



Title	Species-specific use of allochthonous resources by ground beetles (Carabidae) at a river-land interface
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1 **Species-specific use of allochthonous resources by ground**
2 **beetles (Carabidae) at a river–land interface**

3

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17

18 **Abstract**

19 A variety of organisms mediate river–terrestrial linkages through spatial subsidies.
20 However, most empirical studies have classified organisms rather broadly (e.g., by
21 functional group or taxonomic family) and have dismissed species-level linkages at the
22 interface of ecosystems. Here, we show how allochthonous resource use varies among
23 taxonomically similar species of ground beetles (family Carabidae) across seasons
24 (June–September). We investigated seasonal shifts in the distribution of five beetle
25 species and their dietary responses to spatial subsidies (emerging aquatic insects) in a
26 Japanese braided river. Despite their taxonomic closeness, the ground beetles showed
27 species-specific responses to spatial subsidies, and beetle distribution patterns tended to
28 coincide with their diets. Overall, 1–56% of ground beetle diets were derived from
29 aquatic prey. One genus (*Bembidion* spp.) mainly consumed aquatic prey, while three
30 species fed primarily on terrestrial prey across all seasons. However, one species
31 (*Lithochlaenius noguchii*) showed shifts in its diet from aquatic to terrestrial prey
32 according to subsidy availability. The observed variation in allochthonous resource use
33 was likely related to species-specific foraging modes, physiological tolerance to dry
34 conditions, and interspecific competition. Our findings suggest that considering

35 species-specific interactions is necessary to fully understand cross-system interactions

36 and recipient food-web dynamics.

37 **Key words:** food web, cross-system interaction, river, ground beetle, stable isotope

38 **Introduction**

39 Energy flow across ecosystems, commonly known as allochthonous inputs or spatial
40 subsidies, is a fundamental property of nature (Polis *et al.* 1997). Seminal studies of
41 cross-habitat linkages stressed material transfer governed by gravity (Vannote *et al.*
42 1980; Leroux & Loreau 2008). However, ecologists now recognize the importance of
43 energy flows in the form of organismal movements, which can work against
44 gravitational forces (Baxter *et al.* 2005). In river–terrestrial ecotones, for example,
45 emerging aquatic insects are preyed upon by terrestrial consumers, mediating nutritional
46 backflows from rivers to terrestrial food webs (Kato *et al.* 2004).

47 A variety of trophic interactions mediate cross-ecosystem linkages (Baxter *et al.*
48 2005; Giery *et al.* 2013). Nevertheless, most empirical studies have classified organisms
49 rather broadly (e.g., by functional group or taxonomic family), especially for small
50 consumers like carnivorous insects, and have dismissed species-level variation in
51 allochthonous resource use (but see Nakano & Murakami 2001; Paetzold *et al.* 2005;
52 Paetzold *et al.* 2006). Although this simplification makes complex systems more
53 tractable, it masks an important aspect of trophic interactions. That is, even within a
54 functional guild, small differences in foraging modes (Marczak *et al.* 2007; Giery *et al.*
55 2013) and/or physiological tolerance to environmental conditions (Ahrens & Kraus

56 2006) can result in differing uses of resource subsidies. For example, terrestrial
57 consumers highly specialized on aquatic prey may rely on spatial subsidies across
58 seasons (Paetzold *et al.* 2005), while generalist foragers capable of adapting to a wide
59 range of environmental conditions may exhibit flexible dietary shifts according to
60 resource availability (e.g., Kato *et al.* 2004). Thus, lumping organisms too broadly has
61 the potential to provide inaccurate estimates of biomass flux into the recipient consumer
62 community. Therefore, quantification of how allochthonous resource use varies within
63 seemingly similar taxonomic groups is essential for better understanding cross-system
64 interactions. This issue is particularly relevant to temperate regions, where the effect of
65 the subsidy depends strongly on consumers' responses to the seasonally pulsed
66 emergence of aquatic insects.

67 In braided rivers, the highly variable flow regime creates relatively
68 unproductive areas of exposed gravel. This simple and rather barren habitat provides an
69 excellent opportunity to test species-level differences in subsidy use for several reasons.
70 First, owing to low *in situ* prey availability, riparian arthropods are expected to rely
71 mainly on allochthonous inputs, such as emerging aquatic insects, which largely
72 originate from rivers (Paetzold *et al.* 2005; Paetzold *et al.* 2006). Second, the fairly
73 barren and homogeneous nature of exposed gravels requires organisms to be capable of

74 adapting to such a severe environment, leading to relatively simple biological
75 communities characterized by similar taxonomic groups of carnivorous arthropods (e.g.,
76 Carabid beetles). If variability in subsidy use occurs in a simple system where
77 allochthonous production is expected to be the primary source of production, then this
78 would suggest the importance of inter-specific variation in more complex systems with
79 multiple sources of production (i.e., higher *in situ* productivity).

80 Here, we aimed to determine whether allochthonous resource use varies among
81 taxonomically similar ground beetles (family Carabidae) across seasons
82 (June–September). To test the hypothesis that differences would occur in subsidy use
83 among ground beetle species, we investigated the distribution and diet of ground beetles
84 as well as subsidy availability (emerging aquatic insects). We examined whether spatial
85 distribution of ground beetles coincided with their diets. Few previous studies have
86 investigated more than one component of a consumer’s response to spatial subsidies.
87 Therefore, combining multiple factors may provide a compelling evidence for
88 species-level variation in subsidy use among closely related species.

89

90 **Methods**

91 *Study system*

92 We conducted our investigation at the Tottabetsu River, Hokkaido, Japan (42°40'N,
93 140°18'E). The mean annual air temperature and cumulative precipitation in 2014 were
94 5.7°C and 1061.5 mm, respectively (Japan Meteorological Agency; available at
95 <http://www.jma.go.jp/jma/index.html>). The water catchment area encompasses 304 km²
96 of agricultural and forested terrain. This medium-sized, alluvial fan river (ca. 20–30-m
97 wetted width) is characterized by a highly variable flow regime with the highest average
98 discharge in early spring during snowmelt runoff and unpredictable peak flows in
99 autumn owing to typhoons. In 2014, major precipitation events (ca. 50–150 cm rise in
100 water level) occurred at least once a month from June to September.

101 We sampled emerging aquatic insects and ground beetles at four exterior gravel
102 bars along a 2-km stretch of river (median particle size, $D_{50} = 42.5$ mm). For this stretch,
103 the rough estimate of the active floodplain width was ca. 100–120 m, and one to three
104 braids run through this area. The gravel bars were ca. 500–2,000 m apart from each
105 other, and their respective areas varied from ca. 0.3 ha to 0.9 ha with 30–100-m widths
106 (see Fig S2 in ESM).

