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Effects of coarse woody debris with morphological complexity on organic matter retention and the aquatic biodiversity in a stream ecosystem

Mana Honda

t95k24221@stu.tamagawa.ac.jp

Tamagawa University College of Agriculture Graduate School of Agriculture: Tamagawa Daigaku Nogakubu Daigakuin Nogaku Kenkyuka https://orcid.org/0009-0001-0685-2314

Yoshi Minami

Tamagawa University College of Agriculture Graduate School of Agriculture: Tamagawa Daigaku Nogakubu Daigakuin Nogaku Kenkyuka

Kurumi Yoshinaga

Tamagawa University College of Agriculture Graduate School of Agriculture: Tamagawa Daigaku Nogakubu Daigakuin Nogaku Kenkyuka

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Abstract

To clarify how morphological differences in Coarse woody debris (CWD) influence riparian ecosystems, we compared physical environments and leaf litter retention around CWD with-branches (hereafter, with-branches sections) and CWD without-branches (hereafter, without-branches sections) in the headwaters of the Kushiro River, eastern Hokkaido, Japan, and examined whether differences occurred in aquatic biota. Benthic invertebrate assemblages differed between with-branches and without-branches sections during the flood season. Several predator taxa were observed in with-branches sections, whereas grazer taxa dominated without-branches sections. Assemblage composition in with-branches sections was influenced by the accumulation of particulate organic matter (POM), while that in without-branches sections was associated with gravel aggregation. In with-branches sections, both bottom-up and top-down effects influenced biodiversity index. The accumulation of POM in with-branches sections originated from litter directly trapped by CWD, and litter-associated invertebrate assemblages were also diverse. The presence of both types of woody debris in the creek enhances benthic invertebrate diversity, highlighting the importance of habitats that locally concentrate substrates, particularly gravel and POM, and suggesting that introducing, retaining, or ensuring the continuous input of diverse woody debris is crucial for the conservation of aquatic and riparian biota.

Introduction

Wetland environments have been affected by a wide range of human activities, including the exploitation of natural resources, urbanization, dam construction and groundwater abstraction, grazing and agriculture, and the introduction of non-native species (Sayer et al. 2025). Freshwater ecosystems support a disproportionately large number of threatened species compared with other ecosystems, and this trend is particularly pronounced in river ecosystems (Sayer et al. 2025). Therefore, the conservation of river ecosystems is of critical importance. River ecosystems are strongly influenced by dam construction, channelization, and riparian development (Poff et al. 1997; Bunn and Arthington 2002; Allan 2004). In particular, riparian development such as the stabilization of flow regimes and the removal of riparian vegetation reduces the supply of organic matter to streams, thereby affecting food-web structure through bottom-up processes (Richardson and Béraud 2014; Mor et al. 2018). These effects have been shown to extend to riparian predator communities via changes in aquatic insect production (Nakano and Murakami 2001), indicating that river food webs function across broad spatial scales that include not only the stream channel but also surrounding terrestrial ecosystems.

Organic matter inputs from riparian forests to streams provide an important energy source that supports aquatic food webs (Hall et al. 2000), while large organic matter alters the physical river environment and provides favorable habitats for aquatic organisms (Flebbe and Dolloff 1995). Organic matter inputs are commonly classified by size: fallen trees or large woody materials transported by water are referred to as coarse woody debris (CWD) or large woody debris (LWD), whereas leaf litter and progressively smaller organic particles are termed coarse particulate organic matter (CPOM) and fine particulate organic matter (FPOM), respectively (Yoshimura et al. 2006). In headwater streams, narrow channel widths and

closed riparian canopies result in abundant inputs of CPOM. These materials are subsequently broken down by water flow and consumers such as shredders and transported downstream (Vannote et al. 1980; Webster and Benfield 1986). Consumers inhabiting downstream reaches primarily utilize FPOM produced in upstream sections (Vannote et al. 1980).

