibits invariant  $\delta^{13}\text{C}$  across sites (Finlay 2001), the slope of the consumer-  
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22 192 biofilm regression is directly proportional to the percent contribution of the periphyton/biofilm  
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25 193 food source pathway to the diet (Rasmussen 2010). While this approach assumes similarity in  
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27 194 feeding within taxa across sites, it largely circumvents problems that originate from overlapping  
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30 195  $\delta^{13}\text{C}$  values in the center of the wide  $\delta^{13}\text{C}$  distribution of periphyton (Finlay 2001). Using the  
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32 196 gradient approach, confidence intervals around slope estimates can be used to compare  
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35 197 periphyton reliance among taxa and regions (Jardine *et al.* 2012a). When 95% confidence  
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37 198 intervals include one but not zero, periphyton can be considered to contribute roughly 100% to  
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39 199 the diet. When the 95% C.I. includes zero but not one, periphyton is assumed to contribute nil to  
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41 200 the diet. A 95% C.I. that includes neither zero nor one suggests a mixed contribution from the  
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43  
44 201 two source pathways, and a 95% C.I. that includes both zero and one results from an unsolved  
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46 202 model (Jardine *et al.* 2012a). Though both x and y in these regressions are measured with error  
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48 203 suggesting model II regression would be more appropriate, results reported here are for ordinary  
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50 204 least squares (OLS) regressions because model II regressions commonly result in slopes that are  
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53 205 higher than one or lower than zero (Jardine *et al.* 2012a), and proportions derived from OLS  
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3 206 slopes provide values that are closer to those estimated directly from mixing models at subsets of  
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5 207 sites where sources differ (Jardine, Kidd & Rasmussen 2012b; T.D. Jardine, unpublished data).  
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8 208 By grouping organisms into functional feeding groups and using the resulting consumer-  
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10 209 biofilm  $\delta^{13}\text{C}$  slopes as estimates of % periphyton in the diet, coarse comparisons can be made  
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12 210 among regions of the biomass-specific contribution from periphyton to the invertebrate  
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14 211 community (Jardine *et al.* 2013). This is achieved by multiplying the total biomass of a taxon at  
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16 212 a site by its estimated dietary contribution from periphyton and then summing the totals for the  
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18 213 site. The result is the total amount of biomass that can be attributed to periphyton production,  
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20 214 which can then be divided by the total biomass to estimate the overall percent contribution from  
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22 215 periphyton. Error terms can be derived from slope estimates (e.g. 1 S.E.) and also multiplied by  
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24 216 biomass to obtain error around final totals. While this does not allow formal statistical testing  
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26 217 among regions, it provides a relative indicator of the importance of periphyton and associated  
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28 218 uncertainty along the tropical to temperate gradient.  
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34 219 To estimate trophic level for individual taxa within sites,  $\delta^{15}\text{N}$  data were used (Post  
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36 220 2002). Trophic level was calculated according to:  $(\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{baseline}})/\Delta^{15}\text{N} + 2$ , where  
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38 221  $\Delta^{15}\text{N}$  is an average diet-tissue  $\delta^{15}\text{N}$  fractionation (2.5‰, Vanderklift & Ponsard 2003) and  
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40 222  $\delta^{15}\text{N}_{\text{baseline}}$  is the average value within a site for primary consumers. Primary consumers were  
41  
42 223 classified according to Gooderham and Tsyrlin (2002) and included various combinations of  
43  
44 224 Leptophlebiidae, Psephenidae, Baetidae, Caenidae, Elmidae, Gripopterygidae, Pyralidae,  
45  
46 225 Oligochaeta, Simuliidae, Tipulidae, Scirtidae, Corbiculiidae, Calocidae, Gastropoda, and  
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48 226 Notonemouridae. Trophic level measurements were then linked to wet weights per individual by  
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50 227 regression. Slopes of these regressions in the four regions were compared by testing for overlap  
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52 228 among 95% confidence intervals, using model II regression with the lmodel2 package in R  
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3 229 (Legendre 2001) to facilitate direct comparisons with prior work (Riede *et al.* 2011). Initial  
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6 230 screening removed data from two sites. The entire Endeavour River site (tropical region) was  
7  
8 231 removed because unlike all other sites in the study, predators at that site had lower  $\delta^{15}\text{N}$  than  
9  
10 232 primary consumers, suggesting an inappropriate selection of baseline organism. A single water  
11  
12 233 penny sample (Family Psephenidae) at a site in the temperate mainland region (Thomson River  
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14  
15 234 @ Trevor Platt's) was also removed from the analysis as an outlier because it had  $\delta^{13}\text{C}$  (-27.3‰)  
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17  
18 235 and  $\delta^{15}\text{N}$  (-0.3‰) that greatly differed from the remainder of the food web ( $\delta^{13}\text{C} = -39.9$  to  $-33.0$   
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20 236 and  $\delta^{15}\text{N} = 6.3$  to  $9.3\text{‰}$ ,  $n = 4$ ) resulting in a clearly incorrect trophic level (-0.4).  
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## 238 Results

### 239 *Taxonomic composition of biomass*

240 The four regions differed in taxonomic composition and individual body sizes.  
241 Temperate island sites had communities whose biomass was dominated by small-bodied taxa,  
242 including Leptophlebiid mayflies (mean individual wet mass = 3.5 mg) that made up an average  
243 of  $38 \pm 28\%$  of the biomass (Fig. 1). Omnivorous shrimps (Atyidae,  $19 \pm 29\%$ , mean mass =  
244 70.3 mg) and net-spinning caddisflies (Hydropsychidae,  $11 \pm 16\%$ , mean mass = 5.9 mg) were  
245 also important in this region. This latter taxon also dominated the biomass at temperate  
246 mainland sites, accounting for  $30 \pm 23\%$  of the biomass on average (Fig. 1) at an average size of  
247 5.3 mg. No other taxon contributed more than 10% in this region. In the subtropical region,  
248 large-bodied freshwater prawns (Palaemonidae, mean mass = 395.3 mg) were the dominant taxa  
249 ( $29 \pm 33\%$ ). Leptophlebiids ( $17 \pm 10\%$ , mean mass = 3.5 mg) and two predatory taxa  
250 (Megaloptera dobsonflies  $19 \pm 21\%$ , mean mass = 42.5 mg, and dragonflies Odonata  $11 \pm 14\%$ ,  
251 mean mass = 55.9 mg) also contributed more than 10%. In the tropics, there were five taxa with

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3 252 considerable biomass that were also important in the other regions. The crustaceans Atyidae  
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5 253 (mean mass = 48.8 mg) and Palaemonidae (mean mass = 138.8 mg) made up  $24 \pm 24\%$  and  $13 \pm$   
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7  
8 254  $34\%$  of the biomass, respectively. Other taxa included Hydropsychidae ( $15 \pm 15\%$ , mean mass =  
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10 255 2.4 mg), Odonata ( $18 \pm 19\%$ , mean mass = 39.8 mg) and Leptophlebiidae ( $10 \pm 13\%$ , mean mass  
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12 256 = 1.0 mg). In all regions, the largest individuals at a given site were responsible for the greatest  
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15 257 fraction of the total biomass ( $F_{1,305} = 181.139$ ,  $p < 0.001$ ). There were significant differences  
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17 258 among regions in individual wet mass ( $F_{3,305} = 21.484$ ,  $p < 0.001$ ). On a community-wide basis,  
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19 259 temperate island sites had significantly lower average individual wet mass compared to the other  
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22 260 three regions. However, when comparing the wet mass of individuals within taxa across regions,  
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24 261 the tropics had significantly smaller individuals compared to the other three regions: Baetidae  
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27 262 [ $F_{3,18} = 4.351$ ,  $p = 0.018$ ; tropical < temperate mainland ( $p = 0.003$ ); Hydropsychidae [ $F_{3,29} =$   
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29 263  $4.149$ ,  $p = 0.015$ ; tropical < temperate mainland ( $p = 0.002$ ), temperate island ( $p = 0.018$ ) and  
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31 264 subtropical ( $p = 0.045$ ); and Leptophlebiidae [ $F_{3,29} = 2.837$ ,  $p = 0.055$ ; tropical < subtropical ( $p$   
32  
33 265 =  $0.019$ ), temperate mainland ( $p = 0.022$ ) and temperate island ( $p = 0.028$ )]. There were no  
34  
35 266 differences among the other three regions except for Baetidae, where individuals from temperate  
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37 267 mainland sites were significantly larger than those from temperate island sites ( $p = 0.015$ ).  
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#### 42 43 269 *Carbon sources and $\delta^{13}C$*