107

108 *Seasonal flux of aquatic insect emergence*

109 We quantified aquatic insect emergence from June 2014 to September 2014 (Jun 11–12,
110 Jun 21–23, Jun 27–29, Jul 8–9, Aug 21–23, Sep 13–16; mean interval \pm SD = 19.4 \pm
111 15.8 days). At each gravel bar, we haphazardly placed an emergence trap (pyramidal
112 shape, 470 μ m mesh, 0.36 m²; MegaView Science Co., Taichung City, Taiwan) on the
113 water surface of three local habitats (backwater, riffle, and glide). Thus, a total of 12
114 traps (three traps per bar \times four bars) were placed in the river stretch. The three habitat
115 types encompassed approximately > 80% of the river surface and thus were assumed to
116 provide representative data on insect emergence. Although our sampling did not capture
117 aquatic insects emerging along the shore, the seasonal trend for total emergence was not
118 systematically different to that of the river surface (N. Watanabe, personal
119 communication; comparison of total emergence between shoreline and river surface in
120 the adjacent Satsunai River). Each trap was fixed with four metal bars and kept in place
121 for 1–4 days, during which time emerging insects entered a collecting bottle filled with
122 70% ethanol. In the laboratory, emerging insects were identified to order. Six to 19
123 individuals of each order were dried and weighed to the nearest milligram to estimate
124 average dry weight (see Table S1).

125

126 *Sampling for lateral distribution of ground beetles*

127 We investigated the activity density of ground beetles (hereafter, “density”) using pitfall
128 traps (cup size: 89 mm diameter × 114.5 mm height) concurrent with the sampling of
129 emerging aquatic insects (Jun 19–23, Jul 11–18, Aug 22–28, Sep 13–18). In each gravel
130 bar, we established two sampling units, one at the water’s edge (2.5–6.2 m from the
131 water’s edge; the distance varied owing to varying water levels) and another in the
132 middle of the gravel bar (9.0–52.5 m from the water’s edge), whose distances were
133 proportional to the size of each gravel bar and were measured with a laser distance
134 meter (TruPulse 200; Laser Technology Inc., Centennial, CO). We assumed higher
135 availability of aquatic prey near the water’s edge as emerged insect density is known to
136 decrease rapidly with distance from the emergence site (the river) (Muehlbauer *et al.*
137 2014).

138 An individual sampling unit consisted of 10 pitfall traps with preservative
139 (100% propylene glycol). Pitfall traps were arranged parallel to the waterline, spaced \geq
140 5 m apart, and left for 4–7 days. For traps that had been disturbed by mammals (e.g.,
141 fox) during the study period, we estimated the number of individuals caught based on
142 the remaining undisturbed pitfalls only (8–10 traps per unit). Ground beetles were
143 identified to species or genus. For five major species of ground beetles (see Results and

144 Table S2), we measured their body size with a caliper (to the nearest 0.1 mm) and
145 weighed their dry mass to the nearest milligram (sample size: 25–59 individuals per
146 species or genus; see Table S3).

147

148 *Sample collection for stable isotope analysis*

149 Ground beetles captured during quantitative sampling were also used for stable isotope
150 analysis. We chose the five most prevalent species for this analysis because their
151 impacts on ecosystem processes (e.g., energy transfer) likely outweigh those of rare
152 ground beetles (see Results and Table S2). The dominant species were *Apristus grandis*,
153 *Bembidion* spp., *Lithochlaenius noguchii*, *Pterostichus leptis*, and *Brachinus stenoderus*
154 (family Carabidae). Although we used preservative for sample collection, our
155 preliminary analysis revealed that its influence on isotopic signatures was not
156 significant (Mann-Whitney U-test, $p > 0.1$ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, $n = 20$; see ESM 1
157 for details). We analyzed five to 20 individuals of each ground beetle species (see Table
158 S4 for details).

159 Potential ground beetle prey were collected in June, August, and September
160 along the same stretch of river. We gathered potential aquatic prey at three positions
161 (backwater, riffle, and glide) along each gravel bar where ground beetles were caught.

162 All major orders of invertebrates (Ephemeroptera, Plecoptera, Trichoptera, and Diptera)
163 were gathered using a standard 3-min kick sample with a 500- μ m net (O'Callaghan *et al.*
164 2013), and late instar larvae were selected for stable isotope analysis. Potential
165 terrestrial prey (Coleoptera, larval Lepidoptera, flies, snails, slugs, earthworms, and
166 ground spiders [family Lycosidae]) were collected systematically by timed
167 hand-searching the substrate and >10 host plants (30–60 minutes per gravel bar) and by
168 malaise traps established in the adjacent riparian zone. This choice of potential prey was
169 based on earlier ground beetle dietary analyses (Hering & Plachter 1997; Ikeda *et al.*
170 2010; Okuzaki *et al.* 2010; O'Callaghan *et al.* 2013). The sample size for each
171 taxonomic group ranged from five to 19 individuals (see Table S5).

172 Samples of ground beetles and their potential prey were dried at a constant
173 50°C for > 48 hrs. Whole-body tissues were ground into fine powder individually for
174 most samples, but homogenized composites were obtained from two to four individuals
175 for small-sized taxa. Stable isotope analyses were performed on a continuous flow
176 isotopic ratio mass spectrometer (MAT252; Finnigan MAT Co., Bremen, Germany)
177 coupled with an elemental analyzer (Fisons Instruments, Model EA/NA, Italy) via
178 ConFlo II as an interface. Ratios of $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ were expressed as the relative
179 differences between the sample and conventional standards (Vienna Peedee Belemnite

180 [VPDB] and air N₂, respectively). These ratios were reported in δ notation as: ($R_{\text{sample}} -$
181 $R_{\text{standard}})/R_{\text{standard}}$, where R_{sample} and R_{standard} denote relative abundance of stable isotopes
182 of respective elements in samples and standards (Coplen 2011). Working standards of
183 known δ values (i.e., tyrosine; $\delta^{13}\text{C}_{\text{VPDB}} = -22.2\text{‰}$, $\delta^{15}\text{N}_{\text{air}} = 6.03\text{‰}$) were analyzed at
184 least every 10 runs to confirm the reproducibility ($\pm < 0.2\text{‰}$ for C and $\pm < 0.3\text{‰}$ for N)
185 and accuracy of isotope measurements.