For organic matter to be utilized by consumers such as shredders, it must be retained within the stream channel. The retention of litter is influenced by environmental complexity, including trapping by coarse substrates such as stones and branches, microtopography of the streambed, and retention by woody debris (Speaker et al. 1984; Lepori et al. 2005). In particular, litter retained in pools is less susceptible to removal during floods because flow velocity decreases toward the center of pools (Kishi et al. 1999; Kobayashi et al. 2011). Pools are known to form preferentially in meandering sections of rivers (Lofthouse and Robert 2008), but they can also be created by in-channel obstructions that increase hydraulic resistance, with pool formation by woody debris being especially well documented (Montgomery et al. 1995). Thus, woody debris indirectly contributes to litter retention. However, even in areas where pools are not well developed, litter can still be retained in reaches with abundant woody debris (Kishi et al. 1999). Woody debris also directly traps litter and reduces the loss of organic matter during seasonal floods, such as those occurring in spring, thereby buffering seasonal biases in organic matter supply (Speaker et al. 1984; Kishi et al. 1999; Lepori et al. 2005).

Litter retention is also influenced by the physical characteristics of the litter itself. Small and dense FPOM tends to accumulate in pool centers, whereas larger litter is more readily trapped by obstructions and therefore accumulates in riffles (Kobayashi et al. 2011). As a result, litter of differing quality and size is distributed heterogeneously among river habitats. In such environments, suitable sizes and qualities of litter do not necessarily accumulate in habitats accessible to particular detritivorous consumers such as shredders (Kobayashi et al. 2011). For example, small-bodied benthic insects such as Plecoptera, which experience less drag and can cling to leaf surfaces using tarsal claws, feed on litter in riffles, whereas large-bodied benthic insects such as Trichoptera are more susceptible to hydraulic forces and therefore feed on litter retained in low-velocity habitats such as pools. Fish also utilize similar habitat types (Everett and Ruiz 1993). By forming pools, woody debris provides fish not only with food resources such as insects but also with refugia from high flow velocities and shelter from predators (Bisson et al. 1982).

Roni et al. (2008) reported, based on studies conducted in North America, that reconnection of isolated water bodies, restoration of floodplains, and improvement of in-channel habitats are effective for enhancing habitat quality and biodiversity. Among these approaches, in-channel habitat enhancement through the placement of rocks and wood to increase habitat heterogeneity is the most widely implemented. MacInnis et al. (2008) reported that the installation of woody debris promoted the formation of pools and improved spawning habitats for salmon. Although this approach often elicits biological responses more rapidly than large-scale interventions such as dam removal or floodplain reconnection, outcomes are variable, and long-term monitoring and site-specific evaluations are required (Roni et al. 2008). In some cases, wood placement aimed at conserving specific target species has

resulted in population declines of other species (Langford et al. 2012). Consequently, studies and management practices that consider not only physical habitat but also biological responses at the community level, rather than focusing on single species, are increasingly needed (Richardson 2024).

In Japan, river research has historically focused on flood control and disaster prevention (Takahasi and Uitto 2004). In recent years, however, ecosystem-based river management approaches such as *Tashizen-kawazukuri* ("nature-oriented river management") have gained importance (Ministry of Land, Infrastructure, Transport and Tourism 2024), and woody debris has been studied from ecological perspectives. Compared with rivers in many regions outside Japan, Japanese rivers are generally narrower, and riparian forests are dominated by deciduous rather than coniferous species (Sakio et al. 1995). In low-gradient headwater streams in Hokkaido, even woody debris with relatively small diameters can generate well-developed pools due to narrow channel widths, perpendicular orientations of woody debris relative to flow, and fine streambed substrates (Abe and Nakamura 1996; Urabe and Nakano 1998). Yoshinaga et al. (2022) experimentally installed woody debris in a natural stream and observed increases in benthic invertebrate abundance near the debris, concluding that particulate organic matter trapped by the debris played a key role. Nevertheless, practical implementation has been limited to a small number of rivers in Hokkaido (Takayama et al. 2011), and nationwide river management often relies instead on gabions filled with gravel.

