



Title	Stream Resource Gradients Drive Consumption Rates of Supplemental Prey in the Adjacent Riparian Zone
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1 **Title:** Stream resource gradients drive consumption rates of supplemental prey in the  
2 adjacent riparian zone

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15

16 **Abstract**

17 Decades of research have revealed the crucial roles of cross-system energy flows  
18 (spatial subsidies) in mediating trophic interactions in recipient systems. Food web  
19 theory predicts that the responses of subsidized consumers are a key to understanding  
20 the net impacts of spatial subsidies on *in situ* prey/resources of recipient systems.  
21 However, less is known about the factors triggering the cascading biotic interactions  
22 across coupled ecosystems. Here, we quantify how riverine productivity (donor system)  
23 mediates terrestrial food web interactions through spatial subsidies to simplified gravel  
24 bar communities. Our comparative study in Japan indicated that higher algal biomass in  
25 aquatic systems led to increased supplies of emerging aquatic insects, which were  
26 associated with greater densities of terrestrial consumers (Carabid beetles) and enhanced  
27 consumption rates of supplemental *in situ* prey on gravel bars. Our results highlight the  
28 potential of donor productivity to drive cascading biotic interactions across coupled  
29 ecosystems. Since cross-system energy flows should originate, at least in part, from  
30 primary producers of donor systems, our fundamental finding may form the basis of  
31 future studies exploring the driving factors of cross-system trophic interactions.

32 **Key words:** productivity gradients, apparent competition, Carabidae, river–land  
33 interactions, ecotone

34

35

36 **Introduction**

37 Decades of research have shown that ecosystems are not “stand-alone” entities; instead,  
38 ecosystems are linked to one another through cross-system movements of nutrients,  
39 detritus, and organisms (Polis et al., 1997). The cross-system energy flows, also known  
40 as spatial subsidies, are ubiquitous in nature (Polis et al., 1997; Nakano and Murakami,  
41 2001; Shimazaki and Miyashita, 2005; Spiller et al., 2010; Giery et al., 2013) and are  
42 now recognized as a critical driver of food web interactions in recipient systems (i.e., an  
43 ecosystem that receives spatial subsidies) (Sabo and Power, 2002; Baxter et al., 2005;  
44 Spiller et al., 2010; Ruff et al., 2011; Sato et al., 2012).

45         Substantial debates exist as to whether spatial subsidies from donor systems  
46 (i.e., an ecosystem that produces spatial subsidies) indirectly increase or decrease *in situ*  
47 prey in recipient systems by influencing generalist consumers that feed on both  
48 subsidies and *in situ* resources (cf. Takimoto et al., 2008; hereafter *in situ* prey refers to  
49 the prey originating from recipient systems). Food web theory predicts that persistent  
50 supplies of spatial subsidies may cause excessive abundance of subsidized consumers  
51 via enhanced reproduction and/or spatial aggregation, leading to overexploitation of *in*

52 *situ* prey (akin to "apparent competition"; Polis et al., 1997; Henschel et al., 2001).  
53 Meanwhile, in the absence of numerical responses, spatial subsidies should relax the  
54 predation pressure due to, for example, prey-switching of subsidized consumers (e.g.,  
55 Nakano et al., 1999; Spiller et al., 2010). Which of these mechanisms takes primacy  
56 may govern the net impacts of spatial subsidies on *in situ* resources (Baxter et al., 2005).  
57 However, despite the in-depth understanding of the consequences of spatial subsidies,  
58 little is known about the factors triggering such cascading biotic interactions across  
59 coupled ecosystems (but see Sato et al., 2012).

60           Primary productivity in donor systems can drive the cascading biotic  
61 interactions by mediating subsidy flux. This expectation builds upon the classic concept  
62 of "productivity gradients", in which larger productivity contrasts of donor and recipient  
63 systems strengthen the magnitude of trophic linkages across ecosystems (e.g., Polis et  
64 al., 1997). Notably, Burdon and Harding (2008) has provided partial support for this  
65 concept by showing a positive correlation between the emergence flux of aquatic insects  
66 (spatial subsidies) and the abundance of terrestrial web-building spiders (subsidized  
67 consumers). However, a wider spectrum of trophic interactions has yet to be explored:  
68 we still lack evidence for the potential causal linkages amongst donor productivity,  
69 subsidy flux, and recipient food web interactions.

70           Here, we hypothesize that primary productivity in a donor system may drive  
71   predation pressure on *in situ* prey through cross-system trophic interactions. Gravel bars  
72   can serve as an excellent model system to test our hypothesis for the following reasons.  
73   First, the harsh environments of gravel bars limit the diversity of consumer communities  
74   (Terui et al., 2017). The simple food web structure may allow us to disentangle  
75   sequential trophic links across ecosystems. Second, gravel bars are the dynamic  
76   interface of aquatic–terrestrial ecosystems, in which terrestrial generalist consumers  
77   (e.g., Carabid beetle) are subsidized significantly by emerging aquatic insects (Paetzold  
78   et al., 2005; Terui et al., 2017). Therefore, aquatic systems have great potential to  
79   control the predation pressure on *in situ* prey of gravel bars. Finally, each “island” of  
80   gravel bars operates as a spatially discrete entity, which enables a level of true  
81   replication of independent habitats.