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45  
46 270 As expected,  $\delta^{13}C$  was far more variable in biofilm (periphyton) compared with leaf litter  
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48 271 (Fig. S2). Values for biofilm ranged from  $-37.1\text{‰}$  to  $-17.9\text{‰}$  across all sites in all regions (mean  
49  
50 272 =  $-28.3 \pm 3.7\text{‰}$  S.D.,  $n = 44$ ). Ranges in biofilm  $\delta^{13}C$  were smaller in subtropical ( $-27.9\text{‰}$  to -  
51  
52 273  $21.3\text{‰}$ ) and temperate mainland ( $-32.0\text{‰}$  to  $-23.0\text{‰}$ ) sites compared to tropical ( $-37.1\text{‰}$  to -  
53  
54 274  $17.9\text{‰}$ ) and temperate island ( $-34.0\text{‰}$  to  $-22.8\text{‰}$ ) sites. Leaf litter was analyzed at fewer sites  
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3 275 than biofilm but yielded a similar mean value as that reported elsewhere (-29.9‰) and  
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5 276 unsurprisingly, had limited variation across sites (range = -31.6‰ to -28.2‰, 1 S.D. = 1.0, n =  
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7  
8 277 28).

9  
10 278 The combination of the taxonomic composition of the biomass and use of food source  
11  
12 279 pathways led to differences in the importance of periphyton in the four regions. In the tropics,  
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14 280 primary consumers were strongly linked to the periphyton source pathway (Table 2, Fig. 2a), but  
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16 281 organisms classed as omnivores (Atyidae, Palaemonidae, Hydropsychidae) derived less of their  
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18 282 diet from this pathway (Fig. 2b) and dominated the biomass (Fig. 1). This caused the overall  
19  
20 283 community biomass to be roughly equally reliant on the two food sources in this region (Fig. 3).  
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22 284 Both the subtropical and temperate mainland regions had invertebrate communities that derived  
23  
24 285 the vast majority of their biomass from the periphyton pathway (Table 2, Fig. 3). All three  
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26 286 functional feeding groups in these regions were strongly reliant on periphyton, with consumer-  
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28 287 biofilm  $\delta^{13}\text{C}$  slopes > 0.59 for all taxonomic and functional feeding groups (Table 2, Fig. 2). In  
29  
30 288 the temperate island region, consumers were less strongly linked to biofilm, with slopes ranging  
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32 289 from 0.22 to 0.60 (Table 2). As a result, the average contribution to community biomass was  
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34 290 only 31% in this region (Fig. 3).  
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#### 43 292 Size structuring and $\delta^{15}\text{N}$

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46 293 Average trophic level across all regions for those taxa not classed as primary consumers  
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48 294 ranged from 1.8 (Ceratopogonidae) to 3.3 (Tabanidae). Large-bodied, biomass-dominant  
49  
50 295 omnivores had intermediate trophic levels, including Hydropsychidae (TL = 2.3), Atyidae (TL =  
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52 296 2.7) and Palaemonidae (TL = 2.5). Two predatory taxa that had relatively high biomass  
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54 297 [Megaloptera (Corydalidae) and Odonata] both had an average TL = 2.7.  
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3 298           Body size increased with trophic level in these stream invertebrate food webs (Fig. 4).  
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6 299    Though much variability remained unexplained, regressions of log body size vs. trophic level  
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8 300    were significant in all regions (Tropical:  $r^2 = 0.19$ ,  $F_{1,41} = 9.371$ ,  $p = 0.004$ ; Subtropical:  $r^2 =$   
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10 301     $0.41$ ,  $F_{1,46} = 31.838$ ,  $p < 0.001$ ; Temperate mainland:  $r^2 = 0.16$ ,  $F_{1,82} = 16.157$ ,  $p < 0.001$ ;  
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12 302    Temperate island:  $r^2 = 0.18$ ,  $F_{1,57} = 12.687$ ,  $p = 0.001$ ). As estimated from the slopes of body  
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14 303    size vs. trophic level regressions, there were slight differences in the size-structuring of  
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16 304    invertebrate food webs among the regions (Fig. 4). Despite the biomass dominance of large-  
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18 305    bodied crustaceans in the tropics and the dominance of small-bodied insects at temperate island  
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20 306    sites (Fig. 1), there was no evidence for altered size-structuring between these regions. Only the  
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22 307    temperate mainland region had sites with 95% confidence intervals around slope estimates that  
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24 308    did not overlap with all other regions (Table 2), a pattern that was repeated when a more liberal  
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26 309    comparison with 85% confidence intervals was used. The minor difference in the temperate  
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28 310    mainland region was driven by the presence of non-insect taxa in other regions; crustaceans were  
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30 311    generally larger than insects for a given trophic level, exhibiting positive residuals in the body  
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32 312    size-trophic level regressions (Fig. 4). Removal of non-insects from the regressions resulted in  
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34 313    overlap in 95% C.I.'s among regions and allowed the consolidation of all insect data into a single  
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36 314    common slope estimate (Table 2).  
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## 316 **Discussion**

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48 317           Contrary to predictions, energy pathways and size structuring of invertebrate food webs  
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50 318    in tropical streams were not particularly different from those in temperate regions. Despite  
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52 319    considerable differences in the community composition at the extreme ends of the range (tropical  
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54 320    and temperate island), overall food webs in these two distal regions exhibited a similar  
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3 321 contribution from periphyton and equal slopes of trophic level vs. body size regressions. These  
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5 322 observations suggest that there may be little that is unique about lower trophic levels in tropical  
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8 323 river food webs (Boulton *et al.* 2008). However, the potential role of crustaceans in stream food  
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11 324 webs in general and their greater prominence in the tropics require further investigation because  
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13 325 they exert strong controls on both energy pathways and size-structuring examined here.

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15 326 Large-bodied omnivores that dominated biomass in the tropics exhibited mixed diets  
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17 327 originating from both periphyton and leaf litter, a product of their generalist nature (Covich  
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19  
20 328 1988). Both crustacean taxa (Atyidae and Palaemonidae) likely play a role in breaking down  
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22 329 leaf litter in these streams while supplementing their diet with insect prey of aquatic origin  
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24 330 (March & Pringle 2003), thereby filling similar niches and performing similar functions as  
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26  
27 331 omnivorous crayfish (Parkyn, Collier & Hicks 2001). Their dietary contribution from the  
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29 332 periphyton source pathway measured in this study (Atyidae slope = 0.48, corresponding to  
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31 333 approximately equal contributions from periphyton and detritus) is consistent with values for  
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34 334 streams, rivers and waterholes in the wet-dry tropics, where local biofilm contributions ranged  
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36 335 from 39 to 70% for these taxa (Jardine *et al.* 2012a; Jardine *et al.* 2013). The biomass of  
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38 336 palaemonid prawns can also rival that of fish in tropical waterholes (Jardine *et al.* 2013), and  
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40 337 thus their consumption of detrital and algal material will exert a strong role in transferring this  
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43 338 energy to fish and other predators at higher trophic levels.

