

Stable isotope analyses of web-spinning spider assemblages along a headwater stream in Puerto Rico

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Web-spinning spiders that inhabit stream channels are considered specialists of aquatic ecosystems and are major consumers of emerging aquatic insects, while other spider taxa are more commonly found in riparian forests and as a result may consume more terrestrial insects. To determine if there was a difference in spider taxa abundance between riverine web-spinning spider assemblages within the stream channel and the assemblages 10m into the riparian forest, we compared abundances for all web-spinning spiders along a headwater stream in El Yunque National Forest in northeast Puerto Rico. By using a nonmetric dimensional scaling (NMDS) abundance analysis we were able to see a clear separation of the two spider assemblages. The second objective of the study was to determine if aquatic insects contributed more to the diet of the spider assemblages closest to the stream channel and therefore stable isotope analyses of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for web-spinning spiders along with their possible prey were utilized. The results of the bayesian mixing model (SIAR) however showed little difference in the diets of riverine (0m), riparian (10m) and upland (25m) spiders. We found that aquatic insects made up ~50% of the diet for web-spinning spiders collected at 0m, 10m, and 25m from the stream. This study highlights the importance of aquatic insects as a food source for web-spinning spiders despite the taxonomic differences in assemblages at different distances from the stream.

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1 INTRODUCTION

2

3 Riparian zones have been identified as areas of high importance for maintaining biodiversity in
4 aquatic and terrestrial habitats along with being an important interface for the exchange of
5 resources, resulting in an ecosystem with unique environmental dynamics (Naiman & Decamps
6 1997; Naiman et al. 1993; Nakano & Murakami 2001). The importance of terrestrial subsidies
7 (i.e. resources that are transported across ecosystem boundaries) as an energy source in the food
8 webs of headwater streams has long been recognized (Vannote et al. 1980), but only more
9 recently has it become evident that aquatic subsidies can be equally important in terrestrial food
10 webs (Kato et al. 2003; Nakano & Murakami 2001; Polis et al. 1997; Sanzone 2001; Sanzone et
11 al. 2003). Emerging aquatic insects have been shown to be an important food source for a
12 variety of terrestrial predators (Nakano & Murakami 2001; Polis et al. 1997) and the abundance
13 of aquatic insects can affect the distribution of generalist predators such as insectivorous bats,
14 reptiles, birds and spiders (Chan et al. 2008; Fukui et al. 2006; Iwata et al. 2003; Kato et al.
15 2003; Marczak & Richardson 2007; Sabo & Power 2002).

16

17 Web spinning spiders are a particularly good model organism for studying the exchange
18 of subsidies across riparian ecotones due to the fact that they are major consumers of emerging
19 aquatic insects, and some taxa of web spinning spiders have been associated exclusively with
20 fresh water ecosystems (eg. *Tetragnatha* (Tetragnathidae) and *Wendilgarda* (Theridiosomatidae)
21 (Coddington 1986; Eberhard-Crabtree 1989; Gillespie 1987). The distribution of these spiders
22 has been correlated with aquatic insect abundances and for this reason these taxa of spiders are
23 disproportionally more abundant within the first few meters from the stream channel where
24 emerging insects tend to aggregate (Muehlbauer et al. 2014). The genus *Tetragnatha* has a
25 worldwide distribution and can be found on all continents (except Antarctica)(Aiken & Coyle
26 2000). Juvenile and female *Tetragnatha* typically construct relatively large, horizontal orb-webs
27 directly above the surface of lentic and lotic bodies of freshwater (Gillespie 1987). *Wendilgarda*
28 is another genus of spider known to be associated with freshwater ecosystems; however, they are
29 quite different from *Tetragnatha* in the sense that they are only found in tropical regions and the
30 majority of taxa build a very reduced web structure that consists of one or two structural silk
31 lines attached to rocks or vegetation along the stream with additional lines being attached to the

32 water surface to snag drifting insects (Eberhard-Crabtree 1989; Eberhard 2001). Along with
33 these aquatic specialists there has also been evidence that a variety of other taxa of web-spinning
34 spiders (Araneidae, Lynphiidae and Theridiidae) are also more abundant along streams where
35 there are greater densities of aquatic insects (Marczak & Richardson 2007).