82           In this study, we investigated whether consumption rates of supplemental *in*  
83   *situ* prey on gravel bars can vary along a productivity gradient of adjacent rivers. We  
84   took advantage of comparative approaches, which allowed us to capture the patterns  
85   emerging on large temporal and spatial scales. At our field site (the Tokachi River basin,  
86   Hokkaido, Japan), algal biomass exhibits an asymptotic increase due to sewage water  
87   inputs into one of the tributaries, while other tributaries sustained natural longitudinal

88 gradients for most biological properties. This system enabled us to capture a wide range  
89 of riverine productivity at a comparative spatial scale (i.e., within the same climatic  
90 region). We predicted that increased algal biomass would enhance consumption rates of  
91 supplemental *in situ* prey of gravel bars, as persistent supplies of emerging aquatic  
92 insects should elevate terrestrial consumer densities in the long term.

93

94

## 95 **Methods**

### 96 *Study system*

97 We conducted our investigation in the Tokachi River basin, Hokkaido, Japan, during the  
98 summer and fall of 2015 and 2016. The mean annual air temperature and cumulative  
99 precipitation in 2015–2016 were 8.2°C and 1083 mm, respectively (Japan  
100 Meteorological Agency; available at <http://www.jma.go.jp/jma/index.html>). We chose  
101 one stretch (8–12 km) on each of three alluvial fan rivers (ca. 20–30-m wetted channel  
102 width) for our field surveys (Fig. 1). These three rivers (Satsunai, Bisei, and Tottabetsu  
103 Rivers) are characterized by a highly variable flow regime with the highest average  
104 discharge occurring in early spring during snowmelt runoff. However, the rivers differ  
105 in the longitudinal patterns of biological properties. In the Satsunai River, the

106 downstream half of the stretch has been nutritionally enriched by sewage water ( $\text{NO}_3^-$ :  
107 upstream =  $1.6 \pm 1.0 \text{ mg L}^{-1}$ , downstream =  $4.5 \pm 2.2 \text{ mg L}^{-1}$ ; see Fig. S1 for a full  
108 description) and exhibits excessive algal biomass. In contrast, the Bisei and Tottabetsu  
109 Rivers exhibit no signs of increasing algal biomass along the longitudinal gradient,  
110 although the Bisei contains a point source of sewage water ( $\text{NO}_3^-$ : upstream =  $1.9 \pm 0.6$   
111  $\text{mg L}^{-1}$ , downstream =  $3.8 \pm 2.0 \text{ mg L}^{-1}$ ). The lack of algal response in the Bisei River  
112 seems to be attributable to an imbalance of nutrient availability (the Bisei River has  
113 little inputs of  $\text{PO}_4^-$ ; Fig. S1).

114 We were careful in the selection of sampling sites to overcome the limitations  
115 of comparative studies. We selected and performed a suite of field surveys (see below  
116 for details) at 16 sites (i.e., gravel bars; Satsunai, six sites; Bisei, four sites; Tottabetsu,  
117 six sites). In the Satsunai and Bisei Rivers, half of the sampling sites were located  
118 downstream of the sewage water outlet, while the others were located upstream (see Fig.  
119 1; solid dots are downstream sites). Sampling sites in the Tottabetsu River were located  
120 almost equidistantly along the comparable river stretch (Fig. 1). This design separates  
121 the effects of three possible factors: the effects of algal biomass (Satsunai), unknown  
122 effects of enrichment (i.e., enrichment effects other than increased algal biomass; Bisei)  
123 and unknown effects of natural longitudinal gradients (Tottabetsu). Therefore, this

124 sampling design aids our interpretation of the results (see Discussion for further details).

125

126 *Environmental factors*

127 We surveyed several environmental factors that influence, either directly or indirectly,

128 ground beetle density (family Carabidae) on gravel bars: algal biomass, emerging

129 aquatic insects, terrestrial *in situ* prey, and habitat area. We assessed the ash-free dry

130 mass (AFDM) of benthic algae as a proxy for organic matter availability in the river. We

131 assumed that this measure is an appropriate proxy for donor productivity in our study

132 system because the major energy source in shallow, open-canopy rivers is generally

133 benthic algae (Doi, 2009). At each site, we haphazardly sampled three to four cobbles.

134 After carefully removing attached animals, an area of 100 cm<sup>2</sup> (10 × 10 cm) of each

135 cobble was scrubbed with a toothbrush, and a total area of 300–400 cm<sup>2</sup> was rinsed

136 vigorously to remove benthic algae. In the laboratory, we filtered the filtrate through

137 pre-dried GF/F glass fiber filters. The filters were weighed after drying at 60°C for 24 h,

138 combusted at 500°C for 3 h, and then reweighed to estimate AFDM. We measured

139 AFDM twice across seasons (July and September in 2015) to account for seasonal

140 variation in algal production. AFDM was converted into units of mg m<sup>-2</sup> and averaged

141 across seasons on a logarithmic scale (i.e., geometric mean). However, we were unable

142 to obtain an AFDM estimate at one site during the fall (Tottabetsu) due to unexpected  
143 rainfall. Thus, we interpolated the value via a regression of fall (response variable) and  
144 summer AFDM (explanatory variable).

