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

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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*

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

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

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

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

downstream half of the stretch has been nutritionally enriched by sewage water (NO_3^- : 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 description) and exhibits excessive algal biomass. In contrast, the Bisei and Tottabetsu Rivers exhibit no signs of increasing algal biomass along the longitudinal gradient, although the Bisei contains a point source of sewage water (NO_3^- : upstream = $1.9 \pm 0.6 \text{ mg L}^{-1}$, downstream = $3.8 \pm 2.0 \text{ mg L}^{-1}$). The lack of algal response in the Bisei River seems to be attributable to an imbalance of nutrient availability (the Bisei River has little inputs of PO_4^- ; Fig. S1).

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

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

Environmental factors

We surveyed several environmental factors that influence, either directly or indirectly, ground beetle density (family Carabidae) on gravel bars: algal biomass, emerging aquatic insects, terrestrial *in situ* prey, and habitat area. We assessed the ash-free dry mass (AFDM) of benthic algae as a proxy for organic matter availability in the river. We assumed that this measure is an appropriate proxy for donor productivity in our study system because the major energy source in shallow, open-canopy rivers is generally benthic algae (Doi, 2009). At each site, we haphazardly sampled three to four cobbles. After carefully removing attached animals, an area of 100 cm² (10 × 10 cm) of each cobble was scrubbed with a toothbrush, and a total area of 300–400 cm² was rinsed vigorously to remove benthic algae. In the laboratory, we filtered the filtrate through pre-dried GF/F glass fiber filters. The filters were weighed after drying at 60°C for 24 h, combusted at 500°C for 3 h, and then reweighed to estimate AFDM. We measured AFDM twice across seasons (July and September in 2015) to account for seasonal variation in algal production. AFDM was converted into units of mg m⁻² and averaged across seasons on a logarithmic scale (i.e., geometric mean). However, we were unable

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

We quantified aquatic insect emergence in July 2016. This season is the peak period of emergence in the region (Terui et al., 2017) and was assumed to provide representative data. We placed pairs of emergence traps (0.36 m², 470-μm mesh) at two representative local habitats (riffle and glide; >80% of the river surface): one trap on the water surface and the other trap at the water's edge (0.18 m² covered the water surface).

Thus, a total of four traps were deployed at each site. Traps on the water's edge were intended to capture aquatic insects crawling on the shore to emerge. Each trap was fixed using four metal bars and was kept in place for 2 to 4 days, during which emerging insects entered a collection bottle filled with 70% ethanol. In the laboratory, the total wet mass of emerging insects (Ephemeroptera, Plecoptera, Trichoptera, and Diptera) was measured to the nearest milligram and converted into dry mass via a regression of dry and wet mass ($\text{dry mass} = 0.84 + 0.18 \times \text{wet mass} - 5.76 \times 10^{-6} \times \text{wet mass}^2$, $n = 15$, $R^2 = 0.998$). Although emergence flux was investigated in 2016 only, ongoing long-term surveys suggested that spatial emergence patterns (abundance) in Satsunai and Tottabetsu Rivers were consistent among sampling years (2013 vs. 2014 at 8 sites;

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

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

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

Ground beetles

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

Consumption rate of supplemental in situ prey on gravel bars

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

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

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

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

Statistical analysis

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

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

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

as follows:

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

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

where the parameter γ represents random variation among rivers (same as in the

following equations).

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

an overdispersed Poisson process:

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

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

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

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

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

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:

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

$$\log(cr_{ijt}) = \beta_{0,cr} + \beta_{1,cr} \times st.gb_{it} + \beta_{2,cr} \times \text{TEMP}_{cr,ijt} + \log(\text{TIME}_{ijt}) + \gamma_{3,k} + \delta_{2,it} + \varepsilon_{2,ijt}$$

(3),

where $\text{TEMP}_{cr,ijt}$ 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

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

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

In our model, all explanatory variables were centered prior to analysis; therefore, intercepts (β_0) indicate estimated average values of each response variable. We also report regression slopes (β_{1-4}) in a standardized form (obtained by multiplying by the standard deviation of each explanatory variable) to allow them to be comparable with one another.

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

of 0 and variance of σ_R^2 (subscript R corresponds to each random effect name).

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

Results

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

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

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

Discussion

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

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

There are several explanations for why increased spatial subsidies, which may be driven by higher algal biomass, were associated with greater consumption rates of supplemental prey on gravel bars. First, ground beetles seem to have been fueled by persistent supplies of spatial subsidies for multiple generations. Hence, it is reasonable that their numerical response to spatial subsidies (through reproduction and/or spatial aggregation) led to overconsumption of supplemental prey (“apparent competition”), likely masking the effects of seasonal prey switching by ground beetles to emerging 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,

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

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

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

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

Despite the concerted efforts of food web ecologists, the significance of donor productivity has yet to be explored. Our study highlighted the potential of donor productivity to trigger 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 addressing the driving factors of cross-system cascading interactions. Expanding our findings to

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

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Data accessibility

Data and JAGS code will be uploaded on Dryad.

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Table 1 Values of the variables hypothesized to influence ground beetle density at 16 study sites in the Tokachi River basin, Japan (mean $\pm$ standard deviation). The Satsunai 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 $\pm$ 1649.9	1112.3 $\pm$ 326.5	1212.7 $\pm$ 185.3
Emergence flux (mg m ⁻² day ⁻¹)	59.7 $\pm$ 42.5	125.2 $\pm$ 37.6	74.5 $\pm$ 25.5
Terrestrial <i>in situ</i> prey (mg m ⁻² day ⁻¹)	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

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 <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
	$\sigma_{\gamma 2}$	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
	$\sigma_{\epsilon 2}$	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

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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.