186

187 *Statistical analysis*

188 To test how responses to pulsed subsidies (aquatic insect emergence) varied among
189 ground beetle species, we employed a hierarchical Bayesian approach. The density of
190 ground beetles Y_{ijk} (species i at sampling unit j in month k) was assumed to follow a
191 Poisson error distribution, $Y_{ijk} \sim \text{Poisson}(\lambda_{ijk})$. The parameter λ_{ijk} was related to linear
192 predictors via a log-link function:

$$193 \log(\lambda_{ijk}) = \beta 0_{ik} + \beta I_{ik} \cdot \text{Location}_j + \log(\text{CPUE}_{jk}) + \gamma_i + \varepsilon_i$$

194 where *Location* is a dummy variable that denotes the position of a sampling unit (0 =
195 fringe, 1 = mid-bar). We modeled month-specific intercepts $\beta 0_{ik}$ and location effects βI_{ik}
196 (i.e., a random intercept and slope model; RIS model) because we hypothesized that
197 ground beetles may respond to the seasonally pulsed emergence of aquatic insects. Prior

198 to this analysis, we confirmed that the RIS model was superior to a random intercept
199 model, in which location effects βI_i do not vary among sampling months (ESM 2). The
200 month-specific parameters were distributed normally as $\beta_{ik} \sim \text{Normal}(\beta_{global, i}, \sigma^2_{\beta i})$ (β is
201 either β_0 or β_1). Species-specific global intercepts and slopes ($\beta_{global, i}$) were drawn from
202 normal distributions with hyper means μ_β and hyper variances σ^2_β . Catch per unit effort
203 (CPUE_{jk}) is the product of the number of pitfall traps and the sampling duration (days),
204 and its logarithm was included as an offset term. The random effect of sampling site γ_i
205 (i.e., a gravel bar with two sampling units) allowed the model to account for random
206 spatial variations in ground beetle density. The parameter γ_i was assumed to follow a
207 normal distribution with a mean 0 and variance $\sigma^2_{\gamma i}$. The final parameter (ε_i) is a random
208 effect that mitigates overdispersion (Kéry 2010) and is normally distributed as $\varepsilon_i \sim$
209 $\text{Normal}(0, \sigma^2_{\varepsilon i})$.

210 Vague priors were assigned for the parameters: i.e., normal distributions with
211 large variance for μ_β (mean = 0, variance = 10^2) and truncated normal distributions with
212 large variance for σ_β , $\sigma_{\gamma i}$, $\sigma_{\delta i}$ and $\sigma_{\varepsilon i}$ (mean = 0, variance = 50, min = 0, max = 10^3). The
213 model was fitted to the data with JAGS ver. 3.4.3 and the *rjags* package (Plummer
214 2014) in R software ver. 3.1.1 (R Core Development Team 2014). Three Markov Chain
215 Monte Carlo (MCMC) chains were run with 70,000 iterations (20,000 burn-in), and

216 1000 samples per chain were used to calculate posterior probabilities. Convergence was
217 assessed by examining whether the R-hat indicator of each parameter approached 1
218 (Gelman & Hill 2007). We also evaluated model performance with a Bayesian *P*-value
219 (Kéry 2010). The Bayesian *P*-value with a sums-of-square discrepancy measure
220 approaches 0.50 if the model completely reproduces the data.

221

222 *Mixing model*

223 We used a Bayesian mixing model SIAR (version 4) to estimate the relative proportions
224 of different prey types in the ground beetle diets (Parnell *et al.* 2010). This Bayesian
225 mixing model is designed to incorporate (1) variability of isotopic values within a
226 trophic node and (2) uncertainty associated with trophic enrichment. These extensions
227 help avoid any biases due to oversimplified assumptions (e.g., trophic enrichment with
228 no uncertainty).

229 In the mixing model, we applied an *a posteriori* aggregation method to pool
230 food sources sharing common attributes, such as primary producers with similar $\delta^{13}\text{C}$
231 values (Phillips *et al.* 2005). We aggregated the fractions of “terrestrial prey”
232 (Coleoptera, larval Lepidoptera, flies, snails, slugs, and earthworms) as one prey item.
233 Similarly, aquatic insects (Ephemeroptera, Plecoptera, Trichoptera, and Diptera) were

234 grouped as “aquatic prey”. This grouping reduces statistical uncertainty of diet estimates
235 that can arise from having too many possible sources. We added 1.0 to $\delta^{15}\text{N}$ values of
236 aquatic prey (late instar of aquatic insects) before performing the analysis because the
237 values may be enriched through their metamorphosis into adults (Kraus *et al.* 2014).
238 Ground spiders were treated as an independent prey item (“spiders”) because their $\delta^{13}\text{C}$
239 and $\delta^{15}\text{N}$ values were discernable from other prey items. Although one beetle group,
240 *Bembidion* spp., was unlikely to consume spiders (see Fig. 4), the inclusion of “spiders”
241 as a potential food item had little influence on *Bembidion*’s diet estimates (see Table 2
242 and Table S6 for comparison). Here, we report the results of our three-source mixing
243 model.

244 We assumed that the trophic enrichment factors were $0.5 \pm 0.13\text{‰}$ for carbon
245 and $2.3 \pm 0.18\text{‰}$ for nitrogen as these are the averages for non-fluid-feeding consumers
246 (McCutchan *et al.* 2003). Although some previous studies have employed differential
247 trophic enrichment factors for nitrogen ($3.4 \pm 0.98 \text{‰}$; Paetzold *et al.* 2005), our
248 preliminary analysis confirmed that the results were qualitatively similar when using
249 this value. For the priors of dietary proportions p_{ij} (consumer i and resource j), we used
250 a Dirichlet distribution [$p_{i1}, \dots, p_{ij} \sim \text{Dirichlet}(\alpha_{i1}, \dots, \alpha_{ij})$] with the parameter $\alpha_{ij} =$
251 1.0; these correspond to noninformative uniform priors.

252 We estimated the proportional contribution of each prey item for high- and
253 low-subsidy seasons (June–July and Aug–Sep, respectively; see Results) with the R
254 package *siar* (Parnell *et al.* 2010). This temporal resolution is conservative, because
255 terrestrial arthropods typically require 1–3 weeks to turn over their isotopic signatures
256 (Ostrom *et al.* 1997; Oelbermann & Scheu 2002). In the SIAR model, we ran a single
257 MCMC chain (500,000 iterations, 15 thinning, and 50,000 burn-in) and stored 30,000
258 MCMC samples to obtain posterior probabilities.