145 We quantified aquatic insect emergence in July 2016. This season is the peak  
146 period of emergence in the region (Terui et al., 2017) and was assumed to provide  
147 representative data. We placed pairs of emergence traps (0.36 m<sup>2</sup>, 470- $\mu$ m mesh) at two  
148 representative local habitats (riffle and glide; >80% of the river surface): one trap on the  
149 water surface and the other trap at the water's edge (0.18 m<sup>2</sup> covered the water surface).  
150 Thus, a total of four traps were deployed at each site. Traps on the water's edge were  
151 intended to capture aquatic insects crawling on the shore to emerge. Each trap was fixed  
152 using four metal bars and was kept in place for 2 to 4 days, during which emerging  
153 insects entered a collection bottle filled with 70% ethanol. In the laboratory, the total  
154 wet mass of emerging insects (Ephemeroptera, Plecoptera, Trichoptera, and Diptera)  
155 was measured to the nearest milligram and converted into dry mass via a regression of  
156 dry and wet mass (dry mass = 0.84 + 0.18  $\times$  wet mass - 5.76  $\times$  10<sup>-6</sup>  $\times$  wet mass<sup>2</sup>,  $n = 15$ ,  
157  $R^2 = 0.998$ ). Although emergence flux was investigated in 2016 only, ongoing long-term  
158 surveys suggested that spatial emergence patterns (abundance) in Satsunai and  
159 Tottabetsu Rivers were consistent among sampling years (2013 vs. 2014 at 8 sites;

160 Pearson's  $r = 0.78$ ,  $p < 0.02$ ,  $n = 8$ ) (see Terui et al., 2017 for sampling methods).

161 Concurrent with emergence sampling, we quantified terrestrial *in situ* prey  
162 availability (e.g., arthropods supplied from vegetation patches) using gray-colored pan  
163 traps ( $0.30 \times 0.22$  m<sup>2</sup> area, 0.14-m depth). A total of six traps were deployed at three  
164 locations (upstream, midstream, and downstream) of the gravel bar (put on the  
165 substrate). At each location, traps were arranged near the water's edge (5–10 m to the  
166 water's edge; proportional to the gravel bar size) and in the middle (10–20 m) of each  
167 gravel bar. We then filled six pan traps with water and a few drops of surfactant (liquid  
168 soap) and kept them in place for 2 days. Captured invertebrates were removed using  
169 polyester filters (0.5-mm mesh) and preserved in 70% ethanol. We measured the total  
170 wet mass of terrestrial arthropods (Coleoptera, Diptera, Hemiptera, Lepidoptera and  
171 Orthoptera) to the nearest milligram, which was converted into dry mass values using a  
172 regression of dry and wet masses (dry mass =  $0.04 + 0.12 \times$  wet mass  $- 1.34 \times 10^{-3} \times$   
173 wet mass<sup>2</sup>,  $n = 15$ ,  $R^2 = 0.986$ ). We excluded adult aquatic insects from the samples.

174 Finally, we measured the area of each gravel bar in the field using a function  
175 implemented in a hand-held GPS ( $\pm 5$  m accuracy).

176

177 *Ground beetles*

178 We investigated the activity density of ground beetles (hereafter, “density”) using pitfall  
179 traps (cup size: 72 mm diameter × 95 mm height) containing preservative (100%  
180 propylene glycol). Surveys were conducted in July of 2015 (16 sites) and 2016 (10  
181 sites). At each gravel bar, we established three sampling units consisting of three pitfall  
182 traps (upstream, midstream, and downstream locations). The traps were arranged  
183 parallel to the waterline (<3 m to the water’s edge) spaced  $\geq 5$  m apart and were left for  
184 1–7 days. For cases in which some traps had been disturbed by mammals, we estimated  
185 density using only the undisturbed pitfalls (1–9 traps per site). We repeated the survey if  
186 >5 pitfalls had been disturbed by mammals (two sites in Tottabetsu River in 2015).  
187 Consequently, we obtained 28 observations across 2 years. In the statistical analysis, we  
188 used the total density of four dominant species (*Lithochlaenius noguchii*, *Apristus*  
189 *grandis*, *Brachinus stenoderus*, and *Bembidion* spp.), which represented ca. 99% of  
190 Carabid beetle abundance in the samples. See Table S1 for a full list of Carabid beetles  
191 captured.

192

### 193 *Consumption rate of supplemental in situ prey on gravel bars*

194 We measured *in situ* daily removal of artificially provided beetle larvae (Family  
195 Tenebrionidae, wet condition; Natural Pet Foods, Ibaraki, Japan) on gravel bars. We

196 assumed that removal rates of beetle larvae reflect the consumption rate of naturally  
197 available terrestrial resources on gravel bars. Indeed, various types of terrestrial prey  
198 (Coleoptera [including Tenebrionidae], Diptera, Hemiptera, and Lepidoptera) were  
199 found at the study sites (both larvae and adults were supplied from vegetation patches or  
200 shore strandings). At each site, a total of six plastic cups containing 10 beetle larvae  
201 (average dry mass: 28 mg larva<sup>-1</sup>) were provided at three locations (upstream,  
202 midstream, and downstream of the gravel bar) in pairs: one cup near the water's edge (5  
203 m to the edge) and the other cup at the middle of the gravel bar (10 m). Consequently, a  
204 total of 60 beetle larvae were provided at each site. The amount of supplemental prey is  
205 comparable to naturally available terrestrial prey in the habitat (280 mg cup<sup>-1</sup> vs. 2.7–  
206 941.3 mg m<sup>-2</sup> day<sup>-1</sup>; data from pan trap samples).

207         We gently affixed the cups with surrounding cobbles and kept them in place for  
208 2 days (1.72–2.34 days). We counted the number of beetle larvae removed or consumed,  
209 which was then used as a proxy for consumption rates in the following analysis. In  
210 those cases in which some traps were disturbed by mammals, we estimated the  
211 consumption rates using only the undisturbed cups. In our preliminary experiment,  
212 ground beetles accounted for ~93% of carnivorous animals attracted by beetle larvae  
213 (ESM 1). We measured the daily removal rates of beetle larvae three times (2015: early

214 and late July at 16 sites, 2016: mid-July at 10 sites) to account for temporal variability  
215 (a total of 42 observations were available).