36

37 Originally food web studies were generally conducted using observations in the field and
38 gut content analyses but recently the use of stable isotopes has become a preferred method for
39 several reasons. One benefit of using stable isotopes is that gut content analyses are not viable
40 methods for some organisms due to their feeding habits (e.g. spiders who feed on liquefied
41 tissue) (Foelix 2011). Another advantage of stable isotopes is that it is able to infer relatively
42 long term feeding habits due to the bioaccumulation of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ into the tissue of the
43 consumer. A third advantage is that naturally occurring stable isotopes have been shown to be
44 effective at identifying the contribution of different prey items in the diets of consumers through
45 the use of mixing models (Parnell & Jackson 2013; Peterson & Fry 1987; Phillips & Gregg
46 2003). This final aspect of stable isotope analyses is especially useful in aquatic and riparian
47 food webs when determining the importance of subsidies that cross ecosystem boundaries, such
48 as leaf litter falling into streams or emerging aquatic insects becoming food for terrestrial
49 predators (Akamatsu et al. 2004; Burdon & Harding 2008; Davis et al. 2011; Hicks 1997; Lau et
50 al. 2009; Sanzone 2001; Sanzone et al. 2003; Walters et al. 2007).

51

52 This study had two main objectives. The first was to determine if there were differences
53 in the composition of taxa in the assemblages of web-spinning spiders that were found over the
54 stream channel compared to those 10m from the stream. Due to some spiders being specialists
55 of aquatic ecosystems we predicted that these taxa would be in far greater abundance over the
56 stream channel. The second objective was to determine if there were differences in the diets of
57 these two assemblages using stable isotopic analyses. The majority of emerging aquatic insects
58 remain very close to the stream channel and their abundance can drop exponentially only a few
59 meters into the riparian area (Muehlbauer et al. 2014), so we predicted that the assemblage of
60 web-spinning spiders in the stream channel would have a diet that reflects a greater dependence
61 on aquatic insects while the assemblage in the riparian area would be feeding on a greater
62 number of terrestrial insects.

63

64 **MATERIAL AND METHODS**

65

66 ***Study Area***

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68 This study was conducted along the small headwater stream Quebrada Prieta within El Yunque
69 National Forest in northeastern Puerto Rico at latitude 18°18'N and longitude 65°47'W
70 (Masteller 1993). The stream begins at around 600m above sea level and runs into the Quebrada
71 Sonadora at around 310m above sea level with an average slope of 20% (Masteller 1993). The
72 stream ranges from 2-4m in width and is mainly composed of large boulders and cobble with
73 intermittent small pools with finer sediments of sand and silt. In 2012 total rainfall was 397.7cm
74 and the mean temperature was 23.93(±2.94)°C (Luquillo-LTER). The stream is surrounded by a
75 mainly closed canopy of tabonuco (*Dacryodes excels* Vahl) forest which is the dominant tree
76 species in the Luquillo Mountains until around 600m in elevation (Masteller 1993). Other
77 common plant species include bullwood (*Sloanea berteriana* Choisy) and palms (*Prestoea*
78 *montana* Graham and Nicolson)(Masteller 1993).

79

80 The macroinvertebrate community of Quebrada Prieta is diverse and is composed of a variety of
81 aquatic insects with the most abundant being trichopterans and ephemeropterans (Masteller
82 1993). During a 52 week sampling period from 1990 to 1991 the total number of specimens
83 collected in an emergence trap above Quebrada Prieta found 35% to be ephemeropterans, 24%
84 trichopterans, 21% chironomids and 20% as other dipterans (Masteller & Buzby 1993a). In this
85 study emergence patterns varied somewhat between taxa, although as with most tropical streams,
86 all taxa were present throughout the year (Ferrington et al. 1993; Flint & Masteller 1993;
87 Masteller & Buzby 1993b; Pescador et al. 1993; Wagner & Masteller 1993). For all taxa the
88 abundances were generally lowest during the summer months and highest during late fall to early
89 spring (Ferrington et al. 1993; Flint & Masteller 1993; Masteller & Buzby 1993b; Pescador et al.
90 1993; Wagner & Masteller 1993). For an example, ephemeropterans, trichopterans and
91 chironomids were found to be the most abundant during November, March and January
92 respectively (Ferrington et al. 1993; Flint & Masteller 1993; Pescador et al. 1993). All three taxa

93 were found to be the least abundant during June and July (Ferrington et al. 1993; Flint &
94 Masteller 1993; Pescador et al. 1993).

