Winter gifts for river ecosystems: a massive supply of earthworms in early winter

Ryo Futamura\*1, Chiharu Furusawa2, and Hisanori Okamiya3

1Graduate School of Environmental Sciences, Hokkaido University, Takaoka, Tomakomai, Japan

2Graduate School of Environmental Science, Hokkaido University, N10W5 Sapporo, Japan

3Field Science Center for Northern Biosphere, Hokkaido University, Takaoka, Tomakomai, Japan

\*Corresponding author: [rfutamurattg@gmail.com](mailto:rfutamurattg@gmail.com)

**Abstract**

Terrestrial resource pulses can significantly affect the community dynamics of freshwater ecosystems. Previously, its effect on the river community is considered to be stronger in summer, while weaker in winter when terrestrial invertebrates are less abundant. The movement of the terrestrial earthworms are triggered in winter, so they may be supplied to winter rivers as terrestrial resource pulse, but little is known about it. Here, we report that the massive numbers of the terrestrial earthworms were supplied intensively to an upstream of the small river in early winter. In particular, we found large numbers of Megascolecidae earthworms were supplied in an upstream of the small river in Northern Japan. Furthermore, we observed that supplied earthworms were consumed by salmonid fish species (masu salmon, white spotted char and rainbow trout) and aquatic invertebrates (gammarid amphipod, planarian flatworm and stonefly larvae). These findings suggests that the terrestrial earthworms may play a key role in ecosystem functioning in winter when severe and other resources are scarce.

**Keywords:** aquatic invertebrate, resource subsidy, salmonid, terrestrial–aquatic linkage, terrestrial earthworm, winter ecology

**Main text**

Terrestrial resource pulses, such as large inputs of arthropods into streams (Nakano et al. 1999), can have significant effects on the community dynamics of freshwater ecosystems through energy flows (Richardson and Sato, 2015). The effect of a terrestrial resource pulse on a freshwater ecosystem varies temporally and spatially (Leroux and Loreau, 2012; Collins *et al.*, 2016). Typically, its effect on river communities is considered to be stronger in summer, when terrestrial invertebrates are more abundant, and weaker in winter, when they are less abundant (Nakano and Murakami, 2001).

Terrestrial earthworms are abundant in soils throughout the world and are high-energy food for various organisms (Macdonald, 1983; Baubet, Ropert-Coudert and Brandt, 2003). The movement of many earthworms is triggered in early winter when the temperature drops steeply (Friend, 1921; Kobayashi *et al.*, 2015), and they may enter rivers as a terrestrial resource pulse. However, to the best of our knowledge, only one study has reported the mass movement of terrestrial earthworms into streams in early winter (Kobayashi et al. 2015), and their utilization in streams has not been examined. Here, we report that terrestrial earthworms were supplied in a large numbers to the upper reaches of a small river in northern Japan in early winter and were consumed by aquatic organisms.

In the upper reaches of the Horonai River, a small spring-fed stream in northern Japan (42°40′N, 141°35′E; Fig. 1a), we observed an enormous number of terrestrial earthworms (Megascolecidae) in late November 2021 (Fig. 1b, c) during a fish tracking survey. Most seemed to be dead, some were fragmented, but some were still alive underwater. To count them, we walked through the uppermost 5320-m river reach (the survey reach) on 5 December 2021 (Fig. 1a). Further downstream it was difficult to count them because the riverscape is altered artificially (see Futamura et al. 2022 for detail). We walked upstream and counted the living and dead worms in each 100-m section. Since some dead worms were fragmented, we counted only parts with a visible clitellum. Because the worms’ spatial distribution seemed to be non-linear, we modeled their abundance by using a generalized additive model, with river section (i.e., distance from the headwaters) and life status (dead or alive) as predictors. Statistical analysis was conducted in the “mgcv” package of R v. 4.1.2 software (R Core Team, 2021).

In total, we found 740 dead and 71 live earthworms in the 5320-m survey reach. Their mean abundance was 15 ± 16.34 (mean ± SD) per 100-m section. The largest number was 68, found at 200–300 m from the headwaters. The live earthworms seemed to have been supplied to the river within 1 day, because Megascolecidae earthworms die within several hours after entering the water (Chuang and Chen, 2008). Both dead and live worms were found intensively between the headwaters and the middle reach (Fig. 1d) (GAM, *P* < 0.001; Appendix S1: Table S1). This result indicates that dead worms were not transported further downstream but were supplied intensively near the headwaters.

We observed aquatic organisms consuming the worms in the upper reaches of the river. During a fish gut contents survey conducted on 11 December 2021, we found three salmonid species that had consumed the worms: masu salmon (*Oncorhynchus masou*; Fig. 2a), rainbow trout (*Oncorhynchus mykiss*; Fig. 2b), and white-spotted char (*Salvelinus leucomaenis*; Fig. 2c). Although a previous study showed that rainbow trout consumes earthworms in spring to autumn (Kawaguchi *et al.*, 2007), it remained unknown whether fish consume them in winter. Here, we provide rare evidence that fish do, in fact, consume earthworms in early winter. Additionally, we observed aquatic invertebrates such as gammarid amphipoda (Amphipoda; Fig. 2d), planarian flatworms (Tricladida; Fig. 2e), and stonefly larvae (Plecoptera) consuming them on 7 December 2021.