216

### 217 *Statistical analysis*

218 To assess how riverine productivity gradients mediate terrestrial food web interactions,  
219 we performed path analysis within a Bayesian framework. Our path model incorporated  
220 a wide spectrum of trophic interactions across ecosystems (graphically shown in Fig. 2).  
221 The Bayesian path analysis has a certain merit of flexibility, as it can deal with various  
222 types of error distributions and random effects (cf. Takagi and Miyashita, 2015) that are  
223 difficult to be implemented in the framework of ordinary path analysis or structural  
224 equation modeling (but see Lefcheck, 2016 for recent advance in structural equation  
225 modeling). A generalized linear mixed effect model (GLMM) may be a possible  
226 alternative, but it cannot account for the statistical uncertainty that would inflate along  
227 the sequence of regressions. Therefore, our approach is one of the best options currently  
228 available.

229 In the description of our path model, we used uppercase variable names for  
230 observed data and lowercase variable names for latent variables. The average  
231 emergence flux at site  $i$ ,  $EF_i$  ( $\text{mg m}^{-2} \text{day}^{-1}$ ), was assumed to follow a log-normal

232 distribution (natural logarithm) and was related to algal biomass ( $AB_i$ ; AFDM,  $\text{mg m}^{-2}$ )

233 as follows:

234

235  $\log(EF_i) \sim \text{Normal}(\log.ef_i, \sigma_{EF}^2)$

236  $\log.ef_i = \beta_{0,ef} + \beta_{1,ef} \times \log(AB_i) + \gamma_{1,k}$  (1),

237

238 where the parameter  $\gamma$  represents random variation among rivers (same as in the

239 following equations).

240 Ground beetle density at site  $i$  in survey  $j$  and year  $t$ ,  $GB_{ijt}$ , was modeled using

241 an overdispersed Poisson process:

242

243  $GB_{ijt} \sim \text{Poisson}(gb_{ijt})$

244  $\log(gb_{ijt}) = st.gb_{it} + \beta_{4,gb} \times \text{TEMP}_{gb,ijt} + \log(\text{CPUE}_{ijt}) + \varepsilon_{1,ijt}$

245  $st.gb_{it} = \beta_{0,gb} + \beta_{1,gb} \times \log.ef_i + \beta_{2,gb} \times \log(\text{ISP}_i) + \beta_{3,gb} \times \text{AREA}_{it} + \gamma_{2,k} + \delta_{1,it}$  (2),

246

247 where  $\text{TEMP}_{gb,ijt}$  is the average air temperature during the sampling,  $\text{AREA}_{it}$  is the area

248 of the gravel bar (ha),  $\text{ISP}_i$  is the terrestrial *in situ* prey availability ( $\text{mg m}^{-2} \text{day}^{-1}$ ),  $\delta$  is

249 the site-specific year effect, and  $\varepsilon$  is the data-level random variation that accounts for

250 overdispersion (same in the following equations). The logarithm of catch-per-unit-effort  
 251 ( $CPUE_{ijt}$ ; number of pitfalls  $\times$  number of days elapsed) was included as an offset term.  
 252 In this expression, the latent variable  $st.gb_{it}$  indicates the mean density of ground beetles  
 253 at site  $i$  in year  $t$  on a logarithmic scale.

254 The consumption rate (number of beetle larvae consumed),  $CR_{ijt}$ , was then  
 255 drawn from an overdispersed Poisson distribution:

256

257  $CR_{ijt} \sim \text{Poisson}(cr_{ijt})$

258  $\log(cr_{ijt}) = \beta_{0,cr} + \beta_{1,cr} \times st.gb_{it} + \beta_{2,cr} \times TEMP_{cr,ijt} + \log(TIME_{ijt}) + \gamma_{3,k} + \delta_{2,it} + \epsilon_{2,ijt}$

259 (3),

260

261 where  $TEMP_{cr,ijt}$  is the average air temperature during the experiment, and  $TIME_{ijt}$  is the  
 262 time elapsed during the experiment (1.7–2.3 days; an offset term). Note that, however,  
 263 our consumption measure was “censored” at 60 beetle larvae (or less for disturbed sites;  
 264 hereafter,  $C_{ijt}$  denotes censored values for each sample). We accounted for the nature of  
 265 measurements using a censoring function: when all beetle larvae were removed or  
 266 consumed during the experiment, the observations were treated initially as “NA”, and  
 267 the values of  $> C_{ijt}$  (60 beetle larvae for undisturbed sites; either 40 or 50 for disturbed

268 sites) were randomly generated along the parameter inference of Markov Chain Monte  
269 Carlo (MCMC) simulations (see below). Thus, an observation censored at  $C_{ijt}$  beetle  
270 larvae provides a contribution of  $\Pr(\text{CR}_{ijt} > C_{ijt} | \Theta)$  ( $\Theta$  is a set of specified parameters).  
271 This censoring technique has been proven to provide less biased estimates of parameters  
272 (Lunn et al., 2012).

273 Note that we did not find strong support for species-specific responses of  
274 Carabid beetles to emergence flux (see ESM 2). In addition, per-capita consumption  
275 performance was not statistically distinguishable among the dominant beetle species  
276 (ESM 3). Therefore, we pooled the ground beetle densities.

277 In our model, all explanatory variables were centered prior to analysis;  
278 therefore, intercepts ( $\beta_0$ ) indicate estimated average values of each response variable.  
279 We also report regression slopes ( $\beta_{1-4}$ ) in a standardized form (obtained by multiplying  
280 by the standard deviation of each explanatory variable) to allow them to be comparable  
281 with one another.