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46 339 The approximate 50% contribution from terrestrial inputs to invertebrate food webs in the  
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48 340 tropics likely represents a maximum possible value for this region because samples were largely  
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50 341 collected from forested, lowland streams (Kobayashi *et al.* 2011). Allochthonous inputs can  
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52 342 dominate tropical food webs in heavily shaded, low productivity systems (Yule 1996). Though  
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55 343 site-level shredder species diversity is lower in equatorial regions (Boyero *et al.* 2011), some



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3 344 taxa such as leptophlebiid mayflies and crayfish (*Cherax* spp.) can be common (Cheshire,  
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5 345 Boyero & Pearson 2005; Coughlan, Pearson & Boyero 2010) and can break down leaf litter at a  
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7 346 rate comparable to that found in temperate streams (Covich 1988), likely aided by microbial  
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9 347 degradation at higher temperatures. The sites from the tropical region in this study had low  
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11 348 nutrient concentrations (TP < 10 µg/L, TN < 330 µg/L, Table 1) suggestive of oligotrophic  
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13 349 conditions (Smith, Tilman & Nekola 1999). Despite these limitations to in-stream primary  
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15 350 productivity, periphyton still accounted for half of the invertebrate biomass. Subtropical and  
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17 351 temperate mainland regions both had high contributions from periphyton but were arguably the  
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19 352 most dissimilar in terms of environmental variables (Figure S1). One feature these two regions  
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21 353 had in common was higher phosphorus concentrations (Table 1); therefore, the high  
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23 354 contributions from periphyton observed at those sites may be a function of their mesotrophic  
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25 355 status (Bunn *et al.* 1999). Subtropical sites also were at significantly higher elevations than those  
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27 356 in other regions, and food web contributions from periphyton have been observed to peak at mid-  
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29 357 order, upland sites in stream continua (Kobayashi *et al.* 2011).  
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36 358 The dominance of Leptophlebiidae at the temperate island sites is consistent with prior  
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38 359 work in this region (Read & Barmuta 1999) where this taxon is known to shred leaf litter (Yeates  
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40 360 & Barmuta 1999). The Tasmanian fauna is generally depauperate relative to other parts of the  
41  
42 361 continent due to its isolation and history of glaciation, and insect taxa dominate stream  
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44 362 invertebrate assemblages (Magierowski *et al.* 2012). The low contribution of periphyton to the  
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46 363 invertebrate community biomass was driven largely by Leptophlebiidae and Hydropsychidae that  
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48 364 had lower periphyton-consumer  $\delta^{13}\text{C}$  slopes compared to other regions. Although crustaceans  
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50 365 are present in Tasmanian freshwaters, they include small-bodied amphipods (Fig. 4D), and large  
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52 366 bodied forms are less common (D.M. Warfe, University of Western Australia, pers. comm.).  
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3 367 Running waters in temperate systems worldwide are often dominated by insects (Hall, Likens &  
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5 368 Malcolm 2001) that exhibit a wide variety of feeding habits. As a consequence, the relative  
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8 369 biomass and secondary production of different functional feeding groups will dictate the relative  
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10 370 contribution to overall food web biomass from the two food source pathways (Rasmussen 2010;  
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12 371 Jardine *et al.* 2012b). Because larger animals have lower ratios of annual production to biomass  
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14 372 (Banse & Mosher 1980), stream food webs with biomass dominated by terrestrially-subsidized,  
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16 373 large-bodied crustaceans such as those in the tropics may underestimate a high-production,  
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18 374 rapid-turnover fraction of small-bodied insects that are instead more heavily reliant on  
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20 375 periphyton. While outside the scope of this study, the smaller average body mass of insect taxa  
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22 376 in the tropics (Baetidae, Hydropsychidae, Leptophlebiidae) suggests that a similar investigation  
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24 377 with secondary production as the endpoint could produce a different result than using community  
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26 378 biomass as shown here.

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29 379 Differences among seasons may also have played a role in observed patterns of carbon  
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31 380 source pathways. The majority of sites were sampled between March and May, corresponding to  
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33 381 the end of the Austral growing season. Two sites that were sampled in both April and December  
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35 382 exhibited similar patterns in the dominant taxa despite differences in community developmental  
36  
37 383 stage. Leptophlebiid mayflies accounted for 59% (April) and 66% (December) of the  
38  
39 384 community biomass at the Douglas River bridge site despite this taxa having an average wet  
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41 385 mass that was approximately ten times smaller in December (1.4 mg versus 13 mg). At the  
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43 386 Meredith River site, Leptophlebiids were approximately the same size (3 mg versus 5 mg) and  
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45 387 Atyid shrimps were larger in December (157 mg versus 70 mg) yet their contribution to  
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47 388 community biomass was similar in both seasons (54% and 22% in April and 42% and 46% in  
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49 389 December, respectively). Short-lived producers and consumers such as algae and insects can  
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3 390 also exhibit wide temporal variation in isotope ratios; however, the gradient approach is robust to  
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6 391 these seasonal changes because spatial variation in  $\delta^{13}\text{C}$  across sites exceeds temporal variation  
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8 392 within sites (Jardine *et al. in press*).  
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10  
11 393 Despite the presence of large-bodied crustaceans, food webs in the tropics were not less  
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13 394 size-structured than subtropical or temperate streams. This was likely driven by the fact that  
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15 395 trophic levels for these crustaceans were higher than expected, ranging from 2.3 to 3.7 for  
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17 396 Atyidae and 2.5 to 3.6 for Palaemonidae rather than  $\text{TL} \approx 2$  for both taxa if their diet had been  
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19 397 dominated by plant material (Burns & Walker 2000). Because crustaceans were larger than  
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21 398 insects for a given TL (Fig. 4), their higher TLs tended to drive regressions towards steeper  
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23 399 slopes rather than shallower slopes as was predicted. Tropical streams that are dominated by  
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25 400 these taxa (as has been observed previously, Bright 1982; Jacobsen *et al.* 2008), will therefore  
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27 401 have altered biomass spectra (Morin, Rodriguez & Nadon 1995), with a larger fraction of the  
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29 402 community biomass concentrated at trophic levels 2.5 to 3.0 despite similar slopes of individual  
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31 403 body size versus trophic level. Invertebrates generally exhibit weaker size structuring than other  
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33 404 taxa, with predator-prey body mass ratios less than 1 (Brose *et al.* 2006; Riede *et al.* 2011), and  
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35 405 insects in the current study had shallower slopes when crustaceans and other taxa (bivalves,  
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37 406 gastropods, oligochaetes) were excluded from regressions. As a result, streams dominated by  
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39 407 insects will require longer food chains to support top predators that only forage on prey above a  
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41 408 certain size threshold (Pyke, Pulliam & Nekola 1977).  
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48  
49 409 Stable N isotopes are a promising tool for further exploring body mass vs. trophic level  
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51 410 relationships. Regression slopes using TL derived from  $\delta^{15}\text{N}$  have been proposed as a measure  
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53 411 of the impacts of human activities on lotic systems, with positive relationships observed between  
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55 412 slopes and stream productivity owing to a greater proportion of predators in larger size classes in  
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3 413 productive streams (Anderson & Cabana 2009). These slopes are, however, sensitive to trophic  
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5 414 fractionation that is known to exhibit variation according to animal physiology and diet  
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8 415 (Vanderklift & Ponsard 2003). To illustrate this sensitivity, trophic level estimates were adjusted  
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10 416 using a lower  $\Delta^{15}\text{N}$  value that was empirically determined for algae to predators in riverine  
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12 417 systems such as these (1.8‰, Bunn, Leigh & Jardine 2013). With this lower value, the  
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14 418 regression slope of body mass versus trophic level for all insects combined (0.82, 95% C.I. =  
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16 419 0.73-0.93) was almost identical to the slope of 0.81 (95% C.I. = 0.71-0.91) obtained for stream  
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18 420 invertebrates across a series of food webs worldwide (Riede *et al.* 2011). However, using a  
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20 421 higher, commonly used estimate of  $\Delta^{15}\text{N}$  (3.4‰, Post 2002) would have resulted in slopes that  
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22 422 greatly exceeded those reported from prior studies.  
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27 423 Overall these results suggest that stream invertebrate communities can converge on  
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29 424 common structural attributes despite being separated by a large latitudinal gradient (Boulton *et*  
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31 425 *al.* 2008). The similarity in stream food web structure occurred despite differences in the types  
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33 426 of organisms responsible for the transfer of energy through food webs. Though sites were  
34  
35 427 selected to minimize variation in size (width/depth) and human disturbance to allow fair  
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37 428 comparisons among geographic regions, subtle differences in elevation, land use and nutrient  
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39 429 status may have driven the observed patterns. This further supports the view that local factors  
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41 430 may be as responsible as broad-scale geographic factors in dictating freshwater food web  
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43 431 structure and function (Boulton *et al.* 2008). Evidence presented here does not support a need  
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45 432 for separate food web models for tropical streams (Dudgeon *et al.* 2010), though continued  
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47 433 comparisons across latitudinal gradients (*e.g.* Boyero *et al.* 2011) with a particular focus on the  
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49 434 role of crustaceans will enable a fuller understanding of freshwater food web patterns and  
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53 435 processes.  
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45 588 aseasonal tropical streams on Bougainville Island, Papua New Guinea. *Journal of Tropical*  
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591 Table 1. Limnological information for study streams in eastern Australia, where invertebrates  
 592 were collected to estimate importance of organic matter sources to the food web and size-  
 593 structuring.

