HOKKAIDO UNIVERSITY

Title	Stream Resource Gradients Drive Consumption Rates of Supplemental Prey in the Adjacent Riparian Zone
Author(s)	Terui, Akira; Negishi, Junjiro N.; Watanabe, Nozomi et al.
Citation	Ecosystems, 21(4), 772-781 https://doi.org/10.1007/s10021-017-0183-3
Issue Date	2018-06
Doc URL	https://hdl.handle.net/2115/74526
Rights	© Springer Science+Business Media, LLC 2017., The final publication is available at https://doi.org/10.1007/s10021-017-0183-3
Type	journal article
File Information	MS_R2_final_Ecosystems.pdf



Hokkaido University Collection of Scholarly and Academic Papers : HUSCAP

Title: Stream resource gradients drive consumption rates of supplemental prey in the adjacent riparian zone

Author: Akira Terui[1,2*], Junjiro N Negishi[3], Nozomi Watanabe[3], Futoshi Nakamura[2]

[1] Department of Ecology, Evolution and Behavior, University of Minnesota, 140 Gortner Lab, 1479 Gortner Avenue, St. Paul, MN 55108, USA

[2] Department of Forest Science, Graduate School of Agriculture, Hokkaido University, Kita 9, Nishi 9, Kita-ku, Sapporo 060-8589, Japan

[3] Faculty of Environmental Earth Science, Hokkaido University, N10W5, Sapporo, Hokkaido 060-0810, Japan

* Corresponding author.

E-mail address: hanabi0111@gmail.com (A. Terui)

Abstract

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

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

Introduction

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

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

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

Methods

Study system

We conducted our investigation in the Tokachi River basin, Hokkaido, Japan, during the summer and fall of 2015 and 2016. The mean annual air temperature and cumulative precipitation in 2015–2016 were 8.2°C and 1083 mm, respectively (Japan Meteorological Agency; available at http://www.jma.go.jp/jma/index.html). We chose one stretch (8–12 km) on each of three alluvial fan rivers (ca. 20–30-m wetted channel width) for our field surveys (Fig. 1). These three rivers (Satsunai, Bisei, and Tottabetsu Rivers) are characterized by a highly variable flow regime with the highest average discharge occurring in early spring during snowmelt runoff. However, the rivers differ 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 (NO_3^-:
107 upstream = 1.6 ± 1.0 mg L^{-1}, downstream = 4.5 ± 2.2 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 (NO_3^-: upstream = 1.9 ± 0.6
111 mg L^{-1}, downstream = 3.8 ± 2.0 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 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^2 (10 × 10 cm) of each
135 cobble was scrubbed with a toothbrush, and a total area of 300–400 cm^2 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℃ for 24 h,
138 combusted at 500℃ 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^{-2} 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^2, 470-μm 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^2 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 $- 5.76 \times 10^{-6} \times$ wet mass^2, $n = 15$,
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 (0.30×0.22 m^2 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 (Copleoptera, 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^2, $n = 15$, $R^2 = 0.986$). 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 (±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 ≥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^{-1}) 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^{-1} vs. 2.7–
206 941.3 mg m^{-2} day^{-1}; 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 (mg m^{-2} day^{-1}), was assumed to follow a log-normal

232 distribution (natural logarithm) and was related to algal biomass (AB_i; AFDM, 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 γ 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 $\log(gb_{ijt}) = st.gb_{it} + \beta_{4,gb} \times TEMP_{gb,ijt} + \log(CPUE_{ijt}) + \varepsilon_{1,ijt}$

245 $st.gb_{it} = \beta_{0,gb} + \beta_{1,gb} \times log.ef_i + \beta_{2,gb} \times \log(ISP_i) + \beta_{3,gb} \times AREA_{it} + \gamma_{2,k} + \delta_{1,it}$ (2),

246

247 where $TEMP_{gb,ijt}$ is the average air temperature during the sampling, $AREA_{it}$ is the area

248 of the gravel bar (ha), ISP_i is the terrestrial *in situ* prey availability (mg m^{-2} day^{-1}), δ is