95

96 *Web-Spinning Spider Assemblages*

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98 A 100m reach of Quebrada Prieta was selected and then divided into four 25m subsections. Field
99 work for this portion of the project was conducted from April to August 2012, with at least one
100 week between sampling dates to minimize the possibility of impacting the study area. A 3m x
101 3m riverine quadrat was selected within the stream channel in the first 25m section of stream,
102 measuring 3m from the stream edge into the stream channel. Each quadrat was selected to
103 contain a random mixture of available substrates, such as boulders, vegetation and deadwood
104 which may affect web-spinning spider distribution. All web-spinning spiders within the quadrat
105 up to 2.5m in height were hand collected and preserved in 70% ethanol for later identification.
106 This process was then repeated for a riparian site 10m laterally from the stream edge into the
107 riparian forest from the riverine sampling site. The same sampling procedure was then repeated
108 for the next 25m section of the stream. On the following sampling date we would sample the
109 remaining two 25m sections of the stream not sampled during the previous visit.

110

111 Each sampling date consisted of two riverine and two riparian quadrats. We conducted
112 both diurnal and nocturnal sampling because some taxa of web-spinning spiders (e.g.
113 *Tetragnatha* and *Chrysometa*) are more active at night and rarely build webs during the day.
114 Nocturnal sampling on average was conducted from 1900-2300, while diurnal sampling on
115 average was from 1000-1400. Sampling was only conducted during favorable weather
116 conditions, because spider webs are many times easily destroyed by wind and rain (Foelix 2011).
117 Diurnal and nocturnal samplings were combined and therefore a total of eight riverine and eight
118 riparian quadrats were analyzed for differences in web-spinning spider assemblages.

119 A Nonmetric Dimensional Scaling (NMDS) analysis along with a post-hoc Analysis of
120 Similarity (ANOSIM) were used to determine if there were differences in taxa composition of
121 the two web-spinning spider assemblages. A secondary post-hoc analysis, Similarity
122 Percentages (SIMPER), was used to determine which particular taxa of spiders were causing a

123 difference in the composition of the two assemblages. All of these analyses were conducted with
124 the statistical program PAST (Hammer et al. 2001).

125

126 *Stable Isotopes*

127

128 To verify that the spider assemblages and their prey had stable isotope signatures that fell within
129 realistic ranges of the basal C sources we sampled the three principal energy sources for aquatic
130 and terrestrial arthropods. The three C sources sampled were stream leaf litter, periphyton and
131 terrestrial vegetation. Stream leaf litter was collected at random throughout the 100m stream
132 transect and was gently rinsed to remove any macroinvertebrates. Periphyton was also sampled
133 randomly by collecting rocks from the stream, gently rinsing them to remove any
134 macroinvertebrates, and then scrubbing them with a small wire brush. The resultant slurry was
135 then collected into glass vials to be dried later. For terrestrial vegetation samples, green leaves
136 were collected at random from C3 plants within the riparian forest.

137

138 Possible insect prey of the spider assemblages were collected for isotope analysis using
139 two methods. Flying insects were collected using a passive sampling method with three Malaise
140 traps that were placed within the stream channel for approximately four hours during the diurnal
141 and nocturnal spider sampling. Traps were placed within three different sections of the stream
142 reach (0-25m, 25-75m and 75-100m) during each sampling period. This was done in order to
143 have a representation of the available prey of web-spinning spiders flying along the stream
144 channel. Aquatic insect larvae were collected using hand nets throughout the 100m stream
145 reach. Sampling was conducted in pools, riffles, and cascades to ensure that all major
146 microhabitats were sampled. The larval stages of Ephemeroptera, Trichoptera and
147 Chironomidae were used for isotopic analysis because they no longer feed as adults and thus
148 their isotopic signature is fixed during the aquatic larval stage.

149

150 To compare the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ stable isotope signals for the different spider assemblages,
151 individuals were collected from a riverine transect within the stream channel, from a riparian
152 transect 10m parallel from the stream edge and from an upland transect 25m parallel from the
153 stream edge. In each transect web-spinning spiders were collected from the four most abundant

154 families, Tetragnathidae, Theridiosomatidae, Pholcidae and Uloboridae. Spiders were collected
155 and maintained live in small containers for a day, to allow for the digestion of prey that may
156 have been recently consumed to reduce the influence of the isotopic signal from what they were
157 consuming.