282 In our path model, the random effects for river identity ( $\gamma_{1,k}, \gamma_{2,k}, \gamma_{3,k}$ ) were  
283 assumed to follow a multivariate normal distribution,  $\gamma_{1-3,k} \sim \text{MN}(\mathbf{0}, \Sigma)$ , in which  $\mathbf{0}$  and  
284  $\Sigma$  denote a vector of zeros and a variance–covariance matrix, respectively. The other  
285 random effects were drawn from normal distributions ( $\delta_{1,it}, \delta_{2,it}, \varepsilon_{1,ijt}, \varepsilon_{2,ijt}$ ), with a mean

286 of 0 and variance of  $\sigma_R^2$  (subscript R corresponds to each random effect name).

287 Vague priors were assigned to the parameters: normal distributions (mean = 0,  
288 variance =  $10^4$ ) for regression coefficients  $\beta$ , truncated normal distributions (mean = 0,  
289 variance =  $10^4$ , range: 0–100) for standard deviations ( $\sigma_{EF}$  and  $\sigma_R$ ), and an  
290 inverse-Wishart distribution for  $\Sigma$  (*d.f.* = 4). The model was fitted to the data using  
291 JAGS (ver. 4.1.0) and the package “*runjags*” (Denwood, 2016) in R 3.2.3 (R Core Team,  
292 2016). Three MCMC chains were run with 15,000 iterations (5,000 burn-in), and 500  
293 samples per chain were used to calculate posterior probabilities. Convergence was  
294 assessed by examining whether the R-hat indicator of each parameter approached a  
295 value of 1 (Gelman and Hill, 2007). The goodness of fit of the model was assessed  
296 using the coefficient of determination (conditional  $R^2$ ) following Nakagawa and  
297 Schielzeth (2013).

298

299

## 300 **Results**

301 Descriptive statistics of the environmental variables are summarized in Table 1. Algal  
302 biomass was highly variable in the Satsunai River, whereas only moderate variation  
303 occurred in the Bisei and Tottabetsu Rivers (Table 1, see ESM 4 and Fig. S2 for

304 longitudinal gradients). This pattern was also observed for emergence flux but not for  
305 terrestrial *in situ* prey availability (Table 1).

306           The Bayesian path model had reasonable explanatory power (conditional  $R^2 =$   
307 0.71–0.81 for each response variable), suggesting that our parameter inference was  
308 highly reliable. The model suggested that the donor productivity mediated the  
309 consumption rate of supplemental *in situ* prey (Table 2, Fig. 2). Algal biomass (AFDM)  
310 had a positive effect on the emergence flux of aquatic insects. Increased emergence flux  
311 was associated with high densities of ground beetles and rapid consumption of  
312 supplemental prey on gravel bars (Figs. 2, 3). In contrast, terrestrial variables (terrestrial  
313 prey availability, habitat area, and air temperature) had little influence on ground beetle  
314 density (Table 2, Fig. 2). However, higher air temperature during the experiment  
315 escalated the consumption rate of supplemental prey, likely due to  
316 temperature-dependent activity of ground beetles (Table 2, Fig. 2). A full description of  
317 the estimated parameters is provided in Table 2 and Fig. S3.

318

319

## 320 **Discussion**

321 Standing algal biomass (a proxy for donor productivity) had clear repercussions on the

322 consumption rate of supplemental *in situ* prey (beetle larvae) on gravel bars, even  
323 though the effects had to be transmitted through as many as three trophic linkages  
324 across ecosystems (Fig. 2). Furthermore, these effects remained significant even after  
325 accounting for the influences of terrestrial prey availability and habitat characteristics,  
326 such as gravel bar area (both were insignificant). Although a great deal of attention has  
327 been paid to the consequences of spatial subsidies, few studies addressed the potential  
328 factors triggering the cross-system cascading interactions (e.g., Burdon and Harding,  
329 2008; Sato et al., 2012). The present study provides among the first quantitative and  
330 holistic picture of how resource gradients in a donor system drive cascading biotic  
331 interactions across coupled ecosystems.

332         There are several explanations for why increased spatial subsidies, which may  
333 be driven by higher algal biomass, were associated with greater consumption rates of  
334 supplemental prey on gravel bars. First, ground beetles seem to have been fueled by  
335 persistent supplies of spatial subsidies for multiple generations. Hence, it is reasonable  
336 that their numerical response to spatial subsidies (through reproduction and/or spatial  
337 aggregation) led to overconsumption of supplemental prey (“apparent competition”),  
338 likely masking the effects of seasonal prey switching by ground beetles to emerging  
339 aquatic insects (see Terui et al., 2017 for stable isotope analysis). The enhanced

340 consumption rate was consistently observed over two years, further corroborating our  
341 interpretation. Another, but compatible explanation may stem from the moderate levels  
342 of subsidy use by the dominant beetle species (0.12–0.54 in proportion; see Terui et al.,  
343 2017). Subsidy theory suggests that “apparent competition” appears strongly when  
344 consumer’s proportional preference to prey subsidies ranges from 0.10 to 0.60 (Leroux  
345 and Loreau, 2008). This is mainly because those levels of subsidy use are sufficient to  
346 respond numerically to subsidies while exerting strong top down effects on *in situ* prey  
347 (Leroux and Loreau, 2008). Collectively, our results are in close agreement with the  
348 food web theories that predict the long-term effects of cumulative subsidies.