The effect of terrestrial resource pulses on freshwater ecosystems has previously been considered to be strong in summer but weak in winter (Nakano and Murakami 2001). Furthermore, previous studies have focused on terrestrial arthropods, and other terrestrial invertebrates such as earthworms have received little attention. Here, we show that a large number of earthworms were supplied intensively to the upper reaches of a small river during early winter, and several aquatic organisms were consuming them. This result suggests that terrestrial earthworms play an important role in ecosystem functioning in a freshwater ecosystem in winter, when other food items are scarce.

One of our key findings is that aquatic invertebrates were consuming the worms. Although it is well documented that freshwater fish do so (Mason and MacDonald, 1982; Kawaguchi *et al.*, 2007; Inoue, Sakamoto and Kikuchi, 2013; Itakura *et al.*, 2021), to the best of our knowledge, no studies have shown utilization of earthworms by aquatic invertebrates. We observed a broad range of aquatic invertebrate taxa consuming the worms as allochthonous prey. Although terrestrial invertebrate inputs indirectly affect the aquatic invertebrate community by altering the intensity of fish predation in the food web (Nakano, Miyasaka and Kuhara, 1999), their direct effects remain unclear. This massive supply of earthworms in winter provides a unique opportunity to examine this topic. Further quantitative studies of the utilization of terrestrial resources by aquatic invertebrates are required to reveal the effect of terrestrial resource pulses on freshwater ecosystems.

Why and how did the earthworms enter the river in winter? It is possible that they were accidentally supplied to the river from the riverbank where the soil was exposed. Although the behavioral mechanism is unknown, their movement is triggered in early winter, when the temperature drops and the soil moisture declines (Friend, 1921). This could cause some to inadvertently fall from the riverbank into the river, in particular from steep sites where the soil is exposed. Our additional data support this idea, as we found denuded slopes more frequently in the upper reaches of the stream (Fig. S1), corresponding with the distribution of earthworm supply to the river. Because denuded slopes are often concreted by revetments worldwide (Grill et al. 2019), river development may have decreased the supply of worms to the river in early winter.

Large numbers of earthworms appear to be supplied continually and broadly in early winter. In the Horonai River, they seemed to be supplied for at least a few weeks, because we observed them from 18 November until 11 December (personal observations). They appear to be supplied also to other rivers in northern Japan. A previous study reported that enormous amounts of terrestrial earthworms were supplied to the small Doran River (44°48′N, 142°06′E) in early winter (Kobayashi *et al.*, 2015). We also observed earthworms entering the Yufutsu River, an adjacent tributary of the Horonai River (42°42′N, 141°33′E), on 11 December 2021 (personal observation). Thus, the terrestrial earthworm supply could be a common phenomenon in early winter and may play an important role in northern temperate freshwater ecosystems.

In summary, we found that many terrestrial earthworms were supplied to the upper reaches of a river in early winter and aquatic organisms were consuming them. Winter is severe for aquatic organisms when prey availability is low and metabolic costs are high (Huusko *et al.*, 2007; Sutton *et al.*, 2021). Thus, storing energy before winter is key to survival during winter (Hurst, 2007). Seasonal access to high-energy prey in early winter could provide some aquatic organisms with substantial energy benefits to survive the winter, shaping survivorship and having spillover effects on populations, communities, and ecosystem functioning. In particular, intense earthworm subsidies to the upper stream may increase the heterogeneity of consumer abundance along a stream gradient and shape the food web structure. Our observation emphasizes the need for further studies on the effects of terrestrial resource pulses on freshwater ecosystems, especially in winter, to deepen our understanding of terrestrial–aquatic linkages.

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# ORCID

Ryo Futamura: https://orcid.org/0000-0001-8128-3476

Chiharu Furusawa: https://orcid.org/0000-0001-6928-0571

Hisanori Okamiya: <https://orcid.org/0000-0001-7708-2962>

## Data Accessibility

The data will be uploaded to Figshare after acceptance

**Competing Interests**

We have no conflict of interest.

**Author Contribution**

# R.F., C.F. and H.O. conceived the ideas. All authors designed the methodology and collected the data. R.F. and H.O. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication

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# Figure legends

**Figure 1** (a) Map and representative photograph of the survey reach in the Horonai River. The survey reach (the uppermost 5320 m of the river) is shown in bold. (b) Terrestrial earthworms lying on the riverbed (black arrows). (c) Earthworms accumulating in a slow-flowing pool. (d) Distribution of dead (blue) and live (orange) worms along the survey reach: each point indicates the total abundance of worms in each 100-m section. The regression curve was fitted using a generalized additive model. Gray shading shows the 95% confidence interval.

**Figure 2** Aquatic organisms that had consumed terrestrial earthworms. Salmonid fish species: (a) masu salmon (*Oncorhynchus masou*), (b) rainbow trout (*O. mykiss*), (c) white-spotted char (*Salvelinus leucomaenis*). Benthic invertebrates (black arrows): (d) gammarid amphipod (Amphipoda), (e) planarian flatworm (Tricladida)