158

159 Specimens were frozen (-20°C) for a minimum of 24 hours, then placed in a drying oven
160 for a minimum of 48hrs (70°C) and finally ground to a fine powder for isotopic analysis. Insects
161 were identified to the family level (except for Lepidoptera identified to order) and spiders were
162 identified to the genus level (except for *Wendilgarda clara* Keyserling 1886, identified to
163 species). Composite taxa samples of a minimum of four individuals for spiders 1±0.05mg of
164 animal tissue and 5±0.05mg of plant tissue was measured for the natural abundances of ¹⁵N and
165 ¹³C using ratio mass spectrometry at the Miami Stable Isotope Ecology Lab at the University of
166 Miami in Florida. Natural abundances of stable isotopes for δ¹³C and δ¹⁵N were calculated as:

167
$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$$

168 where, $R_{\text{sample}} = {}^{13}\text{C}:{}^{12}\text{C}$ or ${}^{15}\text{N}:{}^{14}\text{N}$ ratio in the sample and $R_{\text{standard}} = {}^{13}\text{C}/{}^{12}\text{C}$ ratio in Pee Dee
169 Belemnite for δ¹³C and $R_{\text{standard}} = {}^{15}\text{N}/{}^{14}\text{N}$ ratio in the atmosphere for δ¹⁵N (Peterson & Fry
170 1987).

171

172 The stable isotopes ¹⁵N and ¹³C of insects were analyzed as composite samples with
173 aquatic insect taxa compiled first by family into one of five functional feeding groups: collector-
174 gatherers (n=1), filterers (n=2), predators (n=3), scrapers (n=2) and shredders (n=2) (Ramirez &
175 Gutierrez-Fonseca 2014). Terrestrial insects were grouped as either herbivorous (n=3) or
176 predacious (n=2). Terrestrial dipterans were only identified to order and due to their varied
177 feeding behaviors they were not placed into a particular feeding group. The isotopic values for
178 the five aquatic functional groups were then combined into a single aquatic insect group and the
179 values for the three terrestrial insect groups (predators, herbivores and dipterans) were combined
180 as well. Spider taxa were identified to genus and were grouped as either having been collected in
181 riverine (n=7), riparian (n=5) or upland (n=5) transects. Mean averages of δ¹³C and δ¹⁵N for
182 each group (aquatic insects, terrestrial insects, riverine spiders, riparian spiders and upland
183 spiders) were used in subsequent biplots and dietary analyses.

184 Dietary analyses were conducted utilizing Bayesian mixing models in the SIAR package
185 version 4.2 with Stable Isotope Analysis in R (SIAR) (Parnell & Jackson 2013) for R version
186 3.0.3 (R Core Team 2012). Consumers were the three spider groups (riverine, riparian and
187 upland) and the sources were the two insect groups (aquatic and terrestrial). Fractionation
188 factors between consumers and sources ($\delta^{13}\text{C}$: $0.08 \pm \text{SD } 1.90$ and $\delta^{15}\text{N}$: $2.75 \pm \text{SD } 2.20$) were
189 adopted from the work by Yuen and Dudgeon (2015) in which they had reviewed fractionation
190 values for arthropod consumers from a previous comprehensive study (Caut et al. 2009). The
191 proportion of aquatic insects in the diets of the three spider groups were determined from the
192 SIAR package that provides 5, 25, 75 and 95% credibility intervals from the Bayesian mixing
193 models.

194

195 RESULTS

196

197 *Web-Spinning Spider Assemblages*

198

199 Four diurnal and four nocturnal samplings were conducted for both riverine and riparian habitats.
200 Five families of web-spinning spiders (Araneidae, Pholcidae, Tetragnathidae, Theridiosomatidae
201 and Uloboridae) were collected in varying abundances from riverine and riparian quadrats (Table
202 1). The least abundant family was Araneidae with only two individuals collected, while the
203 family Theridiosomatidae was the most abundant with 199 individuals collected from two taxa,
204 *Theridiosoma sp.* and *Wendilgarda clara* (Keyserling) (Table 1). The second most abundant
205 family was Tetragnathidae with 146 individuals collected from three genera, *Chrysometa*,
206 *Leucauge* and *Tetragnatha* (Table 1). Uloboridae was the third most abundant family with 32
207 individuals collected from the *Miagrammopes* genus (Table 1). Pholcidae was the second to
208 least abundant family with 28 individuals collected from the *Modisimus* genus (Table 1). There
209 were 265 spiders collected from the riverine habitat while in the riparian habitat 142 spiders were
210 collected.