259

260

261 **Results**

262 *Seasonality of aquatic insect emergence*

263 The overall average aquatic insect emergence (i.e., over the entire sampling period and
264 across sites) was 284.2 ± 420.7 SD individuals $\text{m}^{-2} \text{day}^{-1}$ and 0.3 ± 0.5 SD $\text{g m}^{-2} \text{day}^{-1}$.

265 During the sampling period, aquatic insect emergence had a clear peak from June to
266 July (Fig. 1). This general trend did not vary among taxonomic orders. Diptera
267 accounted for more than half of emerging individuals (55.4%), followed by Plecoptera
268 (37.1%), Ephemeroptera (6.0%), and Trichoptera (1.6%). However, in terms of biomass
269 Plecoptera was most abundant (43%), followed by Diptera (36%), Ephemeroptera
270 (15%), and Trichoptera (6%) (Fig. 1; see Table S1 for average dry mass of each order).

271

272 *Lateral distribution of ground beetles*

273 In total, we collected 8,545 ground beetle individuals from > 19 species over the study
274 period (Table S2). Numerically abundant species (or genera) included *Lithochlaenius*
275 *noguchii* (48.8%), *Apristus grandis* (30.8%), *Brachinus stenoderus* (7.8%), *Bembidion*
276 spp. (5.3%), *Nebria macrogona* (4.0%), and *Pterostichus leptis* (1.5%). The average
277 body sizes were 15.6 (*L. noguchii*), 4.4 (*A. grandis*), 10.3 (*B. stenoderus*), 5.0
278 (*Bembidion* spp.), 19.2 (*N. macrogona*), and 19.1 mm (*P. leptis*) (see Table S3 for

279 details). These major species (or genera) were recorded in both low-
280 (August–September) and high-subsidy periods (June–July) except for *N. macrogona*,
281 which was not recorded between June and July. The remaining 13 species accounted for
282 < 1% of the total community density. Thus, these were considered sporadic and/or rare
283 species and were omitted from further analyses. *Nebria macrogona* was also omitted
284 because it was not captured in June or July.

285 The Bayesian *P*-value of the hierarchical Bayesian model was 0.49. The model
286 precisely predicted the observed density of ground beetles (see Fig S1) and revealed that
287 their responses to seasonal subsidies differed substantially among species (Fig. 2; see
288 Table 1 for estimated parameters). The activity density of two species *L. noguchii* and
289 *Bembidion* spp. was significantly higher at the water’s edge during the high-subsidy
290 season (June–July), but not during the low-subsidy season (August–September; Fig. 2).
291 The density of *B. stenoderus* was consistently higher at the water’s edge (Fig. 2), and
292 the month-specific location effect was significant in September and marginally
293 significant in July and August (probability of β_1 being negative was 0.95 for both
294 months). The month-specific location effect for *P. leptis* and *A. grandis* was not
295 significant irrespective of season (Fig. 2).

296

297 *Ground beetle diet compositions*

298 Isotope signatures varied greatly among the three potential prey items (spiders,
299 terrestrial prey, and aquatic prey), allowing us to reliably estimate their proportional
300 contributions to ground beetle diets (Fig. 3).

301 The SIAR model revealed that the five species consumed allochthonous inputs
302 to varying degrees (Fig. 4). *Bembidion* spp. was the most reliant on aquatic prey across
303 seasons (mode estimate: 54–56%; Table 2). The most dominant species *L. noguchii*,
304 which showed a strong functional response to spatial subsidies, switched its diet
305 composition significantly between the high and low subsidy periods (35% to 1%; Table
306 2).

307 The other three species (*B. stenoderus*, *P. leptis* and *A. grandis*) consumed
308 some aquatic prey during the high-subsidy season (4–23%; Table 2), but showed almost
309 no reliance during the low-subsidy season (1–2%; Table 2). *Brachinus stenoderus*
310 mainly fed on ground spiders, especially during the high-subsidy season (39–61%;
311 Table 2). In contrast, the major prey of *P. leptis* and *A. grandis* were terrestrial primary
312 consumers (43–80% and 52–55%, respectively; Table 2). However, these estimates of
313 diet composition showed some uncertainty and their 95% credible intervals overlapped
314 across seasons. The large uncertainty in the diet estimates for *P. leptis* (Fig. 4;

315 June-July) was probably because its isotopic composition was out of the isotopic
316 triangle of the three potential prey groups (left panel in Fig. 3).

317

318 **Discussion**

319 Our study revealed that seasonal habitat use of the five ground beetle species (i.e., close
320 or distant to the water's edge) was species-specific. Moreover, allochthonous resource
321 use varied among beetle species, especially during the high-subsidy season. Further,
322 allochthonous resource use tended to coincide with habitat use (except for *B.*
323 *stenoderus*; see below). These multiple lines of evidence (i.e., beetle habitat use and diet
324 composition), strongly suggest that subsidy use can vary even within a taxonomic
325 family. Hence, inappropriate representation by a single recipient consumer or grouping
326 could provide erroneous estimates of allochthonous resource use in seasonally dynamic
327 environments.

328 Differing degrees of specialization on aquatic or terrestrial prey may explain
329 the variable responses to seasonal subsidies. Consistent with previous findings (Paetzold
330 *et al.* 2005), *Bembidion* spp. seems to be a specialist forager of aquatic prey. The
331 dominant species *L. noguchii* may be a generalist forager whose prey selection is likely
332 influenced by seasonal prey availability (see Fig. 4). These two species appear to share a
333 foraging habit of aggregating along the water's edge (see Fig. 2), where they consume
334 aquatic insects crawling on or stranded on the shore. In contrast, *P. leptis* and *A. grandis*
335 were consistently fueled by terrestrial primary consumers across seasons (e.g., snails or

336 slugs), as observed in congeneric species (Ikeda *et al.* 2010). These two species'
337 occasional use of aquatically derived resources may depend on aquatic prey being
338 stranding, mainly after flow pulses, as the two species did not aggregate along the
339 water's edge (see Fig. 2). However, it is important to note that species-specific
340 physiological tolerance to dry conditions can limit habitable areas and, consequently,
341 consumer's access to prey items. For example, wolf spiders are known to move mainly
342 along the water's edge owing, in part, to their sensitivity to desiccation stress (Ahrens &
343 Kraus 2006). Some of the species studied, such as *Bembidion* spp. which are vulnerable
344 to dry conditions (Andersen 1985), could be forced to consume aquatically derived
345 resources owing to physiological constraints. Another possible but not mutually
346 exclusive explanation for this differential resource use is competition among ground
347 beetles (Thiele 1977; Niemelä 1993) because inter-specific competition can cause
348 resource partitioning in the habitat. Currently, we lack information to determine which
349 of these reasons might be most influential, and further explorations are needed.
350 However, it is certainly possible that these three factors (foraging habits, physiological
351 tolerance, and interspecific competition) may act in concert to produce the observed
352 differences in allochthonous resource use.