Although research on woody debris has progressed, no studies have examined how morphological differences in woody debris influence river ecosystems. In general, branches are more easily transported by flow, and most woody debris that remain in streams for extended periods consists only of the main trunk (Abe and Nakamura 1996). However, elucidating organic matter dynamics associated with newly supplied woody debris is important because it can demonstrate the ecological significance of periodic woody debris inputs and contributes to the conservation of headwater ecosystems. While some studies have reported the physical effects of debris complexes in which large logs trap smaller branches (Haga et al. 2017), no studies have investigated temporal changes in biological responses following debris installation. Woody debris with more complex structures, such as debris with branches, is expected to enhance organic matter retention by enabling both direct and indirect retention of litter of diverse sizes and qualities across various in-channel habitats. If the organic matter retention function of woody debris can be quantified and its bottom-up effects and contributions to biodiversity enhancement demonstrated, more ecologically informed riparian conservation strategies could be developed. Therefore, the objective of this study was to determine whether morphological characteristics of woody debris influence litter retention and biodiversity in headwater river ecosystems in Hokkaido, Japan.

Methods

1. Study area

The study was conducted in a tributary of the Kushiro River in eastern Hokkaido, Japan (hereafter referred to as the Birunai Creek, Fig. 1).

The Kushiro River is one of the largest lowland rivers in eastern Hokkaido, Japan, with a catchment area of approximately 2,500 km² and a gently sloping. The river drains from volcanic uplands through extensive wetlands before discharging into the Pacific Ocean (Ministry of Land, Infrastructure, Transport and Tourism 2025). The riverbed gradient in the upstream region is extremely gentle (1/1,000), and the river is characterized by a meandering channel (Sakaguchi et al. 2020). No major weirs or dams are present along the main stem (Ministry of Land, Infrastructure, Transport and Tourism 2025), and the river retains a largely natural flow regime.

Riparian forests in the upper Kushiro River are mainly composed of *Salix* spp. *Betula platyphylla* and *Alnus hirsuta*. Shrub vegetation along the riverbanks includes *Spiraea salicifolia*, and the understory is dominated by *Sasa nipponica*, *Urtica platyphylla*, and *Carex* spp. The aquatic plant *Ranunculus nipponicus* occurs on the riverbed, and fish species such as *Oncorhynchus masou*, *Salvelinus leucomaenis* and *Tribolodon sachalinensis* inhabit the river (Ministry of Land, Infrastructure, Transport and Tourism 2025). Terrestrial fauna includes mammals such as *Cervus nippon* and *Vulpes vulpes*, as well as large birds including *Grus japonensis*.

Teshikaga Town, located in the headwaters of the Kushiro River, lies in eastern Hokkaido, bordered by the central mountain range to the west and north and facing the Pacific Ocean influenced by the Oyashio Cold Current to the south. The region belongs to the eastern Pacific climatic zone (Ministry of Land, Infrastructure, Transport and Tourism 2025). The climate is cool and humid, characterized by frequent fog formed when warm southeasterly winds in summer are cooled over the cold ocean current (Ministry of Land, Infrastructure, Transport and Tourism 2025). According to the Japan Meteorological Agency (2025), the mean annual air temperature from 2010 to 2020 was 5.6°C, with a maximum of 34.4°C and a minimum of − 24.9°C. Mean annual precipitation was 1,091 mm, and the maximum snow depth reached 118 cm in the Kawayu area. Heavy rainfall occurs during limited periods, mainly due to frontal systems from early summer to summer and typhoons from summer to early autumn (Ministry of Land, Infrastructure, Transport and Tourism 2025).

The Birunai Creek is a small, low-gradient stream approximately 3 m wide, located in Biruwa, Teshikaga Town (43°33' N, 144°22' E; Fig. 1). The study reach is straight with few large cobbles. Because the river is closely associated with riparian forest, it is heavily shaded, and fallen trees caused by strong winds are frequently observed. The dominant riparian tree species are similar to those in the main stem.

2. Methods

2.1. Experimental design

From upstream to downstream, the study reach was divided into a control reach (hereafter, C reach), a reach with CWD without branches installed in summer 2021 (hereafter, without-branches sections), and a reach with CWD with branches installed in summer 2023 (hereafter, with-branches sections) (Fig. 1). These reaches were arranged consecutively with 2 m spacing, resulting in a total reach length of 46 m.