211

212 A NMDS analysis of the two web-spinning spider assemblages shows a clear spatial separation
213 of the eight riparian and eight riverine groups (Fig.1). This was statistically verified with the
214 post-hoc test ANOSIM, which showed a significant difference in the degree of separation

215 between the two assemblages (Bonferroni-corrected, $p < 0.002$, $R = 0.722$) (Fig. 1). An additional
216 post-hoc analysis, SIMPER, found that around 48% of the dissimilarity between the assemblages
217 was attributed to the abundance of *Wendilgarda clara*.

218

219 ***Basal Carbon Sources and Prey Taxa***

220

221 Stable isotope analyses of the basal C sources showed a difference of $\delta^{13}\text{C}$ in terrestrial
222 vegetation, periphyton and stream leaf litter. Terrestrial vegetation (-34.90‰) was more
223 depleted in $\delta^{13}\text{C}$ than aquatic periphyton (-32.40‰) and stream leaf litter (-25.50‰) (Table 2).
224 $\delta^{15}\text{N}$ values were very similar for C3 vegetation (-1.30‰) and periphyton (-0.80‰) while stream
225 leaf litter had the highest $\delta^{15}\text{N}$ value (0.80‰). Despite these differences in $\delta^{13}\text{C}$ there was no
226 clear separation between aquatic and terrestrial C signatures.

227 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for individual insect groups varied among taxa. The family
228 Helicopsychidae (Trichoptera) was the most depleted in $\delta^{13}\text{C}$ (-34.88‰), while the family
229 Lampyridae (Coleoptera) was the most enriched in $\delta^{13}\text{C}$ (-25.30‰) (Table 2). The family
230 Cicadoidea (Hemiptera) had the lowest $\delta^{15}\text{N}$ value (-0.55‰), while Lampyridae, a terrestrial
231 predator, was not only the most enriched in $\delta^{13}\text{C}$ but was also the most enriched in $\delta^{15}\text{N}$ (6.31‰)
232 (Table 2). There was also a large amount of variation seen in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values when
233 insects were analyzed according to their functional feeding groups. The terrestrial predator group
234 of insects was the most enriched in $\delta^{13}\text{C}$ ($-26.06 \pm \text{SD}1.75\text{‰}$), followed by collector-gatherers ($-$
235 26.63‰), aquatic predators ($-27.26 \pm \text{SD}0.68\text{‰}$), terrestrial herbivores ($-28.05 \pm \text{SD}0.91\text{‰}$),
236 shredders (-28.55‰), filterers ($-28.59 \pm \text{SD}1.17\text{‰}$) and scrapers ($-31.52 \pm \text{SD}4.75\text{‰}$). Terrestrial
237 predators ($5.07 \pm \text{SD}1.75\text{‰}$) were the most enriched in $\delta^{15}\text{N}$, followed by aquatic predators
238 ($4.35 \pm \text{SD}1.20\text{‰}$), filterers ($3.16 \pm \text{SD}0.76\text{‰}$), collector-gatherers (2.63‰), scrapers
239 ($2.27 \pm \text{SD}0.45\text{‰}$), shredders (0.78‰) and terrestrial herbivores ($0.69 \pm \text{SD}1.76\text{‰}$). When insect
240 taxa were grouped together and analyzed as either terrestrial ($n=5$) or aquatic ($n=10$), no
241 significant difference was found in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between the two groups (Figure 2).
242 Although there was no significant difference in $\delta^{13}\text{C}$, terrestrial insects ($-26.99 \pm \text{SD}1.22\text{‰}$) were
243 overall more enriched than aquatic insects ($-28.66 \pm \text{SD}2.69\text{‰}$). Terrestrial insects
244 ($3.17 \pm \text{SD}2.60\text{‰}$) were also more enriched in $\delta^{15}\text{N}$ although they also showed greater variation
245 than aquatic insects ($3.04 \pm \text{SD}1.47\text{‰}$).