353 Despite the fact that *B. stenoderus* consumed relatively little aquatic prey, the

354 species was consistently distributed along the water's edge (Fig. 2); however, the
355 location effect was marginal. This apparent response to aquatic prey was probably
356 influenced by the presence of small ground spiders (e.g., wolf spiders with < 10 mm
357 body size), which made up the largest proportion the diet of *B. stenoderus* in June and
358 July. These ground spiders were found most often along the shore across all seasons (AT,
359 personal observation). Given the diet composition of *B. stenoderus*, the species seems to
360 have sought out ground spiders rather than emerging aquatic insects. Spiders in gravel
361 bars might also depend heavily on aquatic subsidies (Paetzold *et al.* 2005), which can be
362 inferred from the isotopic signatures of spiders in this study (see Fig. 3). Thus, the
363 aggregation of *B. stenoderus* near the water's edge can be explained as an indirect
364 functional response to aquatic prey.

365 The modest reliance of ground beetles on allochthonous inputs (~56%)
366 deserves attention because earlier studies have reported a much higher contribution of
367 aquatic prey to riparian consumers on gravel bars (~100%) (Hering & Plachter 1997;
368 Paetzold *et al.* 2005). There are two possible explanations for this discrepancy. First, it
369 could be the result of differences in aquatic and/or *in situ* prey availability. According to
370 a meta-analysis by Marczak *et al.* (2007), the effects of subsidies were controlled
371 mainly by the ratio of subsidies to ambient resources of comparable types (e.g., flying

372 aquatic insects vs. flying terrestrial insects). During the summer of 2014, the gravel bars
373 underwent frequent flooding events, which may have disproportionately decreased
374 insect emergence (McCabe & Gotelli 2000) and/or supplemented ground beetles with
375 stranded terrestrial prey (Paetzold *et al.* 2006). In addition, the relatively small size of
376 the gravel bars may have allowed easy access to terrestrial prey originating from
377 adjacent riparian forests. A second possible explanation for this discrepancy lies in the
378 different values assumed for trophic enrichment factors in mixing models (e.g., Paetzold
379 *et al.* 2005 assumed 3.4‰ for nitrogen). However, this is unlikely because our
380 preliminary analysis using this trophic enrichment factor (3.4‰) did not qualitatively
381 change the results. Therefore, the first explanation is more likely, but experimental
382 testing is needed to reveal the mechanism behind this inconsistency with previous
383 findings.

384 Even in a fairly barren habitat like a gravel, respective reliance on
385 allochthonous prey varied within a single taxonomic family. Species-specific
386 allochthonous resource use may be common at most ecosystem boundaries (e.g., the
387 interface of canopy and understory food webs), given the diversity of foraging modes,
388 physiological tolerance, and interspecific interactions among consumers. Thus, we
389 suggest that considering species-specific interactions is necessary for deeper

390 understanding of cross-system interactions and recipient food-web dynamics. However,
391 our study covered only 1 year, and the results represent an initial snapshot of the
392 dynamics of this system. Feeding habits can vary annually in relation to factors that
393 affect the river environment, such as discharge (O'Callaghan *et al.* 2013). Therefore,
394 additional studies are needed to fully reveal long-term patterns.

395

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402

403 **Authorship**

404 AT, TA and JN designed and conducted the sampling. AT led the statistical analysis and
405 writing. All authors participated in conception, discussion of the results, and manuscript
406 preparation.

407

408 **Supporting information**

409 **ESM 1** Influence of propylene glycol on isotopic signatures

410 **ESM 2** Comparison of the RIS and RI models

411 **Table S1** Average dry mass (\pm standard deviation) of emerging aquatic insect

412 individuals

413 **Table S2** Inventory of ground beetle species collected in the Tottabetsu River

414 **Table S3** Average body size and dry mass (\pm standard deviation) of most common
415 ground beetle species

416 **Table S4** Ground beetles used for stable isotope analysis

417 **Table S5** Prey samples used for stable isotope analysis

418 **Table S6** Results of the two-source SIAR model

419 **Figure S1** Comparison of predicted and observed ground beetle density

420 **Figure S2** Photograph of gravel bars in the Tottabetsu River

421

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498

499 **Table 1** Results of the hierarchical Bayesian model explaining the spatial distribution
500 patterns of ground beetles. Values indicate median estimates of partial regression
501 coefficients and their 95% credible intervals (95% CIs, brackets). Coefficients whose
502 95% CIs did not include zero are shown in bold. *A. grandis*, *Apristus grandis*; *B.*
503 *stenoderus*, *Brachinus stenoderus*; *L. noguchii*, *Lithochlaenius noguchii*; *P. leptis*,
504 *Pterostichus leptis*

Species	Global intercept	Month-specific location effect (βI)			
	($\beta 0_{global}$)	June	July	August	September
<i>A. grandis</i>	-0.84	0.00	0.03	0.56	0.71
	[-2.74, 1.30]	[-1.29, 1.13]	[-1.22, 1.14]	[-0.55, 1.73]	[-0.42, 2.16]
<i>Bembidion</i> spp.	-1.47	-2.15	-2.72	-0.64	-2.78
	[-3.98, 0.61]	[-3.40, -0.94]	[-4.38, -1.36]	[-2.17, 0.80]	[-11.27, -0.48]
<i>B. stenoderus</i>	-1.06	-0.55	-0.71	-0.72	-0.87
	[-2.44, 0.30]	[-1.39, 0.48]	[-1.55, 0.17]	[-1.64, 0.14]	[-2.05, -0.05]
<i>L. noguchii</i>	0.04	-0.87	-0.93	0.24	0.17
	[-2.10, 1.71]	[-1.76, -0.02]	[-1.78, -0.13]	[-0.65, 1.15]	[-0.71, 1.08]
<i>P. leptis</i>	-2.11	-0.23	-0.19	0.51	0.18
	[-5.67, 0.51]	[-5.47, 1.84]	[-1.77, 1.03]	[-0.66, 1.90]	[-1.04, 1.52]