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

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

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

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

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

where $TEMP_{cr,ijt}$ is the average air temperature during the experiment, and $TIME_{ijt}$ is the time elapsed during the experiment (1.7–2.3 days; an offset term). Note that, however, our consumption measure was "censored" at 60 beetle larvae (or less for disturbed sites; hereafter, C_{ijt} denotes censored values for each sample). We accounted for the nature of measurements using a censoring function: when all beetle larvae were removed or consumed during the experiment, the observations were treated initially as "NA", and 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 $\Pr(CR_{ijt} > C_{ijt}|\boldsymbol{\Theta})$ ($\boldsymbol{\Theta}$ 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 (β_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, $\gamma_{1–3,k} \sim \mathrm{MN}(\mathbf{0}, \sum)$, in which $\mathbf{0}$ and
284 $\sum$ 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 σ_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 β, truncated normal distributions (mean = 0,

289 variance = 10^4, range: 0–100) for standard deviations (σ_{EF} and σ_R), and an

290 inverse-Wishart distribution for $\sum$ (*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

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

Importantly, a meta-analysis by Marczak et al. (2007) did not reveal consistent significant effects of donor productivity on the recipient consumer responses. The deviation from the general trend may be attributable to the nature of gravel bar habitats. Gravel bars are relatively open to the neighboring donor systems, allowing effective physical transport of spatial subsidies across ecosystems (i.e., no apparent barriers for migration of emerging aquatic insects). Moreover, *in situ* productivity of gravel bars may be so limited that most individuals/species must feed, at least in part, on emerging aquatic insects (Paetzold et al., 2005; Terui et al., 2017). Indeed, we directly observed 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 autochthonofus 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.
397
398
399 **Acknowledgements**
400 We are grateful to B. Nessa, H. Imai, T. Akasaka and student volunteers for their
401 field/laboratory assistance. This study is partly supported by the research fund for the
402 Ishikari and Tokachi Rivers provided by the Ministry of Land, Infrastructure, Transport,
403 and Tourism of Japan.
404
405 **Data accessibility**
406 Data and JAGS code will be uploaded on Dryad.
407
408
409 **Reference**
410 Baxter CV, Fausch KD, Saunders WC. 2005. Tangled webs: reciprocal flows of invertebrate prey link
411 streams and riparian zones. Freshwater Biology 50: 201-220.
412 Burdon FJ, Harding JS. 2008. The linkage between riparian predators and aquatic insects across a
413 stream‐resource spectrum. Freshwater Biology 53: 330-346.

414 Collins SM, Kohler TJ, Thomas SA, Fetzer WW, Flecker AS. 2016. The importance of terrestrial
415 subsidies in stream food webs varies along a stream size gradient. Oikos 125: 674-685.
416 Denwood MJ. 2016. runjags: An R package providing interface utilities, model templates, parallel
417 computing methods and additional distributions for MCMC models in JAGS. Journal of Statistical
418 Software 71: 1-25.
419 Doi H. 2009. Spatial patterns of autochthonous and allochthonous resources in aquatic food webs.
420 Population Ecology 51: 57-64.
421 Gelman A, Hill J. 2007. Data Analysis Using Regression and Multilevel/Hierarchical Models. New York,
422 USA: Cambridge University Press.
423 Giery ST, Lemoine NP, Hammerschlag-Peyer CM, Abbey-Lee RN, Layman CA. 2013. Bidirectional
424 trophic linkages couple canopy and understorey food webs. Functional Ecology 27: 1436-1441.
425 Henschel JR, Mahsberg D, Stumpf H. 2001. Allochthonous aquatic insects increase predation and
426 decrease herbivory in river shore food webs. Oikos 93: 429-438.
427 Lefcheck JS. 2016. piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution,
428 and systematics. Methods in Ecology and Evolution 7: 573-579.
429 Leroux SJ, Loreau M. 2008. Subsidy hypothesis and strength of trophic cascades across ecosystems.
430 Ecology Letters 11: 1147-1156.
431 Lunn D, Jackson C, Best N, Thomas A, Spiegelhalter D. 2012. The BUGS book: A practical introduction
432 to Bayesian analysis. Boca Raton, USA: CRC press.
433 Marczak LB, Thompson RM, Richardson JS. 2007. Meta-analysis: trophic level, habitat, and productivity
434 shape the food web effects of resource subsidies. Ecology 88: 140-148.
435 Nakagawa S, Schielzeth H. 2013. A general and simple method for obtaining R^2 from generalized linear
436 mixed‐effects models. Methods in Ecology and Evolution 4: 133-142.
437 Nakano S, Miyasaka H, Kuhara N. 1999. Terrestrial-aquatic linkages: Riparian arthropod inputs alter
438 trophic cascades in a stream food web. Ecology 80: 2435-2441.
439 Nakano S, Murakami M. 2001. Reciprocal subsidies: dynamic interdependence between terrestrial and
440 aquatic food webs. Proceedings of the National Academy of Sciences of the United States of
441 America 98: 166-170.
442 Paetzold A, Schubert CJ, Tockner K. 2005. Aquatic terrestrial linkages along a braided-river: Riparian
443 arthropods feeding on aquatic insects. Ecosystems 8: 748-759.
444 Polis GA, Anderson WB, Holt RD. 1997. Toward an integration of landscape and food web ecology: The
445 dynamics of spatially subsidized food webs. Annual Review of Ecology and Systematics 28:
446 289-316.
447 Rahel FJ, Hubert WA. 1991. Fish assemblages and habitat gradients in a Rocky Mountain–Great Plains
448 stream: biotic zonation and additive patterns of community change. Transactions of the American
449 Fisheries Society 120: 319-332.