Location	Date	S	E	Order	Catch area	Elevation (m)	Canopy (%)	pH	turb	DO	temp	TP (mg/L)	TN (mg/L)	benthic chlor
TROPICAL - NORTH QUEENSLAND														
Endeavour R.	26-May-10	15.429	145.118	4	372.8	22	40	6.8	5.1	7.7	24.9	0.009	0.19	32.4
Trevathan Cr.	26-May-10	15.620	145.221	3	75.9	47	70	6.6	6.6	7.4	24.8	0.002	0.17	3.6
Bloomfield R.	27-May-10	15.960	145.319	4	314.4	18	10	6.9	1.6	8.1	23.7	0.002	0.11	3.2
Thompson Cr.	27-May-10	16.102	145.459	2	8.6	12	90	5.9	0.1	7.6	23.3	0.002	0.10	11.6
Douglas Cr.	28-May-10	16.280	145.297	3	60.3	13	10	6.7	1.1	7.9	22.5	0.006	0.14	0.7
Cooper Cr.	28-May-10	16.166	145.416	2	9.5	29	90	6.5	0.5	7.0	23.7	0.002	0.06	1.4
Saltwater Cr.	29-May-10	16.417	145.356	2	33.4	25	50	6.6	0.0	8.4	21.8	0.002	0.21	1.1
Mossman R.	29-May-10	16.450	145.360	4	87.5	21	80	6.7	0.0	8.3	22.2	0.002	0.20	2
Freshwater Cr.	30-May-10	16.907	145.704	4	93.2	19	80	6.7	2.7	7.6	23.8	0.008	0.32	6.7
SUBTROPICAL - SOUTHEAST QUEENSLAND														
Coomera R. upper	23-Apr-10	28.047	153.190	3	84.7	119	70	7.6	5.8	8.5	21.0	0.077	0.05	27.3
Coomera R. @ Durston's	23-Apr-10	28.056	153.179	3	84.7	125	70	7.6	1.9	8.4	21.3	0.067	0.05	16.5
Canungra Cr. @ Sarabah Road	06-Oct-11	28.095	153.115	2	74.6	165	30	6.4	2.5	8.7	16.5	0.047	0.16	12.2
Canungra Cr. @ Double crossing	06-Oct-11	28.037	153.141	2	99.5	115	60	6.4	3.0	7.2	17.1	0.053	0.18	2.6
Albert R. @ Ward Bridge	07-Oct-11	28.172	153.042	3	92.8	155	30	6.4	7.8	8.9	17.5	0.060	0.18	2.4
Cedar Cr.	07-Oct-11	27.840	153.179	2	26.9	28	60	6.3	2.7	7.2	17.1	0.012	0.14	1.6
TEMPERATE MAINLAND - VICTORIA														
Avon R. @ Stratford	15-Mar-10	37.973	147.078	5	1513.5	12	10	6.5	3.0	12.1	22.6	0.009	0.14	1.4
Avon R. @ Weir's Crossing	15-Mar-10	37.951	147.055	5	1432.5	17	10	6.8	8.7	11.4	24.2	0.011	0.13	1.8
Avon R. @ Bushy Park	15-Mar-10	37.863	147.008	5	1326.1	34	30	6.6	4.8	11.9	27.5	0.008	0.12	1.4
Avon R. @ Huggett's Crossing	16-Mar-10	37.811	146.855	3	49.4	103	20	.	.	.	.	0.008	0.11	1.5
Avon R. @ Avon-Turton Track	16-Mar-10	37.722	146.880	4	256.7	195	30	7.3	0.1	8.5	20.8	0.007	0.08	1
Avon R. @ 3rd Crossing	16-Mar-10	37.712	146.886	4	256.7	211	30	7.3	0.4	9.3	22.4	0.007	0.08	1
Avon R. @ Wombat Road	16-Mar-10	37.817	146.945	5	589.3	59	20	7.1	0.6	13.0	26.5	0.007	0.09	2.1
McAllister R. @ Trevor Platt's	17-Mar-10	38.035	146.982	5	2111.9	22	60	7.0	16.2	6.9	21.8	0.150	0.50	
Thomson R. @ Trevor Platt's	17-Mar-10	38.034	146.972	5	1480.4	19	60	6.8	18.3	9.5	22.4	0.076	0.32	
McAllister R. @ Davis Bridge	17-Mar-10	38.022	146.980	5	2111.9	23	70	6.7	64.0	10.0	23.7	0.120	0.38	
Thomson R. @ Riverview Road	17-Mar-10	38.007	146.871	5	1326	28	70	7.0	15.0	6.8	23.8	0.011	0.11	
Thomson R. @ Denison	18-Mar-10	38.003	146.794	5	1312.7	41	20	6.8	10.9	8.4	22.2	0.017	0.25	21.2
Thomson R. @ Reilly's Bridge	18-Mar-10	37.986	146.694	5	1175	60	30	7.1	5.0	8.7	22.4	0.011	0.18	1.8
Thomson R. @ Higgins Road	18-Mar-10	37.986	146.757	5	1242.5	47	80	6.9	10.0	7.5	24.2	0.017	0.19	16.7
Avon R. @ Valencia Creek Road	19-Mar-10	37.825	146.986	5	869.8	52	20	6.8	1.1	7.3	23.4	0.039	0.30	2.1
Rainbow Creek @ Neilson's Road	19-Mar-10	38.013	146.715	5	1107.4	53	50	6.9	4.0	7.4	22.4	0.017	0.22	0.9
TEMPERATE ISLAND - TASMANIA														
Douglas R. @ Bridge	14-Apr-10	41.781	148.256	3	72.2	9	50	7.5	1.0	10.2	14.6	0.020	1.10	11.3
Douglas R. @ Bridge	08-Dec-11	41.781	148.256	3	72.2	9	50	7.8	.	9.8	21.0	<0.005	0.19	6.3
Meredith R.	15-Apr-10	42.116	148.061	3	97.9	10	50	6.8	0.2	7.9	14.6	0.012	0.34	4.8
Meredith R.	10-Dec-11	42.116	148.061	3	97.9	10	50	7.3	.	6.5	18.4	0.008	0.46	3.8
Swan R.	15-Apr-10	41.996	148.079	4	251	19	30	7.0	1.2	9.6	14.6	0.010	0.21	0.6
Apsley R.	15-Apr-10	41.863	148.186	3	83.2	89	10	7.2	1.1	9.7	14.0	0.009	0.10	0.3
Scamander R.	16-Apr-10	41.450	148.162	3	147.3	38	50	7.3	0.6	9.4	15.1	0.008	0.19	0.4
Boobyalla R.	17-Apr-10	40.924	147.861	4	242.9	13	90	7.0	7.3	9.0	14.3	0.051	0.66	22.5
Groom R.	17-Apr-10	41.257	148.054	2	35.1	120	90	7.0	1.9	9.8	13.7	0.014	0.39	6
Trout Cr.	09-Dec-11	41.443	148.194	4	272.6	15	50	7.1	.	9.4	17.8	<0.005	0.45	0.7
Swan R.	09-Dec-11	42.007	148.076	4	256.9	17	20	7.5	.	9.5	23.3	<0.005	0.20	2.7
Buxton R.	10-Dec-11	42.261	148.001	3	60.11	11	60	7.4	.	8.8	20.0	0.005	0.26	1.4
Douglas R. upstream	10-Dec-11	41.776	148.220	3	72.2	88	10	7.6	.	9.7	18.4	<0.005	0.18	3.9
Wye R.	11-Dec-11	42.068	148.064	3	162.13	8	70	7.3	.	6.8	19.2	0.469*	0.51	1.5
*this sample was re-analyzed to confirm the high value														