349           Importantly, a meta-analysis by Marczak et al. (2007) did not reveal consistent  
350 significant effects of donor productivity on the recipient consumer responses. The  
351 deviation from the general trend may be attributable to the nature of gravel bar habitats.  
352 Gravel bars are relatively open to the neighboring donor systems, allowing effective  
353 physical transport of spatial subsidies across ecosystems (i.e., no apparent barriers for  
354 migration of emerging aquatic insects). Moreover, *in situ* productivity of gravel bars  
355 may be so limited that most individuals/species must feed, at least in part, on emerging  
356 aquatic insects (Paetzold et al., 2005; Terui et al., 2017). Indeed, we directly observed  
357 that many Carabid beetles preyed upon aquatic insects crawling on the shore (AT,

358 personal observation), supporting our statistical inference from stable isotope analysis  
359 (Terui et al., 2017). These two factors, the effective physical transport of spatial  
360 subsidies and unproductive nature of gravel bars, were likely combined to produce the  
361 prevailing impacts of donor productivity across coupled ecosystems.

362           It should be borne in mind that sewage water inputs could also affect detritus  
363 food webs in the study rivers. For example, enriched terrestrial plants may provide  
364 greater amount of leaf litter inputs into adjacent rivers, thereby increasing detritivorous  
365 aquatic insects (and spatial subsidies in the form of emerging aquatic insects). However,  
366 in our study system, the contribution of detritus food webs to spatial subsidies seems to  
367 be limited because the river surface was rarely covered with riparian  
368 canopies/vegetation (see Fig. 1c; ~0% canopy cover). In such rivers, the relative  
369 importance of autochthonous production often exceeds that of allochthonous inputs  
370 (Collins et al., 2016), forming the major energy source of developing food webs (Doi,  
371 2009). The above mechanism must not be ignored, but may be more relevant to small  
372 streams in which stream secondary production (aquatic insect biomass) relies heavily on  
373 leaf litter inputs from riparian canopies.

374           Another possible issue with our system involves the longitudinal arrangement  
375 of our sampling sites. Many biological factors vary longitudinally (Rahel and Hubert,

376 1991; Terui and Miyazaki, 2016, 2017), and such patterns might explain the variations  
377 observed in a suite of variables in this study. However, we can exclude this possibility,  
378 as all of the response variables (emergence flux, ground beetle density, and  
379 consumption) exhibited minimal changes over the stretches of the rivers with little algal  
380 biomass variation (Bisei and Tottabetsu; ESM 4). These facts suggest that the lengths of  
381 our study stretches were short enough to avoid any naturally occurring longitudinal  
382 gradients. Furthermore, enrichment without increased algal production (the Bisei River;  
383 see Fig S1 and S2) caused ambiguous responses in the terrestrial variables (ground  
384 beetle densities and consumption rates). Therefore, enrichment alone appears to be  
385 insufficient to explain the observed patterns. Considering this evidence, algal biomass  
386 was very likely to be the variable controlling the consumption rate of supplemental *in*  
387 *situ* prey in the recipient system.

388         Despite the concerted efforts of food web ecologists, the significance of donor  
389 productivity has yet to be explored. Our study highlighted the potential of donor  
390 productivity to trigger cascading biotic interactions across coupled ecosystems. Since  
391 cross-system energy flows should originate, at least in part, from primary producers of  
392 donor systems, our fundamental finding may form the basis of future studies addressing  
393 the driving factors of cross-system cascading interactions. Expanding our findings to

394 broader members of recipient systems (e.g., intraguild prey) may provide intriguing  
395 insights into how ecological communities are organized in intimately coupled  
396 ecosystems.

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398

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403 and Tourism of Japan.

404

### 405 **Data accessibility**

406 Data and JAGS code will be uploaded on Dryad.

407

408

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478 **Table 1** Values of the variables hypothesized to influence ground beetle density at 16  
 479 study sites in the Tokachi River basin, Japan (mean  $\pm$  standard deviation). The Satsunai  
 480 and Bisei Rivers each have a point source of eutrophication at midstream (see Fig. 1).

Variable	River name		
	Satsunai	Bisei	Tottabetsu
Algal biomass (AFDM; mg m <sup>-2</sup> )	2825.1 $\pm$ 1649.9	1112.3 $\pm$ 326.5	1212.7 $\pm$ 185.3
Emergence flux (mg m <sup>-2</sup> day <sup>-1</sup> )	59.7 $\pm$ 42.5	125.2 $\pm$ 37.6	74.5 $\pm$ 25.5
Terrestrial <i>in situ</i> prey (mg m <sup>-2</sup> day <sup>-1</sup> )	93.8 $\pm$ 72.4	70.4 $\pm$ 74.6	52.9 $\pm$ 20.7
Bar area (ha)	0.41 $\pm$ 0.13	0.49 $\pm$ 0.34	0.51 $\pm$ 0.28

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484 **Table 2** Parameters estimated in the Bayesian path model. See Fig. 2 for graphical

485 representation.