2.2. Installation of branched CWD

Branched CWD used in this study consisted of crown sections of white birch (*Betula platyphylla*) and willow species (*Salix* sp.), which are components of the riparian forest along the Birunai Creek. To fit the approximately 3 m channel width, the logs were cut to a length of approximately 4 m using a chainsaw. The diameter at the basal end of the trunk ranged from 7 to 10 cm. After removing naturally accumulated woody debris when present, two birch logs and two willow logs were installed at 6 m intervals (Fig. 2A). The basal end of each log was fixed to the right bank. Leaf litter directly accumulated on the without-branches sections was removed prior to the experiment. The unbranched CWD units were labeled U (upstream, φ10 cm), M (middle, φ20 cm), and D (downstream, φ30 cm), and the branched CWD units were labeled B-i (Birch-i), B-ii (Birch-ii), W-i (Willow-i), and W-ii (Willow-ii).

2.3. Sampling points

Physical environmental variables were measured at the intersections of channel-parallel lines (a–c) and channel-perpendicular lines (1–6), indicated by black circles in Fig. 2B (hereafter, environmental measurement points). Benthic invertebrates were collected at intermediate points between environmental measurement points, indicated by white circles (hereafter, biological sampling points). Line-a passed near submerged branches of the CWD shown in Fig. 2A, line-b ran through the center of the channel, and line-c was located near the fixed basal trunk.

2.4. Physical environment

To compare environmental conditions between with-branches and without-branches sections, physical variables were measured at environmental measurement points in the experimental and control reaches. Riverbed topography was recorded by measuring water depth (m) from the water surface to the riverbed using a ruler. River water level (cm) was also measured as the difference between the water surface and a reference line installed on the riverbank. Flow velocity (cm s^{-1}) was measured using a propeller-type current meter (Global Water CGW-FP101, Kenek) at both just below the water surface (hereafter, surface-layer) and just above the riverbed (hereafter, bottom-layer) for 20 s at each point, and mean values were calculated. Measurements were not conducted at points where the propeller could not be inserted due to accumulated litter or CWD.

Substrate composition was assessed using a 50 cm × 50 cm quadrat centered on each environmental measurement point. Coverage (%) of sand (< 5 mm), small gravel (5–20 mm), medium gravel (20–40 mm), large gravel (> 40 mm), and riverbed organic matter including litter and humus (particulate organic matter; POM) was recorded following Yoshinaga et al. (2022). The riverbed was photographed using an underwater camera (WG-70, RICOH) mounted on a viewing box, and coverage was calculated from images after the survey.

2.5. Benthic invertebrates

To examine whether differences in litter accumulation affected benthic invertebrate diversity, benthic invertebrates were collected in the experimental and control reaches. Substrates within a 30 cm × 30 cm area centered on each biological sampling point were disturbed two to three times using a rake or foot, and dislodged materials were collected downstream using a D-frame net with 1 mm mesh. Benthic invertebrates were sorted using forceps and fixed in 10% formalin solution. After fixation, specimens were identified under a stereomicroscope. Based on Maruyama and Takai (2000), Takemon (2005), and Kawai and Tanida (2018), organisms were classified into functional feeding groups, and assemblages were compared between with-branches sections and without-branches sections. Scientific names followed Kawai and Tanida (2018).

2.6. Organisms inhabiting litter accumulated directly on CWD

To clarify the composition of organisms inhabiting litter directly accumulated on CWD, including organisms other than benthic invertebrates, approximately 2700 cm^3 of litter accumulated on each CWD sections was collected. Organisms were then fixed and identified following the same procedures used for biological sampling points, and assemblage composition was compared among reaches.

2.7. Litter directly accumulated on CWD

Litter directly accumulated on CWD was distinguished from POM and its area (m^2) was calculated using ImageJ based on aerial images obtained by an unmanned aerial vehicle (Mavic 2 Pro, DJI).

2.8. Dye tracer experiment

To assess flow disturbance around CWD, dye tracer experiments were conducted in the experimental and control reaches. A capful of biodegradable fluorescent tracer dye (Techno International Co., Ltd.) was released approximately 1 m upstream of the CWD, and its movement was recorded from above using an unmanned aerial vehicle and from within the river using underwater cameras. Underwater cameras were installed both upstream and downstream of the CWD at positions 25 cm away from the log, oriented toward the flow so that the CWD was visible.