450 R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for
451 Statistical Computing, Vienna, Austria. https://www.R-project.org/.
452 Ruff CP, Schindler DE, Armstrong JB, Bentley KT, Brooks GT, Holtgrieve GW, McGlauflin MT,
453 Torgersen CE, Seeb JE. 2011. Temperature-associated population diversity in salmon confers
454 benefits to mobile consumers. Ecology 92: 2073-2084.
455 Sabo J, Power M. 2002. River-watershed exchange: effects of riverine subsidies on riparian lizards and
456 their terrestrial prey. Ecology 83: 1860-1869.
457 Sato T, Egusa T, Fukushima K, Oda T, Ohte N, Tokuchi N, Watanabe K, Kanaiwa M, Murakami I,
458 Lafferty KD. 2012. Nematomorph parasites indirectly alter the food web and ecosystem function
459 of streams through behavioural manipulation of their cricket hosts. Ecology Letters 15: 786-793.
460 Shimazaki A, Miyashita T. 2005. Variable dependence on detrital and grazing food webs by generalist
461 predators: aerial insects and web spiders. Ecography 28: 485-494.
462 Spiller DA, Piovia-Scott J, Wright AN, Yang LH, Takimoto G, Schoener TW, Iwata T. 2010. Marine
463 subsidies have multiple effects on coastal food webs. Ecology 91: 1424-1434.
464 Takagi S, Miyashita T. 2015. Time‐scale dependency of host plant biomass‐and trait‐mediated
465 indirect effects of deer herbivory on a swallowtail butterfly. Journal of Animal Ecology 84:
466 1657-1665.
467 Takimoto G, Iwata T, Murakami M. 2008. Timescale hierarchy determines the indirect effects of
468 fluctuating subsidy inputs on in situ resources. The American Naturalist 173: 200-211.
469 Terui A, Akasaka T, Negishi JN, Uemura F, Nakamura F. 2017. Species-specific use of allochthonous
470 resources by ground beetles (Carabidae) at a river–land interface. Ecological Research 32: 27-35.
471 Terui A, Miyazaki Y. 2016. Three ecological factors influencing riverine fish diversity in the Shubuto
472 River system, Japan: habitat capacity, habitat heterogeneity and immigration. Limnology 17:
473 143-149.
474 Terui A, Miyazaki Y. 2017. Combined effects of immigration potential and habitat quality on diadromous
475 fishes. Limnology 18: 121-129.