505

506

507 **Table 2** Results of the three-source SIAR model. Values represent mode estimates and
 508 associated 95% credible intervals (in brackets) of the relative contributions of each prey
 509 item. *A. grandis*, *Apristus grandis*; *B. stenoderus*, *Brachinus stenoderus*; *L. noguchii*,
 510 *Lithochlaenius noguchii*; *P. leptis*, *Pterostichus leptis*

511 Species	Source	Relative contributions	
		June—July	August—September
<i>A. grandis</i>	Aquatic prey	0.23 [0.06, 0.38]	0.01 [0.00, 0.16]
	Terrestrial prey	0.52 [0.38, 0.64]	0.55 [0.44, 0.68]
	Spiders	0.27 [0.13, 0.41]	0.39 [0.21, 0.53]
<i>Bembidion</i> spp.	Aquatic prey	0.54 [0.33, 0.74]	0.56 [0.32, 0.71]
	Terrestrial prey	0.44 [0.22, 0.60]	0.39 [0.25, 0.51]
	Spiders	0.01 [0.00, 0.14]	0.02 [0.00, 0.25]
<i>B. stenoderus</i>	Aquatic prey	0.12 [0.02, 0.22]	0.01 [0.00, 0.10]
	Terrestrial prey	0.27 [0.18, 0.36]	0.59 [0.35, 0.75]
	Spiders	0.61 [0.51, 0.70]	0.39 [0.19, 0.64]
<i>L. noguchii</i>	Aquatic prey	0.35 [0.24, 0.46]	0.01 [0.00, 0.15]
	Terrestrial prey	0.24 [0.13, 0.34]	0.46 [0.34, 0.59]
	Spiders	0.42 [0.32, 0.50]	0.50 [0.32, 0.63]
<i>P. leptis</i>	Aquatic prey	0.04 [0.00, 0.56]	0.02 [0.00, 0.16]
	Terrestrial prey	0.43 [0.22, 0.89]	0.80 [0.68, 0.90]
	Spiders	0.22 [0.00, 0.41]	0.15 [0.00, 0.27]

512 **Fig. 1** Pulsed emergence of aquatic insects in 2014 (a–d: abundance, e–h: biomass). The
513 box boundaries represent the 25th and 75th percentiles, the horizontal lines are the
514 median, and the whiskers extend to the most extreme data point that was no more than
515 1.5 times the interquartile range from the box. Data points outside of whiskers are
516 represented by open circles.

517

518 **Fig. 2** Relationships between the activity density of ground beetles and location within
519 the gravel bar (water's edge or mid-bar): *Apristus grandis* (a), *Bembidion spp.* (b),
520 *Brachinus stenoderus* (c), *Lithochlaenius noguchii* (d), and *Pterostichus leptis* (e).
521 Colored dots indicate median values, while gray dots denote individual data points.
522 Solid and broken lines represent significant and insignificant relationships, respectively.
523 See Table 1 for estimated parameters.