2.9. Data analysis

To compare benthic invertebrate assemblages collected simultaneously in the branched and without-branches sections, TWINSPAN (Two-Way Indicator Species Analysis; PC-ORD ver. 6.0, Wild Blueberry Media LLC) was conducted, excluding unidentified taxa. To examine which environmental factors influenced the resulting assemblage groups, principal component analysis (PCA; R 4.2.3, FactoMineR) was used to extract environmental variables characterizing with-branches, without-branches and control sections. Path analysis (R 4.2.3, lavaan) was then conducted. Among environmental variables, the top three variables with the highest combined contributions to the first and second principal components were selected. Pools are characterized by deeper water and reduced near-bed flow velocity relative to surface flow (Robert 1997; Yoshinaga et al. 2022). Using this hydraulic characteristic, we constructed a continuous variable (“pool”) defined as the ratio of surface-layer to bottom-layer flow velocity. Higher

values indicated more developed pools. Small and medium gravel were combined into a single variable, hereafter referred to as pebble. Path analysis was used to examine causal relationships among environmental variables, benthic invertebrates, and overall biological diversity in each section of experimental and control reaches. Benthic invertebrate diversity was evaluated using Simpson's diversity index.

$$D = 1 - \sum_{i=1}^{s} \left(\frac{n_i}{N} \right)^2$$

D; Simpson's diversity index, S; the number of taxa, n_i; the number of individuals of taxon i, N; the total number of individuals

Comparisons of the number of the organisms inhabiting litter accumulated directly on CWD between branched and without-branches sections were conducted using the Mann–Whitney U test.

Seasonal comparisons of POM coverage and directly accumulated litter were conducted using Wilcoxon signed-rank tests based on mean values across all measurement periods for each CWD sections. Comparisons of POM coverage and directly accumulated litter between branched and without-branches sections were conducted using the Mann–Whitney U test. To evaluate whether seasonal effects differed between branched and without-branches sections, linear mixed models (LMMs; R 4.2.3, lme4) were applied, with sub-reach and year as random effects and season and reach as an interaction term.

2.10. Study period

The study was conducted from 2020 to 2025, mainly during the high-flow and leaf-fall seasons. Physical environmental measurements were conducted at least two months after installation of the branched CWD. To compare biological assemblages after stabilization of riverbed conditions and benthic invertebrate colonization, benthic invertebrates were collected during the leaf-fall season in 2024 and the high-flow season in 2025. The high-flow season occurs in spring (around May), and the leaf-fall season in autumn (around October).

Results

1. Benthic invertebrates and habitat conditions

The TWINSPAN results for benthic invertebrates in the with-branches sections and the without-branches sections during the leaf-fall season and the flood season are shown in Fig. 3.

During the leaf-fall season, benthic invertebrates were classified into three groups, and clusters from both sections were intermingled. In contrast, during the flood season, benthic invertebrates were classified into four groups, and clusters from the two sections were clearly separated. In the flood season, predator taxa were more abundant in the with-branches sections, whereas grazers were more abundant in the without-branches sections. In the with-branches sections, except for site B-i, community

composition differed between sites located upstream and downstream of individual CWD (i.e., sites aggregated on either side of a CWD). The control section showed a benthic assemblage similar to that of the upstream-side sites in the without-branches sections.

The PCA results for benthic invertebrates in the with-branches sections and the without-branches sections during the leaf-fall and flood seasons are shown in Fig. 4. Table 1 summarizes the contribution rates and the seven environmental variables (bottom-layer velocity, water depth, pool, sand, pebble, POM, and *Ranunculus nipponicus*).