246

247 ***Web-Spinning Spiders***

248

249 Stable isotope analyses of the individual spider taxa showed less variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$
250 values than was seen in the insect taxa. The genus *Miagrammopes* (Uloboridae) along the
251 upland transect was the most depleted in $\delta^{13}\text{C}$ (-33.30‰), while *Theridiosoma*
252 (*Theridiosomatidae*) also from the upland transect was the most enriched in $\delta^{13}\text{C}$ (-26.50‰)
253 (Table 2). The genus *Chrysometa* (*Tetragnathidae*) from the riverine transect had the highest
254 $\delta^{15}\text{N}$ value (5.19‰), while upland *Miagrammopes* (Uloboridae) had the lowest $\delta^{15}\text{N}$ value
255 (0.10‰) (Table 2). There were no significant differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between the
256 three spider groups. The group the most enriched in $\delta^{13}\text{C}$ were riverine spiders (-
257 $27.07 \pm \text{SD}0.38\%$), followed by riparian spiders ($-27.62 \pm \text{SD}0.52\%$) and finally upland spiders (-
258 $28.30 \pm \text{SD}2.82\%$) (Fig.2). Similarly the group with the highest $\delta^{15}\text{N}$ values were riverine spiders
259 ($4.00 \pm \text{SD}0.75\%$), followed by riparian spiders ($3.76 \pm \text{SD}0.89\%$) and finally upland spiders
260 ($2.92 \pm \text{SD}1.93\%$) (Fig.2). The greatest amount of variation in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values was
261 seen in upland spiders (Fig.2).

262

263

264 ***Bayesian Mixing Model Analyses***

265

266 Bayesian mixing models determined that the proportion of aquatic insects in the diets of the three
267 spider groups was relatively similar. However, the proportion of aquatic insects in the diets of
268 the spiders increased slightly in the groups further away from the stream channel (Fig.3). The
269 analyses revealed that riverine spiders had the least amount of aquatic insects in their diet (45-
270 47%) although there was considerable variation (12-71%) (Fig.3). In the riparian spider group
271 aquatic insects made up a slightly greater proportion (47-49%) but again a great deal of variation
272 was seen (10-80%) (Fig.3). The proportion of aquatic insects was greatest in the upland spiders
273 (50-53%) although this group also had the greatest amount of variation (10-98%) (Fig.3).

274

275 **DISCUSSION**

276

277 The influence of emerging aquatic insects has been shown to affect web-spinning spider
278 distributions in riparian areas, especially within the first 10m from the stream edge (Collier et al.
279 2002; Kato et al. 2003; Kato et al. 2004; Sanzone et al. 2003). Most emerging aquatic insects
280 follow a negative power function abundance curve and over 50% of their “signature” has been
281 found to be within only 1.5m from the stream, although some variation has been found
282 depending on the taxa of aquatic insect (Muehlbauer et al. 2014). We established our working
283 hypotheses based on the strong link between web-spinning spiders and emerging aquatic insects
284 and the fact that the majority of the insects congregate within only a few meters of the stream
285 edge. First we proposed that there would be a different assemblage of web-spinning spiders, due
286 to the presence of aquatic specialists (*Tetragnatha* and *Wendilgarda*), within the stream corridor
287 compared to 10m into the riparian forest. We then proposed that because the majority of aquatic
288 insects congregate within only a few meters of the stream, that the riverine spider assemblage in
289 the stream corridor would be consuming more aquatic insects than riparian and upland spiders.
290 We found that there was indeed a significant difference between the riverine and riparian
291 assemblages and that around 48% of the dissimilarity between the assemblages was attributed to
292 the abundance of *Wendilgarda*, a specialist of aquatic habitats. The results did not entirely
293 support our second hypothesis. The analyses of stable isotopes showed no clear separation
294 between the $\delta^{13}\text{C}$ signature for aquatic and terrestrial prey due to the fact that the aquatic food
295 web was driven by leaf litter inputs from the terrestrial vegetation that resulted in similar $\delta^{13}\text{C}$
296 ranges for both terrestrial and aquatic primary consumers. As a result the biplot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$
297 showed significant overlapping of the three spider groups along with the aquatic and terrestrial
298 insects. This resulted in the inability to visually separate the consumer groups or their prey. The
299 Bayesian SIAR dietary analysis showed that the upland group of spiders relied the most heavily
300 on aquatic insects (50-53%) although only slightly more so than riverine (45-47%) and riparian
301 (47-49%) spiders (Fig.3). Overall aquatic insects were found to be an important food source for
302 web-spinning spiders even up to 25m from the stream channel.