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596 Table 2. Estimated contributions of the biofilm/periphyton source pathway to the diet of stream  
 597 invertebrates, based on  $\delta^{13}\text{C}$  consumer versus  $\delta^{13}\text{C}$  biofilm regressions. Slopes indicate mean  
 598 biofilm contribution to the diet and 95% confidence intervals around slopes (not shown) indicate  
 599 dietary source categories (superscripts, see Methods).

Group	Tropical			Subtropical			Temperate mainland			Temperate island			All regions		
	Slope	r	n	Slope	r	n	Slope	r	n	Slope	r	n	Slope	r	n
<i>Functional feeding groups</i>															
Primary consumers	1.12 <sup>a</sup>	0.83	8	0.76 <sup>a</sup>	0.86	6	1.56 <sup>a</sup>	0.76	15	0.37 <sup>c</sup>	0.48	11	0.90 <sup>a</sup>	0.65	40
Omnivores	0.47 <sup>d</sup>	0.57	8	0.82 <sup>a</sup>	0.92	6	0.95 <sup>a</sup>	0.80	16	0.22 <sup>c</sup>	0.33	10	0.55 <sup>b</sup>	0.58	40
Predators	0.19 <sup>c</sup>	0.22	8	0.78 <sup>a</sup>	0.93	6	0.81 <sup>a</sup>	0.77	7	N/A			0.43 <sup>b</sup>	0.57	24
<i>Families</i>															
Baetidae	N/A			N/A			2.27 <sup>a</sup>	0.80	7	0.44 <sup>d</sup>	0.42	5	1.44 <sup>a</sup>	0.72	17
Leptophlebiidae	1.13 <sup>a</sup>	0.96	6	0.75 <sup>a</sup>	0.88	6	N/A			0.60 <sup>a</sup>	0.62	11	0.86 <sup>a</sup>	0.76	27
Psephenidae	N/A			1.34 <sup>d</sup>	0.85	5	1.24 <sup>a</sup>	0.85	6	N/A			1.25 <sup>a</sup>	0.92	14
Simuliidae	N/A			N/A			N/A			N/A			0.84 <sup>d</sup>	0.52	10
Hydropsychidae	0.47 <sup>b</sup>	0.95	6	0.59 <sup>a</sup>	0.88	6	1.07 <sup>a</sup>	0.88	13	0.43 <sup>d</sup>	0.53	6	0.64 <sup>b</sup>	0.62	32
Atyidae	0.48 <sup>d</sup>	0.50	6	N/A			1.26 <sup>a</sup>	0.96	5	N/A			0.51 <sup>d</sup>	0.43	15
Corydalidae	N/A			0.81 <sup>a</sup>	0.96	6	N/A			N/A			0.80 <sup>a</sup>	0.88	10
Odonata	0.18 <sup>c</sup>	0.22	8	N/A			1.14 <sup>a</sup>	0.89	5	N/A			0.34 <sup>c</sup>	0.45	18

<sup>a</sup>biofilm dominant, <sup>b</sup>mixed diet, <sup>c</sup>terrestrial dominant, <sup>d</sup>unresolved

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3 612 Table 3. Slopes of regressions of log wet weight per individual (Wgt) versus trophic level (TL)  
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6 613 for invertebrates in streams from four regions of eastern Australia. Two different values for  $\delta^{15}\text{N}$   
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8 614 trophic fractionation ( $\Delta^{15}\text{N}$ ), or the expected increase in  $\delta^{15}\text{N}$  per TL, are shown because this  
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10  
11 615 variable is uncertain (Bunn et al. 2013).  
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		$\Delta^{15}\text{N} = 2.5\text{‰}$	$\Delta^{15}\text{N} = 1.8\text{‰}$			
Taxa	Region	Wgt-TL Slope (95% C.I.)	Wgt-TL Slope (95% C.I.)	$r^2$	n	p
All invertebrates	Tropical	1.44 (1.09-1.90)	1.04 (0.78-1.37)	0.19	42	0.004
	Subtropical	1.53 (1.22-1.92)	1.10 (0.88-1.38)	0.41	47	<0.001
	Temperate mainland	0.98 (0.80-1.19)	0.70 (0.58-0.86)	0.16	83	<0.001
	Temperate island	1.45 (1.14-1.83)	0.96 (0.78-1.18)	0.18	58	0.001
Insects only	Tropical	1.30 (0.98-1.73)	0.93 (0.70-1.24)	0.29	37	<0.001
	Subtropical	1.25 (0.98-1.59)	0.90 (0.71-1.15)	0.41	43	<0.001
	Temperate mainland	0.90 (0.71-1.13)	0.65 (0.51-0.81)	0.15	65	<0.001
	Temperate island	1.15 (0.88-1.50)	0.83 (0.63-1.08)	0.11	51	0.008
Insects only	All regions	1.14 (1.01-1.30)	0.82 (0.73-0.93)	0.20	196	<0.001