476

477

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 ± 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^{-2})	2825.1 ± 1649.9	1112.3 ± 326.5	1212.7 ± 185.3
Emergence flux (mg m^{-2} day^{-1})	59.7 ± 42.5	125.2 ± 37.6	74.5 ± 25.5
Terrestrial *in situ* prey (mg m^{-2} day^{-1})	93.8 ± 72.4	70.4 ± 74.6	52.9 ± 20.7
Bar area (ha)	0.41 ± 0.13	0.49 ± 0.34	0.51 ± 0.28

481

482

483

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
	σ_{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 *in situ* 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
	$\sigma_{\varepsilon 1}$	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
	$\sigma_{\gamma 2}$	SD of among-river error	0.44	0.10 to 3.56
Consumption rate	$\beta_{0,cr}$	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
	$\sigma_{\varepsilon 2}$	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

Figure captions

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

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

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

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

Fig. 1 Terui et al.

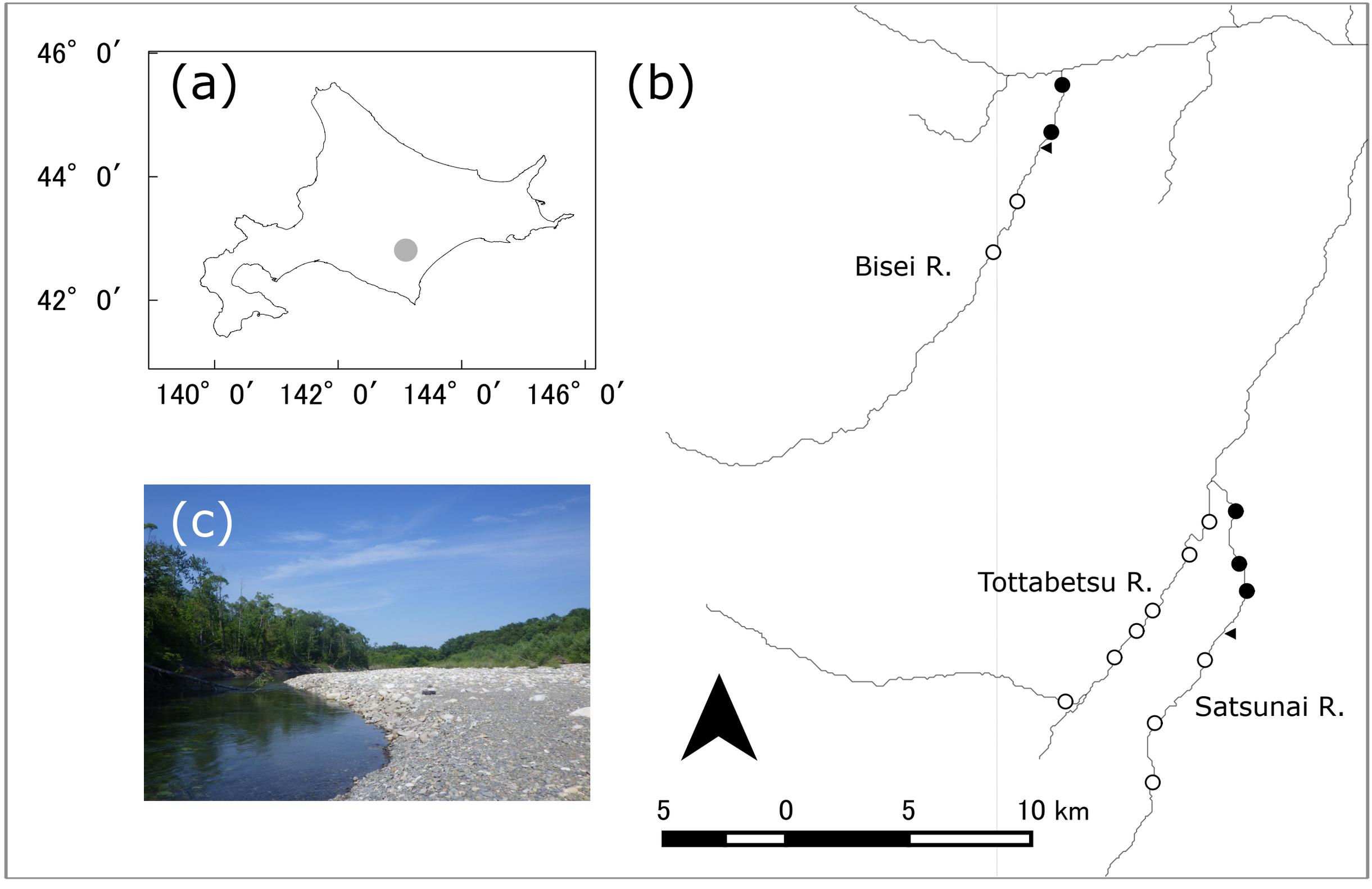


Fig. 2 Terui et al.