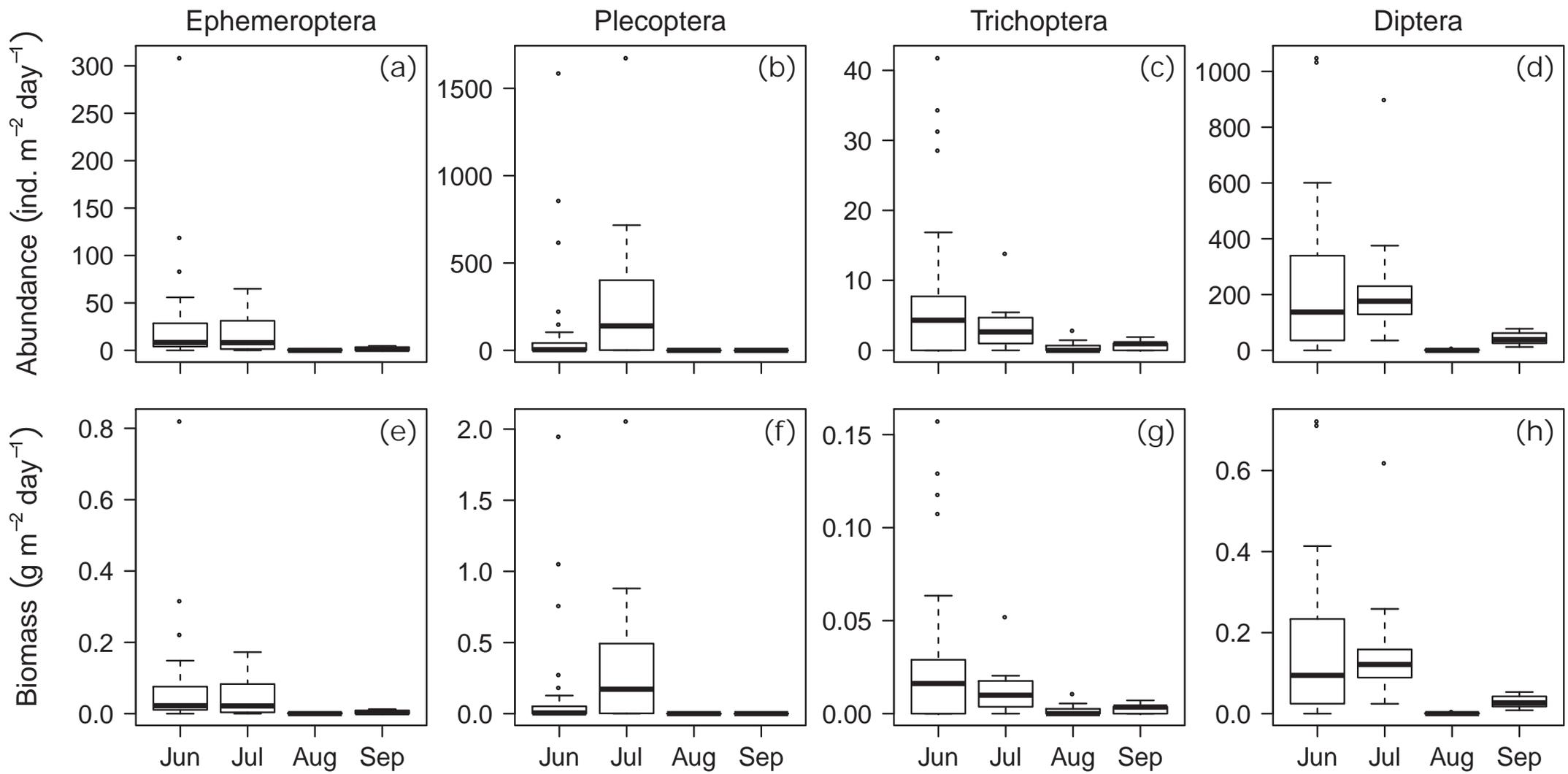
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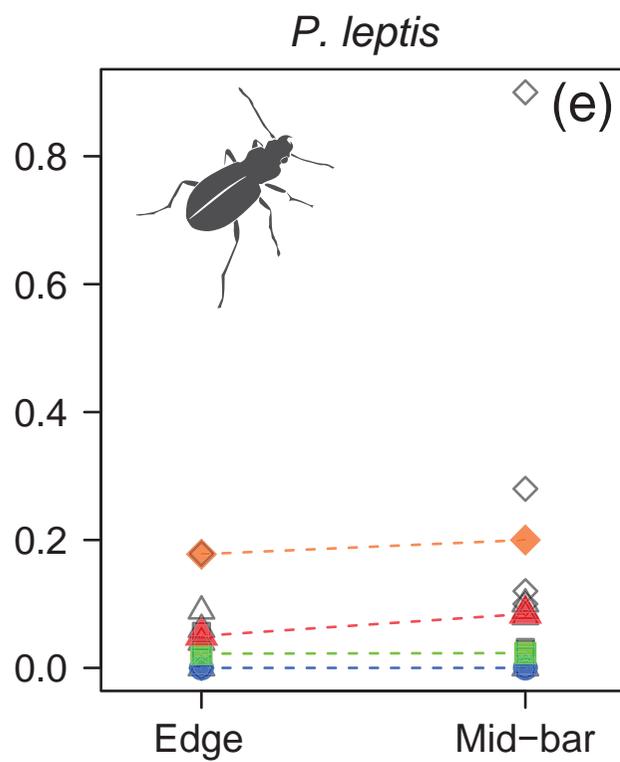
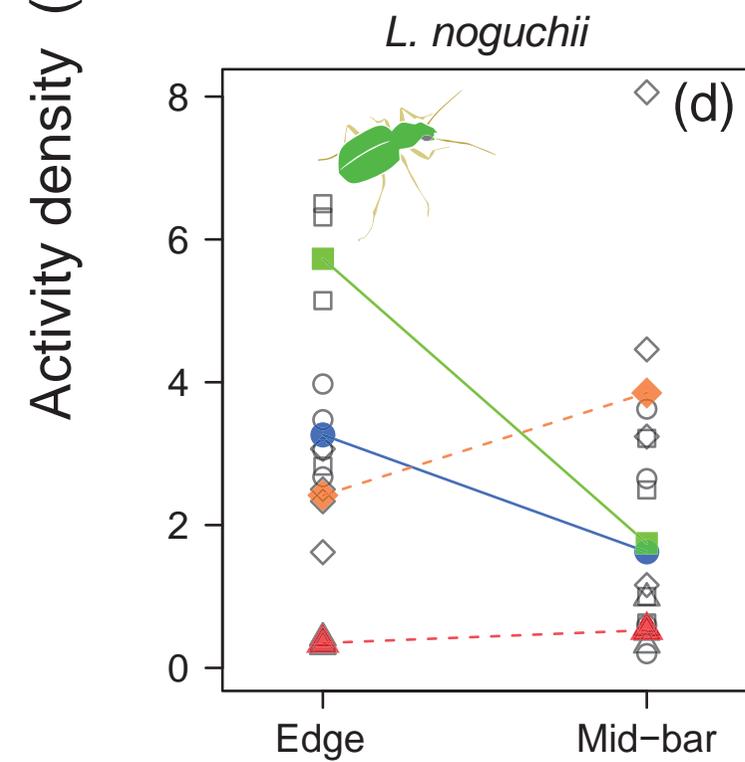
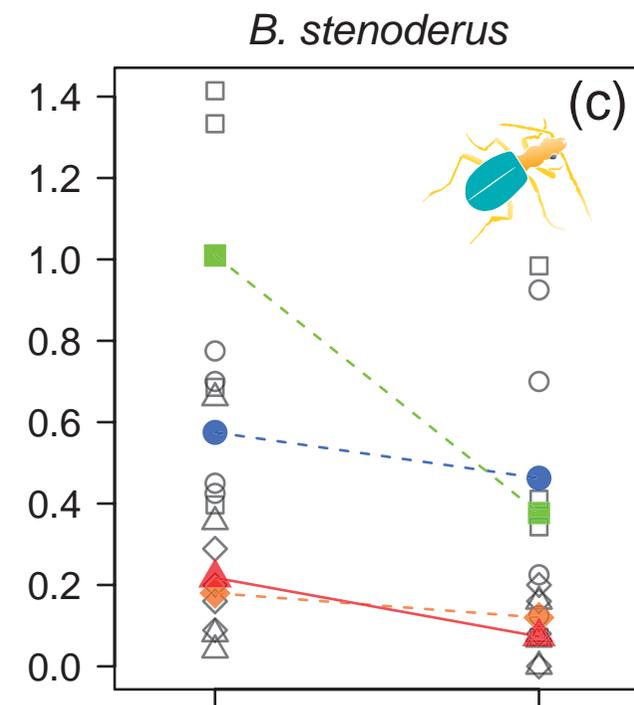
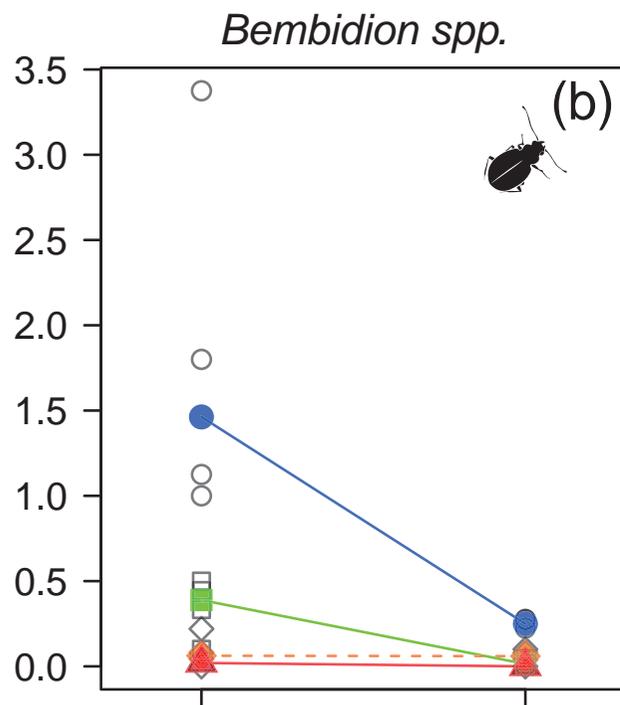
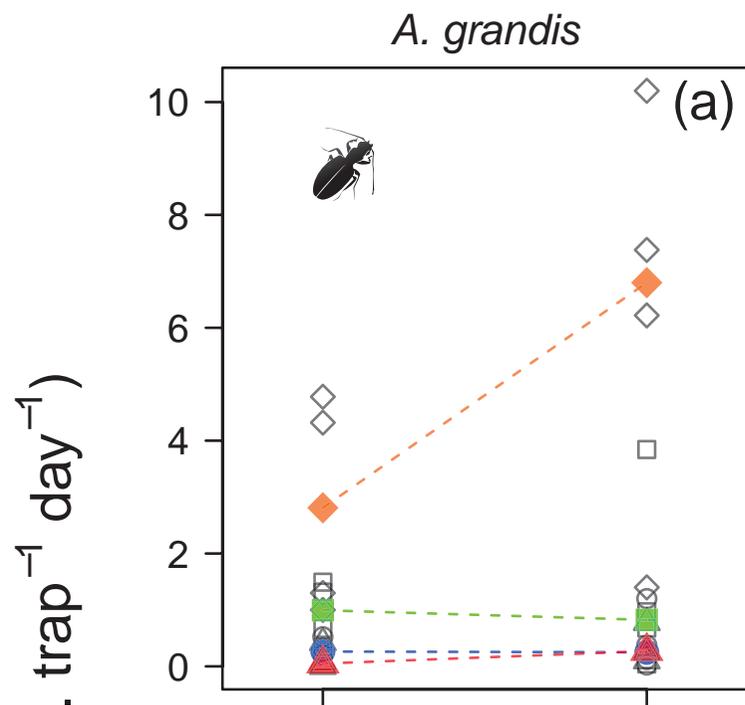
525 **Fig. 3** Mean estimates of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and associated standard deviations (error bars)
526 for ground beetles (open squares) and potential prey items (filled squares). Note that we
527 added 1.0 to the $\delta^{15}\text{N}$ values of aquatic prey given the estimated isotopic enrichment
528 during their metamorphosis into adults. AG, *Apristus grandis*; B, *Bembidion spp.*; BS,
529 *Brachinus stenoderus*; LN, *Lithochlaenius noguchii*; NM, *Nebria macrogona*; PL,