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3 628 **Figure legends**  
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5 629 **Figure 1.** Average percent contribution to the standing biomass of invertebrates in rivers in four  
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7  
8 630 regions of eastern Australia: (A) Tropical (North Queensland; 7 sites), (B) Subtropical (southeast  
9  
10 631 Queensland; 6 sites), (C) Temperate mainland (Victoria; 16 sites), (D) Temperate island  
11  
12 632 (Tasmania; 11 sites). Taxon identifiers are: Am = Amelotopsidae, Ap = Amphipoda, At =  
13  
14 633 Atyidae, Ba = Baetidae, Ca = Caenidae, Cb = Corbiculiidae, Ce = Ceratopogonidae, Co =  
15  
16 634 Corydalidae, Di = Diptera, Ec = Ecnomidae, El = Elmidae, Ep = Ephemeroptera, Ga =  
17  
18 635 Gastropoda, Gr = Griptopterygidae, Gy = Gyrinidae, Hb = Hydrobiosidae, Hy = Hydropsychidae,  
19  
20 636 Le = Leptophlebiidae, No = Notonemouridae, Od = Odonata, Ol = Oligochaeta, Ot = Other, Pa =  
21  
22 637 Palaemonidae, Ph = Philopotamidae, Ps = Psephenidae, Py = Pyralidae, Sc = Scirtidae, Si =  
23  
24 638 Simuliidae, Ta = Tabanidae, Ti = Tipulidae, Zy = Zygoptera  
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29 639 **Figure 2.** Regressions of consumer  $\delta^{13}\text{C}$  vs biofilm  $\delta^{13}\text{C}$  as a measure of the contribution of the  
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31 640 periphyton food source pathway to the diet of primary consumers (A), omnivores (B) and  
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33 641 predators (C) in tropical (open circles), subtropical (shaded triangles), temperate mainland  
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35 642 (shaded squares) and temperate island (solid diamonds) regions of Australia. Slopes  
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37 643 significantly  $>0$  are shown with best-fit lines, and correspond to values in Table 2.  
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40 644 **Figure 3.** Site-specific invertebrate biomass from four regions in eastern Australia showing the  
41  
42 645 percent contribution from periphyton (solid) and terrestrial (open) source pathways. %  
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44 646 periphyton for a site is calculated by multiplying the estimated % periphyton contribution to a  
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46 647 given feeding group by its biomass and summing the totals. The remaining biomass is assumed  
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48 648 to be contributed by terrestrial detrital pathways.  
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51 649 **Figure 4.** Regressions of the  $\log_{10}$  of invertebrate individual wet mass vs. trophic level  
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53 650 (calculated from  $\delta^{15}\text{N}$ ) for riverine sites in tropical (A), subtropical (B), temperate mainland (C)  
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3 651 and temperate island (D) sites in Australia. Open symbols represent insects, solid symbols are  
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6 652 crustaceans (Atyidae and Palaemonidae with the exception of a single amphipod sample with TL  
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8 653 = 1.1 in D), and shaded symbols are other taxa (Oligochaeta, Gastropoda, Bivalvia). Best-fit  
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11 654 lines are for all taxa combined.

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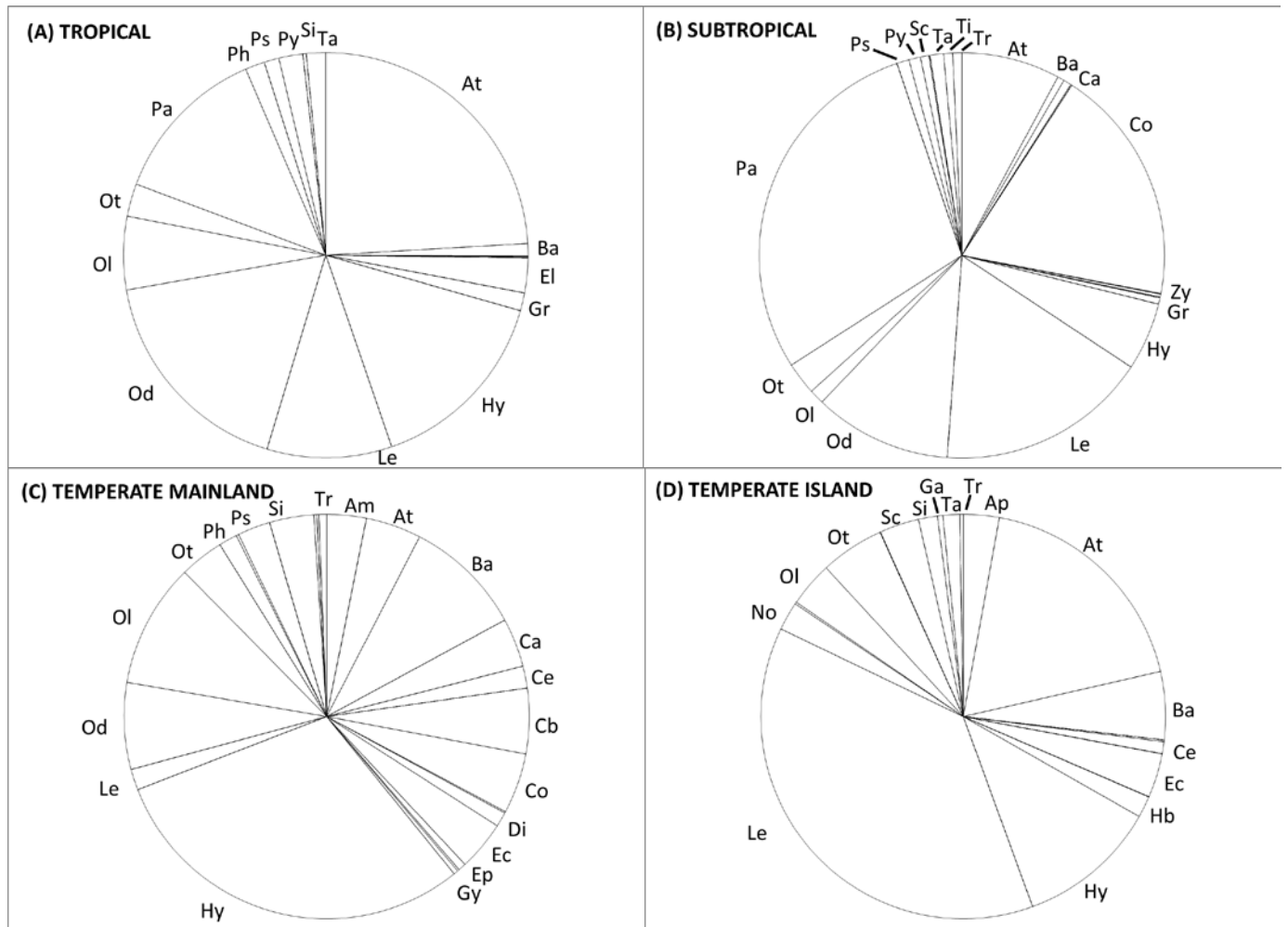
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674 **Figure 1.**