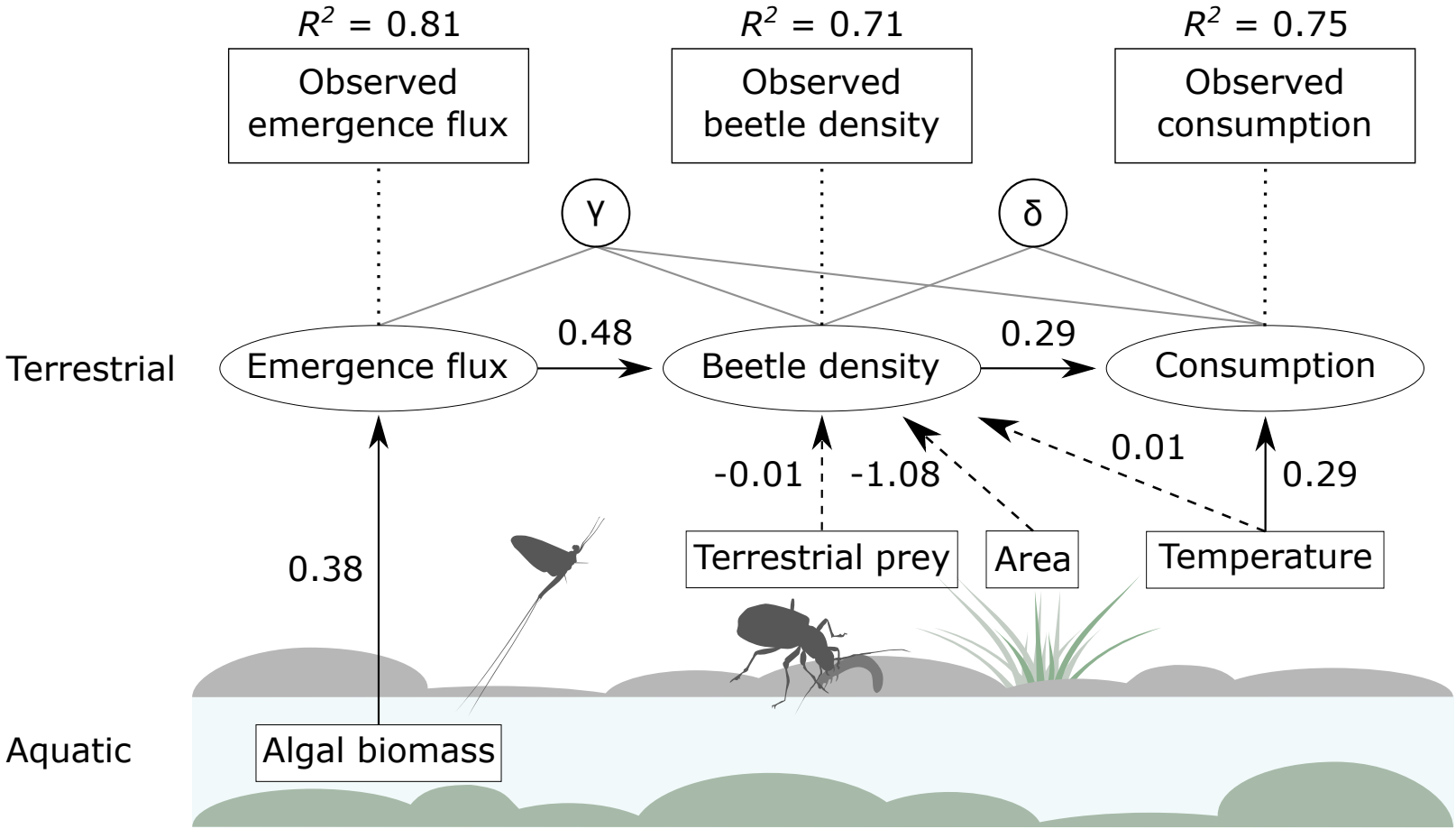


Fig.3 Terui et al.