530 *Pterostichus leptis*.

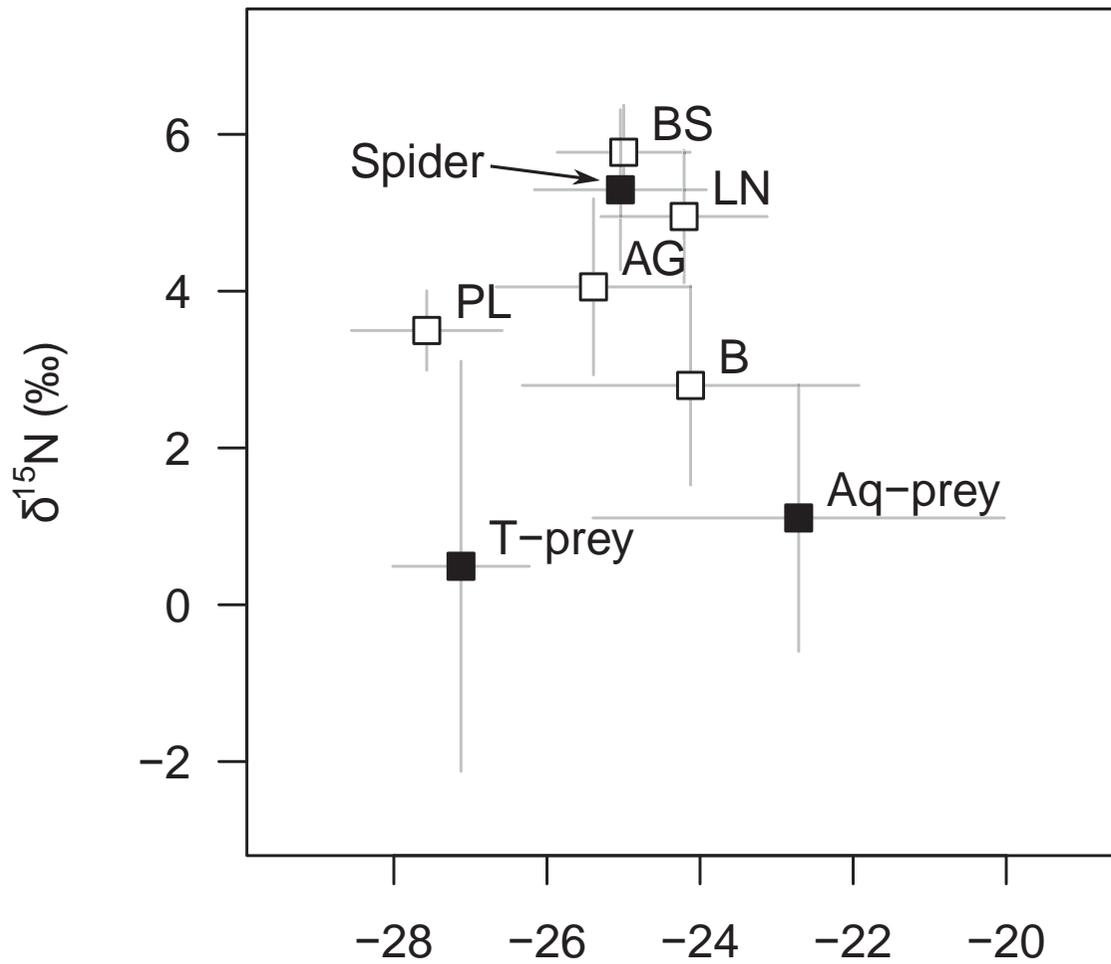
531

532 **Fig. 4** SIAR estimates of the relative contributions of each prey item for different
533 seasons (a–e, June to July; f–j, August to September). Vertical bars are shaded in
534 proportion to the posterior probability density, and white and black horizontal lines
535 mark the mode estimates and 95% credible intervals, respectively. *A. grandis*, *Apristus*
536 *grandis*; *B. stenoderus*, *Brachinus stenoderus*; *L. noguchii*, *Lithochlaenius noguchii*; *P.*
537 *leptis*, *Pterostichus leptis*; Ap, aquatic-prey; Tp, terrestrial prey; S, spiders





Jun-Jul



Aug-Sep