Response	Parameter	Note	Median	95% CI
Emergence flux	$\beta_{0,ef}$	Intercept	4.29	3.21 to 5.72
	$\beta_{1,ef}$	Effect of algal biomass	0.38	0.10 to 0.64
	$\sigma_{EF}$	SD of residual error	0.40	0.27 to 0.67
	$\sigma_{\gamma 1}$	SD of among-river error	0.56	0.15 to 4.07
Beetle density	$\beta_{0,gb}$	Intercept	1.87	0.68 to 2.88
	$\beta_{1,gb}$	Effect of emergence flux	0.48	0.02 to 1.10
	$\beta_{2,gb}$	Effect of terrestrial <i>in situ</i> prey	-0.01	-0.42 to 0.40
	$\beta_{3,gb}$	Effect of bar area	-1.08	-5.50 to 3.45
	$\beta_{4,gb}$	Effect of air temperature	0.01	-0.03 to 0.05
	$\sigma_{\epsilon 1}$	SD of data-level error	0.40	0.07 to 0.92
	$\sigma_{\delta 1}$	SD of site-year-specific error	0.76	0.31 to 1.20
Consumption rate	$\sigma_{\gamma 2}$	SD of among-river error	0.44	0.10 to 3.56
	$\beta_{0,cr}$	Intercept	3.35	2.49 to 4.13
	$\beta_{1,cr}$	Effect of beetle density	0.29	0.06 to 0.53
	$\beta_{2,cr}$	Effect of air temperature	0.29	0.17 to 0.44
	$\sigma_{\epsilon 2}$	SD of data-level error	0.22	0.04 to 0.48
	$\sigma_{\delta 2}$	SD of site-year-specific error	0.32	0.02 to 0.61
	$\sigma_{\gamma 3}$	SD of among-river error	0.30	0.09 to 1.84

486

487

488 **Figure captions**

489 **Figure 1** Locations of the study system and sampling sites. (a) Tokachi River basin,  
490 Hokkaido, Japan (gray dot). (b) Sampling sites (dots) were located among the three  
491 alluvial fan rivers (Satsunai, Bisei, and Tottabetsu). Black triangles indicate outlets of  
492 sewage water. Filled and open dots represent sampling sites located downstream and  
493 upstream of sewage water outlets, respectively. (c) Typical gravel bar surveyed in this  
494 study.

495

496 **Figure 2** Graphical representation of the Bayesian path analysis. Rectangles and ovals  
497 represent observed (i.e., data) and latent variables, respectively. Solid and dashed arrows  
498 connecting boxes show significant and non-significant effects, respectively. Numbers  
499 next to the arrows indicate the standardized slopes. Dotted lines connecting rectangles  
500 and ovals denote stochastic relationships. The parameters  $\gamma$  and  $\delta$  indicate random  
501 effects ( $\gamma$ : river identity effect;  $\delta$ : site-specific year effect). See Table 2 and Figure S3  
502 for a full description of the estimated parameters.

503

504 **Figure 3** Relationships between (a) algal biomass and emergence flux, (b) emergence  
505 flux and beetle density, and (c) beetle density and daily loss of worm carcasses. Lines

506 represent values predicted by the Bayesian path model (black: average; gray: individual  
507 rivers). Different symbols denote data from different rivers (square, Satsunai; circle,  
508 Bisei; diamond, Tottabetsu). Filled and open dots represent sampling sites located  
509 downstream and upstream of sewage water outlets, respectively. Predicted lines for  
510 consumption rates (c) were shifted upward than observed values due to censoring (see  
511 *Statistical Analysis*). Note that emergence flux and beetle density along the x-axis are  
512 latent variables (*log.ef* and *st.gb*, respectively, in equations 1 and 2) derived from the  
513 Bayesian path model. Duplicated measurements were averaged for each site

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Fig. 1 Terui et al.