303

304 The difference in assemblage composition between the stream channel and the riparian
305 forest was found to be driven mainly by an aquatic specialist, *Wendilgarda*, which snare their
306 prey directly from the water surface (Coddington 1986; Eberhard-Crabtree 1989). *Tetragnatha*,
307 another aquatic specialist (Aiken & Coyle 2000; Alvarez-Padilla & Hormiga 2011; Gillespie

1987), was also only found only in riverine quadrats however there were too few individuals to have any statistical significance. Studies of riparian spider assemblages in other parts of the world have found similar shifts in taxa composition, in which the abundance of some spiders was directly related to the distance from the stream edge and that significant differences could be found within only 10m into the riparian zone (Sanzone 2001; Sanzone et al. 2003). However, most studies have only been conducted in temperate regions and so far few studies that have investigated whether this distribution of spider taxa also occurs along tropical streams. Some of the proposed biotic and abiotic factors that could explain the shift in spider distributions range from differences in vegetative complexity and structure (Chan et al. 2009) to changes in humidity and temperature, but the most common factor associated with the distribution of web spinning spiders has been associated with the abundance of aquatic insects (Kato et al. 2003; Kato et al. 2004; Sanzone 2001; Sanzone et al. 2003).

320

Basal carbon sources (stream leaf litter, periphyton and C3 vegetation), prey items (terrestrial and aquatic insects) and web spinning spiders (riverine, riparian and upland) (Table 2) were all found to have isotopic signals within the range of reported values from other studies (Fry 1991; Kato et al. 2004; Lau et al. 2009; March & Pringle 2003; Ometto et al. 2006; Trudeau 2003). Terrestrial vegetation was the most depleted in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, stream leaf litter was the most enriched in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and periphyton was the intermediate of the two (Table 2). The difference between the stable isotopic signals of the stream leaf litter and terrestrial vegetation could be a result of the stream leaf litter having been derived from other vegetation found upstream that were not necessarily present long the section of stream that was sampled during the study. The differences in the type of terrestrial vegetation found upstream could account for some of the difference in isotopic values. Allochthonous and autochthonous C sources in riparian food webs can vary considerably in their $\delta^{13}\text{C}$ signature ($\pm 10\%$) depending on several factors such as plant taxa, water velocity, and canopy cover (Lau et al. 2009; March & Pringle 2003; Ometto et al. 2006; Trudeau 2003). Basal carbon sources were utilized in determining a reasonable range in which subsequent consumers should be found.

336

Isotopic values of insect taxa were all found to be within the range of basal C sources; however there was no clear separation in the isotopic signals between terrestrial and aquatic

338

339 insects (Fig.2). Terrestrial predators and herbivores showed little variation in their $\delta^{13}\text{C}$ signal, -
340 $28.05\pm 0.91\text{‰}$ and $-26.06\pm 1.08\text{‰}$ respectively. The enriched $\delta^{13}\text{C}$ signal in the predators is most
341 likely associated with bioaccumulation more so than a change in C sources. Of all the insect
342 groups, terrestrial herbivores and predators had the lowest and highest $\delta^{15}\text{N}$ values respectively,
343 similar to what was reported in a study done by Kato et al. (2004) in Japan where they also found
344 a difference of around 4‰ between terrestrial herbivores and predators (Kato et al. 2004).

345

346 The $\delta^{13}\text{C}$ signature for the aquatic insect groups, as mentioned earlier, was not
347 statistically different from the terrestrial insects and most of the functional feeding groups had
348 overlapping values with terrestrial herbivores emphasizing the importance of leaf litter inputs in
349 the aquatic food web. Overall, aquatic insects were more depleted in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ than
350 terrestrial insects, similarly to what has been found in other studies (Kato et al. 2004). Scrapers
351 were found to be the most depleted in $\delta^{13}\text{C}$ and this group also showed the greatest range in their
352 $\delta^{13}\text{C}$ signature (-1.52 ± 4.75). This variation is most likely the result of the two taxa that were
353 collected for this functional group. Helicopsychidae were severely depleted in $\delta^{13}\text{C}$ due to them
354 being obligate scrapers, feeding on C sources depleted in $\delta^{13}\text{C}$ such as periphyton and possibly
355 other more depleted C sources that were not sampled in this study (e.g. aquatic moss).
356 Leptophlebiidae are considered to be more generalists and at times may feed as collector-
357 gatherers, despite the families overall classification as scrapers (Ramirez & Gutierrez-Fonseca
358 2014). Similar isotopic values were found for Leptophlebiidae in a nearby stream ($\delta^{13}\text{C}$: -
359 $24.25\pm 0.72\text{‰}$ and $\delta^{15}\text{N}$: $2.51\pm 0.20\text{‰}$) (March & Pringle 2003). The small change in $\delta^{13}\text{C}$ could
360 have been a result of the stream in the study by March and Pringle (2003) having a more open
361 canopy and therefore a possible greater presence of algae. The aquatic insect groups had $\delta^{15}\text{N}$
362 signatures that fell within the two terrestrial extremes with aquatic predators ($4.35\pm 1.20\text{‰}$) and
363 shredders (0.78‰) having respectively the highest and lowest $\delta^{15}\text{N}$ signatures. Collector-
364 gatherers, scrapers and filterers were found to be intermediary with relatively little variation in
365 their $\delta^{15}\text{N}$ values ($1.96\text{-}3.69\text{‰}$).