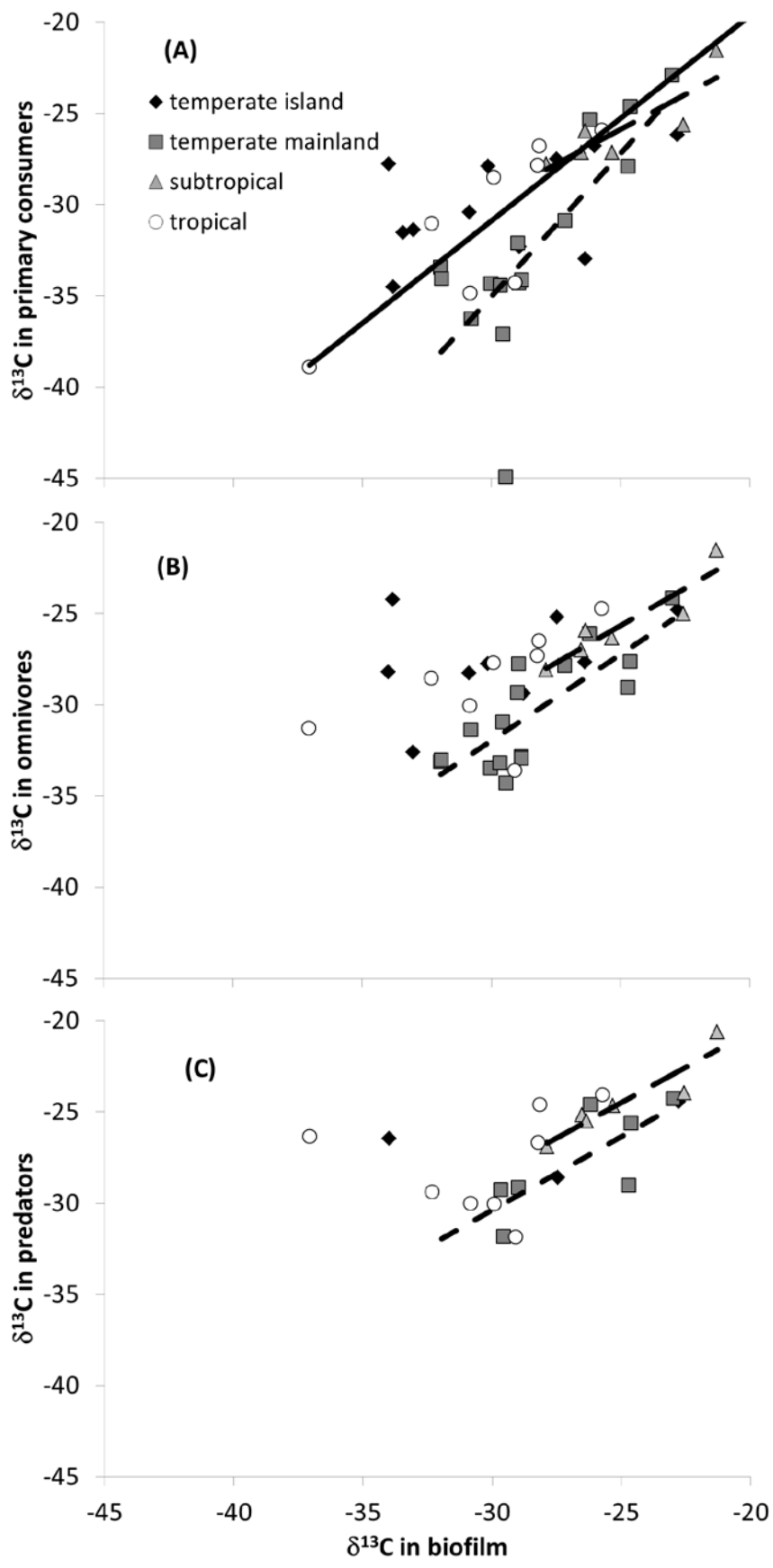


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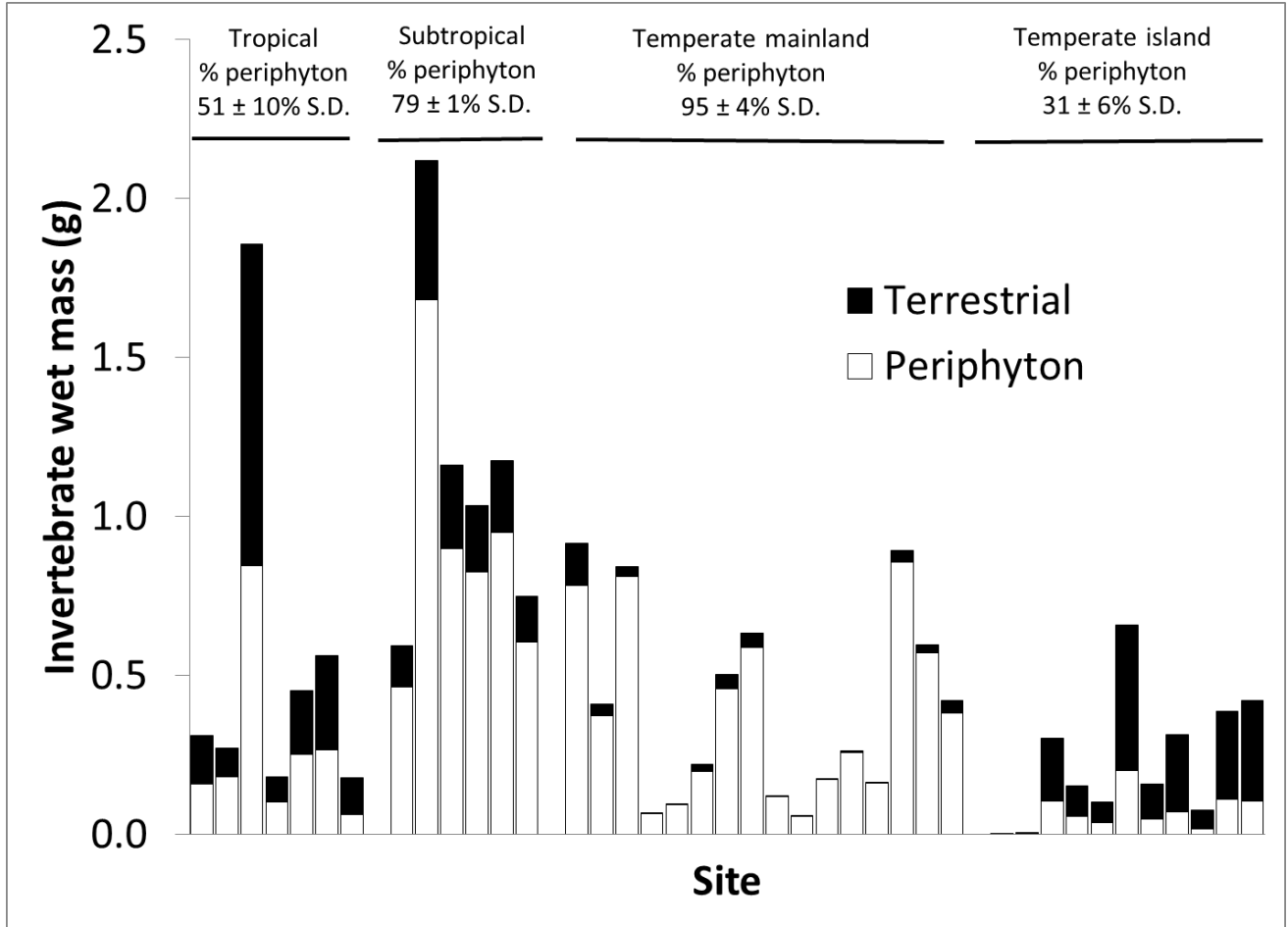
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691 **Figure 2.**