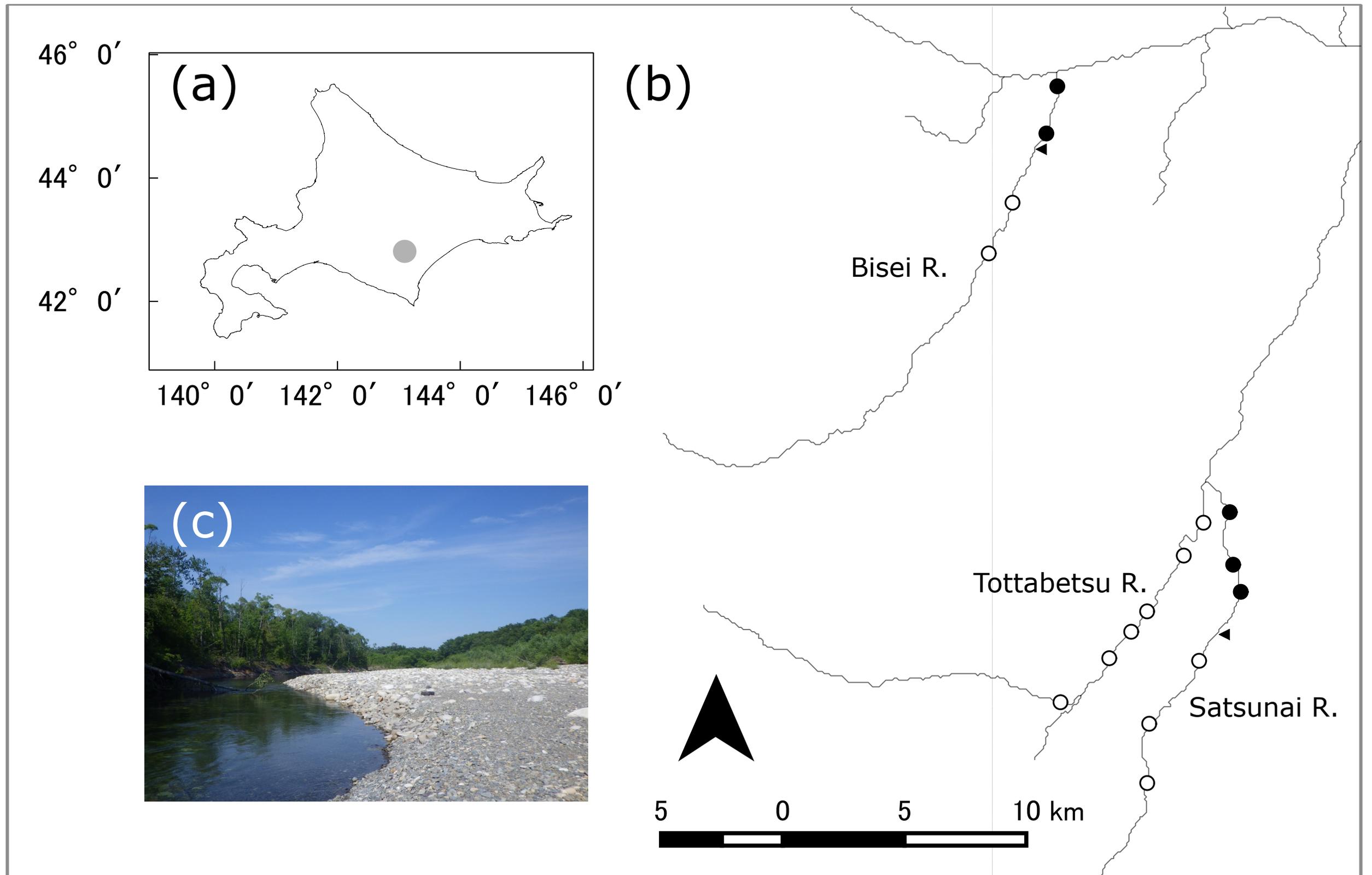


Fig. 2 Terui et al.

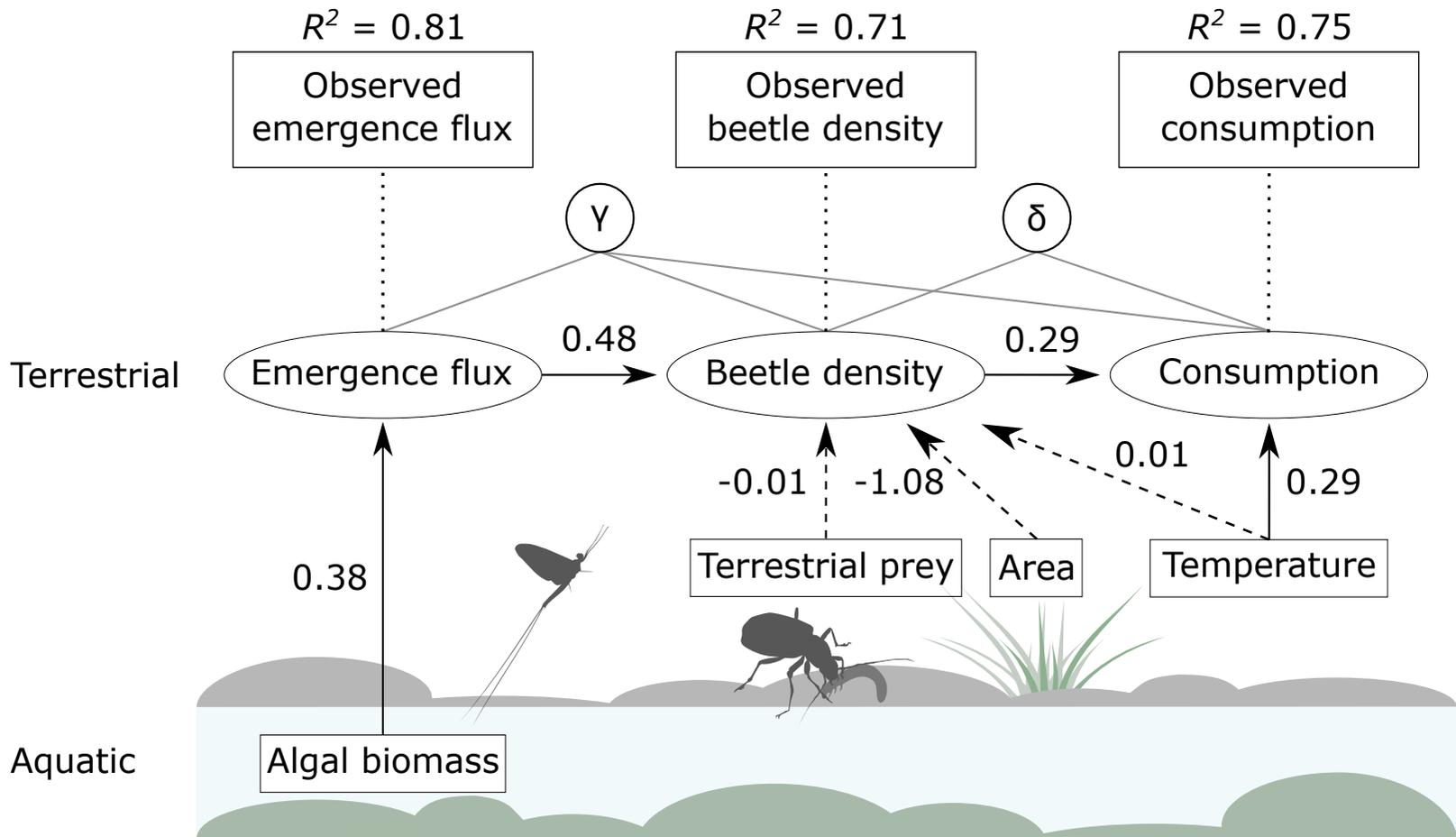


Fig.3 Terui et al.