In the with-branches sections during the leaf-fall season, PC1 was strongly correlated with water depth (r = 0.77), pebble (r = − 0.76), sand (r = − 0.72), POM (r = 0.70), and bottom-layer velocity (r = − 0.68), whereas PC2 was strongly correlated with *R. nipponicus* (r = 0.85). Sites W (W-i and W-ii) were characterized by sandy and pebbly substrates, whereas sites B (B-i and B-ii) showed accumulation of POM. In the without-branches sections and the control section, PC1 was strongly correlated with bottom-layer velocity (r = − 0.87), pool (r = 0.83), POM (r = 0.73), and water depth (r = 0.72), while PC2 was strongly correlated with sand (r = 0.81), pebble (r = − 0.82), and *R. nipponicus* (r = 0.70). Sites U, M, and D were classified as pools; site U was sandy, whereas sites D and M were pebbly. Measurement lines near the CWD at site M showed high POM accumulation. In the with-branches sections during the flood season, PC1 was strongly correlated with sand (r = − 0.78), POM (r = − 0.78), *R. nipponicus* (r = 0.66), and bottom-layer velocity (r = − 0.63), while PC2 was strongly correlated with pebble (r = 0.93). Sites W were characterized by sandy substrates, and measurement lines near the CWD at both W and B sites showed high POM accumulation. In the without-branches sections and the control section, PC1 was strongly correlated with water depth (r = 0.93), sand (r = − 0.88), POM (r = 0.78), and bottom-layer velocity (r = − 0.66), whereas PC2 was strongly correlated with pool (r = − 0.70), *R. nipponicus* (r = 0.67), and pebble (r = 0.65). Measurement lines in the control section were characterized by relatively high flow velocity. Sites U and M were pools with low flow velocity, and POM accumulated at measurement lines located close to CWD.

In the with-branches sections during the flood season, the top three environmental variables were pebble, sand, and POM. Path analysis examining causal relationships among these environmental variables, benthic invertebrate groups derived from TWINSPAN, and Simpson's diversity index showed that benthic invertebrate group 1 was strongly positively correlated with POM (Simuliidae, r = 0.60; Tricladida, r = 0.43; Perlodidae, r = 0.75) and negatively correlated with sand (Tricladida, r = − 0.47; Acari, r = − 0.45). Benthic invertebrate group 3 also showed a strong positive correlation with POM (Perlodidae, r = 0.75). Simpson's diversity index showed a strong positive correlation with Perlodidae. In the without-branches sections during the flood season, the top three environmental variables were pebble, pool, and bottom-layer velocity. Path analysis showed that benthic invertebrate group 2 was positively correlated with pebble (Heptageniidae, r = 0.51), whereas benthic invertebrate group 4 showed no correlation with any environmental variable. Simpson's diversity index also showed no correlation with either biological or environmental variables.

2. Organisms associated with litter directly retained by CWD

During the flood season, species richness was higher in the with-branches sections (12.0 ± 4.0, n = 4) than in the without-branches sections (4.0 ± 4.0, n = 2). In the with-branches sections, five predator taxa (Hirudinoidea, Perlodidae, Rhyacophilidae, Tabanidae, and Araneae) were recorded, whereas only Rhyacophilidae was recorded in the without-branches sections. Adult Coleoptera were observed only in the with-branches sections (Hydraenidae, Hydrophilidae, and Dryopidae). In addition, soil-associated organisms (Entomobryidae) and final-instar Lepidostomatidae were observed in the with-branches sections. As in the flood season, during the leaf-fall season, Coleoptera (Hydraenidae and Scirtidae) were more abundant in the with-branches sections (42.8 ± 31.4, n = 5) than in the without-branches sections (14.0 ± 8.4, n = 4) (U test, $p = 0.032$). Predators (Tricladida, Perlodidae, Rhyacophilidae, Phryganeidae, Pediciidae, Tabanidae, Araneae) were also more abundant in the with-branches sections (9.8 ± 3.8, n = 5) than in the without-branches sections (6.3 ± 4.6, n = 4), although the difference was not statistically significant (U test, $p > 0.05$). At site B-i, small detritivores such as Oligochaeta and Chironomidae tended to be abundant. Lepidostomatidae and Phryganeidae were observed in both sections.