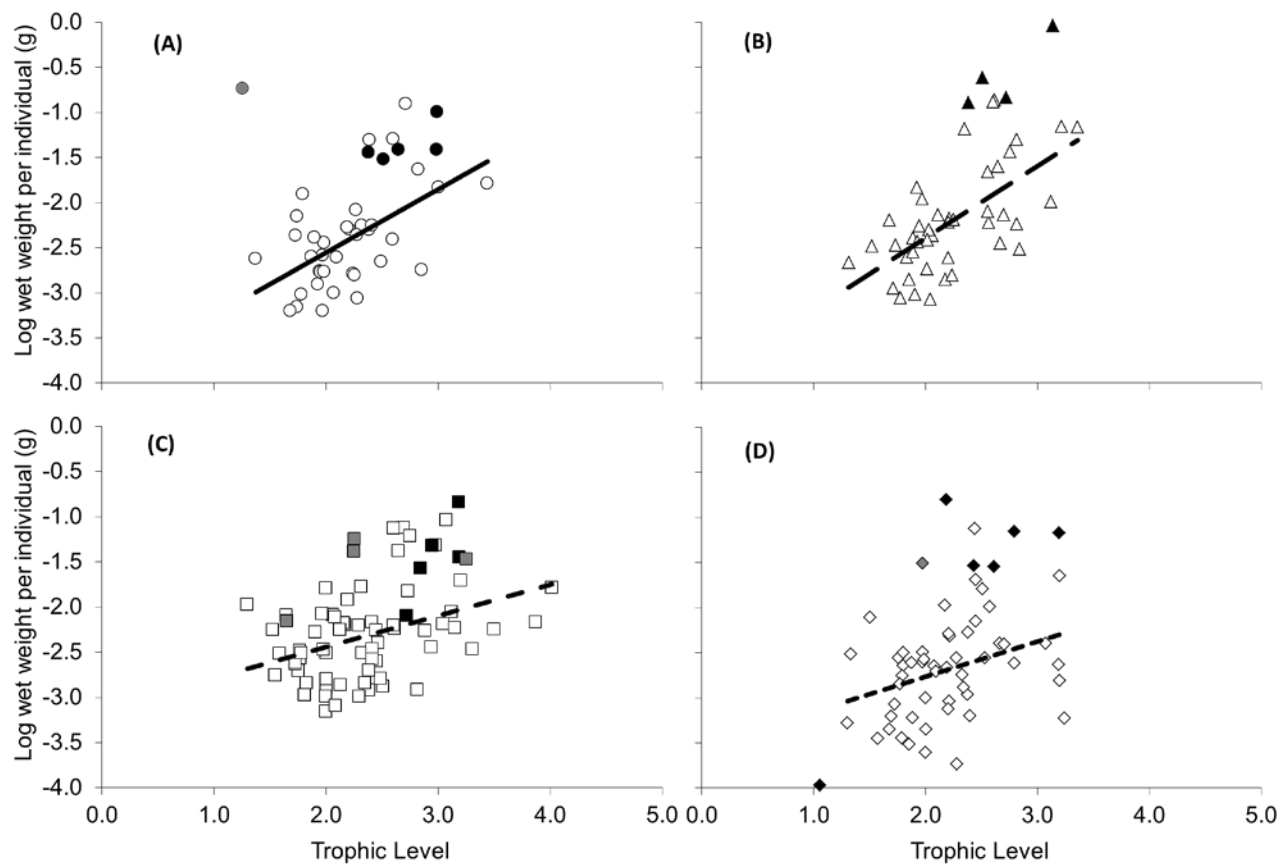
714 **Figure 3.**



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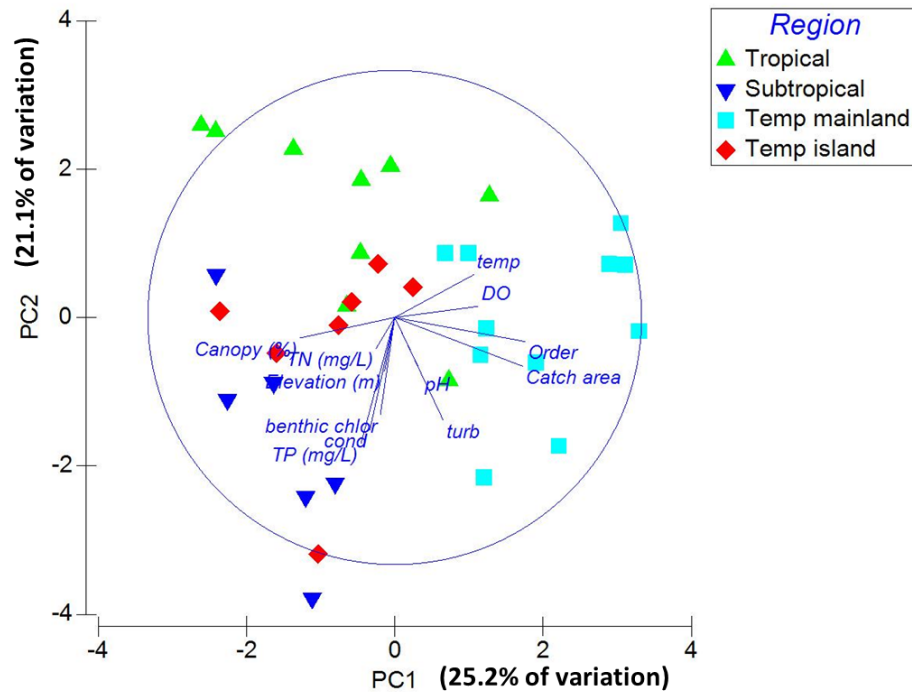
725 **Figure 4.**



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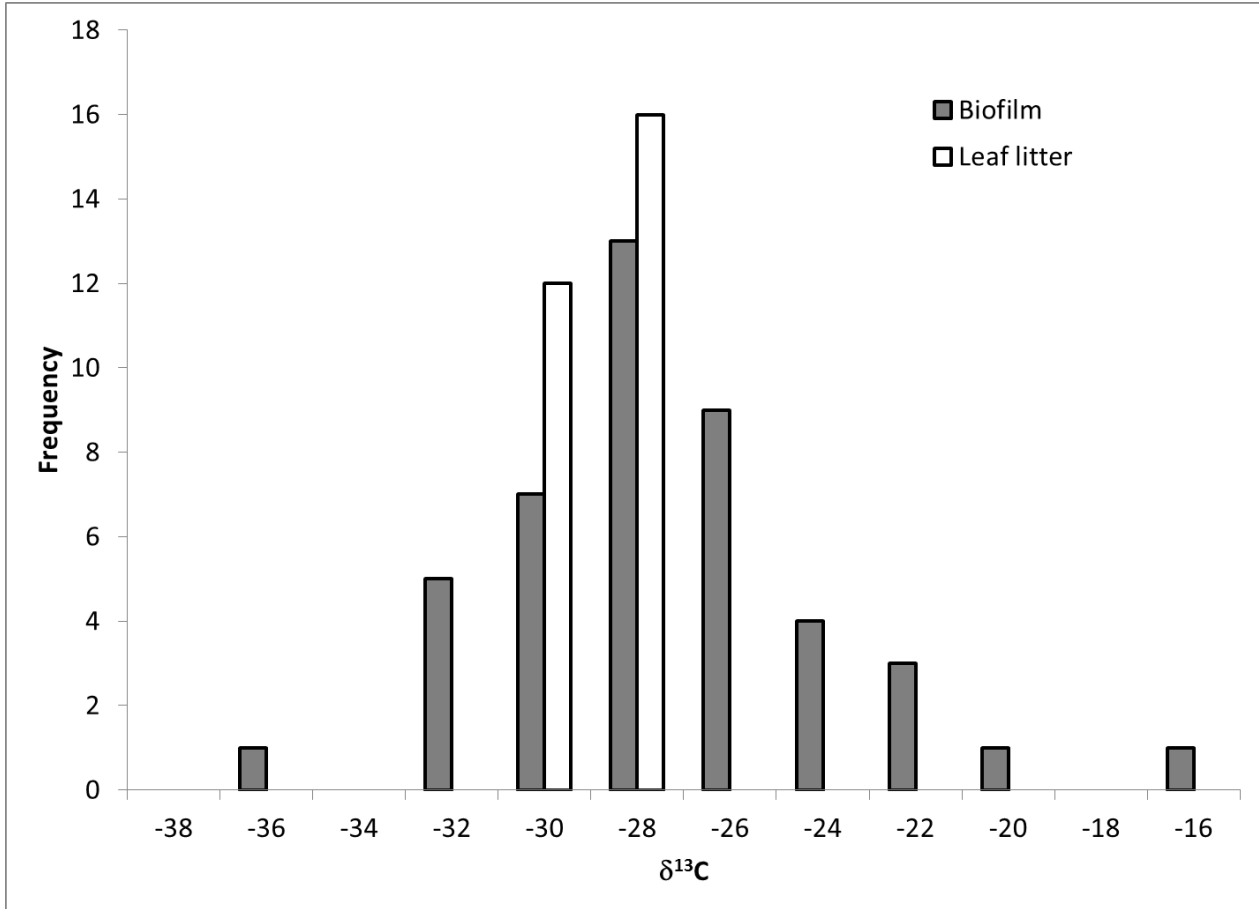
Supplementary material for Jardine, T.D. In review. Organic matter sources and size structuring in stream invertebrate food webs across a tropical to temperate gradient. *Freshwater Biology*.

**Figure S1.** Principal component analysis of environmental variables for streams in four regions of eastern Australia. Variable codes as follows: temp = temperature, DO = dissolved oxygen, Order = stream order, Catch area = upstream catchment area, turb = turbidity, TN = total nitrogen, benthic chlor = benthic chlorophyll *a*, cond = conductivity, TP = total phosphorus.



**Figure S2.** Frequency histogram for stable carbon isotope ratios ( $\delta^{13}\text{C}$ ) of biofilm and leaf litter in streams of eastern Australia.

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