366

367 The three spider groups showed only slight differences in their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures
368 with upland spiders being the most depleted in both instances. A study conducted in Japan
369 similarly found only minimal changes in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between riparian and upland

370 web spinning spiders of the same taxa (Kato et al. 2004). However, in our study we did not
371 analyze individual taxa and included only web-spinning spiders. This may explain some of the
372 similarity between riverine, riparian and upland groups. Other studies have found that
373 differences in stable isotopes values can be associated with different hunting strategies (i.e. sit
374 and wait, wandering or web building) (Collier et al. 2002; Kato et al. 2004; Sanzone et al. 2003;
375 Yuen & Dudgeon 2015).

376

377 The bayesian analysis in SIAR found that upland spiders relied the most upon aquatic
378 insects although there were only slight differences among the three spider groups. Although the
379 vast majority of aquatic insect biomass is concentrated within the first few meters or so from the
380 stream edge, some taxa are known to disperse laterally up to hundreds of meters from the stream
381 (Muehlbauer et al. 2014). For an example, even at around 13.3m from the stream edge an
382 estimated 50% of the abundance of chironomids would still be present (Muehlbauer et al. 2014).
383 Around 10% of the abundance for ephemeropterans and trichopterans was estimated to be found
384 still even 160m and 650m respectively from the stream edge (Muehlbauer et al. 2014). We
385 found that aquatic insects made up around 50% of the spiders' diet which was slightly less than
386 what has been reported in some other studies which have found that aquatic insects can make up
387 ~70-90% of the diet of riparian spiders (Akamatsu et al. 2004; Sanzone et al. 2003). The
388 dominant riparian taxa in those studies however were species of *Tetragnatha*, which have been
389 found to be specialists in trapping emerging aquatic insects. Along our site there were extremely
390 few *Tetragnatha* and were therefore not included in our isotopic analyses. Our results were more
391 similar to those reported for other tropical (Yuen & Dudgeon 2015) and sub-tropical (Collier et
392 al. 2002) sites. In Hong Kong, Yuen and Dudgeon (2015) found that riparian web-building
393 spiders had a mean dependence of ~36-55% on aquatic insects. In New Zealand, Collier et al.
394 (2002) found that the mean contribution of aquatic insects to all riparian spider taxa was ~58%.
395 Emergence patterns of aquatic insects can vary greatly among and even within tropical, sub-
396 tropical and temperate streams and this could have a large influence on the importance of stream
397 subsidies to surrounding terrestrial predators. Some of the variability found among studies may
398 be related to the type of isotopic mixing model that was applied (linear, algorithmic, or
399 bayesian), differences in which spider taxa were present, or differences between stream localities
400 (tropical, subtropical and/or temperate).

401 Our study highlights the importance of riparian ecotones as areas that contain a unique
402 biodiversity of web-spinning spider taxa that are specialists in aquatic habitats and are rarely
403 found even after only a few meters from the water's edge. Dietary analyses revealed that aquatic
404 insects comprised ~50% of the diet in riverine, riparian and upland spiders with only a slightly
405 greater dependence on aquatic insects in the upland spider group. We found that isotopic signals
406 between terrestrial and aquatic insects were not exclusively distinct and this can impact the
407 effectiveness of isotopic mixing models, which has been shown to be a problem for other studies
408 along forested headwater streams. Despite the overlapping of isotopic signals the results of the
409 dietary analysis were similar to other studies conducted along tropical streams. Our study
410 provides further evidence for the importance of aquatic subsidies for terrestrial consumers even
411 within upland areas from the stream.

412

413 CONCLUSION

414

415 The environment provided by the stream channel and that of the riparian forest clearly created
416 two unique web-spinning spider assemblages, in which specialized taxa of aquatic ecosystems
417 were shown to be the major difference between the two study areas. However, differences
418 between these two habitats were potentially the result of structure and microenvironment, rather
419 than prey resources.

420

421

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428

429

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