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

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## Abstract

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

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

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

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

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

## Methods

### *Study system*

We conducted our investigation at the Tottabetsu River, Hokkaido, Japan (42°40'N, 140°18'E). The mean annual air temperature and cumulative precipitation in 2014 were 5.7°C and 1061.5 mm, respectively (Japan Meteorological Agency; available at <http://www.jma.go.jp/jma/index.html>). The water catchment area encompasses 304 km<sup>2</sup> of agricultural and forested terrain. This medium-sized, alluvial fan river (ca. 20–30-m wetted width) is characterized by a highly variable flow regime with the highest average discharge in early spring during snowmelt runoff and unpredictable peak flows in autumn owing to typhoons. In 2014, major precipitation events (ca. 50–150 cm rise in water level) occurred at least once a month from June to September.

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

*Seasonal flux of aquatic insect emergence*

We quantified aquatic insect emergence from June 2014 to September 2014 (Jun 11–12, Jun 21–23, Jun 27–29, Jul 8–9, Aug 21–23, Sep 13–16; mean interval  $\pm$  SD = 19.4  $\pm$  15.8 days). At each gravel bar, we haphazardly placed an emergence trap (pyramidal shape, 470  $\mu$ m mesh, 0.36 m<sup>2</sup>; MegaView Science Co., Taichung City, Taiwan) on the water surface of three local habitats (backwater, riffle, and glide). Thus, a total of 12 traps (three traps per bar  $\times$  four bars) were placed in the river stretch. The three habitat types encompassed approximately > 80% of the river surface and thus were assumed to provide representative data on insect emergence. Although our sampling did not capture aquatic insects emerging along the shore, the seasonal trend for total emergence was not systematically different to that of the river surface (N. Watanabe, personal communication; comparison of total emergence between shoreline and river surface in the adjacent Satsunai River). Each trap was fixed with four metal bars and kept in place for 1–4 days, during which time emerging insects entered a collecting bottle filled with 70% ethanol. In the laboratory, emerging insects were identified to order. Six to 19 individuals of each order were dried and weighed to the nearest milligram to estimate average dry weight (see Table S1).

*Sampling for lateral distribution of ground beetles*

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

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

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

#### *Sample collection for stable isotope analysis*

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

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

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

Samples of ground beetles and their potential prey were dried at a constant 50°C for > 48 hrs. Whole-body tissues were ground into fine powder individually for most samples, but homogenized composites were obtained from two to four individuals for small-sized taxa. Stable isotope analyses were performed on a continuous flow isotopic ratio mass spectrometer (MAT252; Finnigan MAT Co., Bremen, Germany) coupled with an elemental analyzer (Fisons Instruments, Model EA/NA, Italy) via 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 differences between the sample and conventional standards (Vienna Peedee Belemnite

[VPDB] and air N<sub>2</sub>, respectively). These ratios were reported in  $\delta$  notation as:  $(R_{\text{sample}} - R_{\text{standard}})/R_{\text{standard}}$ , where  $R_{\text{sample}}$  and  $R_{\text{standard}}$  denote relative abundance of stable isotopes of respective elements in samples and standards (Coplen 2011). Working standards of known  $\delta$  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 least every 10 runs to confirm the reproducibility ( $\pm < 0.2\text{‰}$  for C and  $\pm < 0.3\text{‰}$  for N) and accuracy of isotope measurements.

#### *Statistical analysis*

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

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

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

to this analysis, we confirmed that the RIS model was superior to a random intercept model, in which location effects  $\beta I_i$  do not vary among sampling months (ESM 2). The month-specific parameters were distributed normally as  $\beta_{ik} \sim \text{Normal}(\beta_{global, i}, \sigma^2_{\beta i})$  ( $\beta$  is either  $\beta_0$  or  $\beta_1$ ). Species-specific global intercepts and slopes ( $\beta_{global, i}$ ) were drawn from normal distributions with hyper means  $\mu_\beta$  and hyper variances  $\sigma^2_\beta$ . Catch per unit effort (CPUE<sub>jk</sub>) is the product of the number of pitfall traps and the sampling duration (days), and its logarithm was included as an offset term. The random effect of sampling site  $\gamma_i$  (i.e., a gravel bar with two sampling units) allowed the model to account for random spatial variations in ground beetle density. The parameter  $\gamma_i$  was assumed to follow a normal distribution with a mean 0 and variance  $\sigma^2_{\gamma i}$ . The final parameter ( $\varepsilon_i$ ) is a random effect that mitigates overdispersion (Kéry 2010) and is normally distributed as  $\varepsilon_i \sim \text{Normal}(0, \sigma^2_{\varepsilon i})$ .

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

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

#### *Mixing model*

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

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

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

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

## Results

### *Seasonality of aquatic insect emergence*

The overall average aquatic insect emergence (i.e., over the entire sampling period and across sites) was  $284.2 \pm 420.7$  SD individuals  $\text{m}^{-2} \text{day}^{-1}$  and  $0.3 \pm 0.5$  SD  $\text{g m}^{-2} \text{day}^{-1}$ . During the sampling period, aquatic insect emergence had a clear peak from June to July (Fig. 1). This general trend did not vary among taxonomic orders. Diptera accounted for more than half of emerging individuals (55.4%), followed by Plecoptera (37.1%), Ephemeroptera (6.0%), and Trichoptera (1.6%). However, in terms of biomass Plecoptera was most abundant (43%), followed by Diptera (36%), Ephemeroptera (15%), and Trichoptera (6%) (Fig. 1; see Table S1 for average dry mass of each order).

### *Lateral distribution of ground beetles*

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

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

The Bayesian *P*-value of the hierarchical Bayesian model was 0.49. The model  
precisely predicted the observed density of ground beetles (see Fig S1) and revealed that  
their responses to seasonal subsidies differed substantially among species (Fig. 2; see  
Table 1 for estimated parameters). The activity density of two species *L. noguchii* and  
*Bembidion* spp. was significantly higher at the water’s edge during the high-subsidy  
season (June–July), but not during the low-subsidy season (August–September; Fig. 2).  
The density of *B. stenoderus* was consistently higher at the water’s edge (Fig. 2), and  
the month-specific location effect was significant in September and marginally  
significant in July and August (probability of  $\beta_1$  being negative was 0.95 for both  
months). The month-specific location effect for *P. leptis* and *A. grandis* was not  
significant irrespective of season (Fig. 2).

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

## Discussion

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

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

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

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

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

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

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

Even in a fairly barren habitat like a gravel, respective reliance on allochthonous prey varied within a single taxonomic family. Species-specific allochthonous resource use may be common at most ecosystem boundaries (e.g., the interface of canopy and understory food webs), given the diversity of foraging modes, physiological tolerance, and interspecific interactions among consumers. Thus, we 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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## **Authorship**

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

## **Supporting information**

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

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

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

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

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

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

| 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] |

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

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

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

530 *Pterostichus leptis*.

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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