3. POM and litter directly retained by CWD

POM cover rate from the leaf-fall season of 2024 to the leaf-fall season of 2025 was significantly higher during the leaf-fall season (26.0 ± 6.0) than during the flood season (15.1 ± 4.2)(Wilcoxon signed-rank test, $p = 0.02$)POM cover rate did not differ between the with-branches sections (24.0 ± 2.9, n = 4) and the without-branches sections (22.8 ± 3.1, n = 3) (U test, $p > 0.05$). At site B-i, POM cover tended to be higher at downstream-side sites than at upstream-side sites relative to the CWD. Even in the control sections, a certain amount of POM was presentleaf-fall season 14.6, flood season 14.1

The area of litter directly retained by CWD (m^2) from the leaf-fall season of 2023 to the leaf-fall season of 2025 was significantly higher during the leaf-fall season (0.40 ± 0.30, n = 7) than during the flood season (0.040 ± 0.033, n = 7) (LMM, $p = 0.003$; Wilcoxon signed-rank test, $p = 0.02$; Fig. 5). No significant difference was detected between the with-branches sections (0.34 ± 0.22, n = 4) and the without-branches sections (0.14 ± 0.037, n = 3) (LMM: area, $p > 0.05$; season × area, $p > 0.05$; U test, $p > 0.05$). However, during the high-flow season, the with-branches sections (0.058 ± 0.024, n = 4) captured more litter than the without-branches sections (0.018 ± 0.030, n = 3) (U test, $p > 0.05$).

5. Dye experiment

Dye movement within the CWD sections is shown in Fig. 6, with representative images from the with-branches sections and the without-branches sections.

At sites U and M, the dye passed through with little retention. At site D, the dye split toward the left bank and the channel center and passed downstream over a longer period. Underwater observations showed

that most dye passed just below the water surface at the channel center but gradually accumulated in the center of the pool before dispersing downstream. At site B-i, the dye did not pass through the CWD but instead bypassed it via a backwater area along the left bank. At site B-ii, the dye passed through all areas except measurement line b. At sites B-ii and W (W-i and W-ii), dye tended to be retained downstream of submerged portions of the CWD; in particular, at site W-ii, eddies formed and retained the dye for an extended period. At sites W, dye accumulated in a small pool formed upstream of the CWD and, downstream, was retained throughout the water column from the surface to the riverbed.

Discussion

Both CWD with branches and without branches were shown to exert distinct ecological functions by enhancing substrate heterogeneity during high-flow periods, thereby influencing benthic invertebrate assemblages. Among predators occurring in the with-branches sections, Tricladida and Perlodidae were likely dependent on the high availability of particulate organic matter (POM), which is a characteristic environmental feature of this section. Tricladida and Perlodidae are known to prey on small benthic invertebrates such as Oligochaet, which primarily feed on fine particulate organic matter (FPOM) (Takemon 2005). Because Oligochaet were particularly abundant downstream of B-i and upstream of W (W-i and W-ii) within the with-branches sections (Table 2), this section can be characterized as an environment where humic materials and FPOM tend to accumulate. Analyses of riverbed morphology based on water depth revealed that the without-branches sections formed a continuous pool, whereas the with-branches sections consisted of multiple small-scale pools. In addition, dye-tracer experiments demonstrated that dye residence time was longer in the with-branches sections than in the without-branches sections. Although the total amount of benthic organic matter did not differ between sections, differences in riverbed complexity likely influenced the size and retention dynamics of POM. In contrast, gravels were aggregated in the without-branches sections. The frequent occurrence of Heptageniidae, which graze algae attached to gravels (Takemon 2005), suggests that algal-covered gravels were abundant in without-branches section. Substrate grain size is closely associated with the accumulation and structure of periphytic algae, and larger substrates tend to support thicker algal assemblages (Albariño et al. 2022).

The distinct benthic invertebrate assemblages formed in this manner contributed to an overall increase in diversity across CWD sections. This pattern can be explained not only by bottom-up effects but also by top-down effects. At sampling sites where Perlodidae were absent, Chironomidae dominated, while Leptophlebiidae—another FPOM feeder—were scarce. In contrast, at sites where Perlodidae were present, the abundance of Leptophlebiidae was comparable to that of Chironomidae (Table 2). Ceneviva-Bastos et al. (2017) reported that litter addition during river restoration in degraded systems led to dominance by omnivorous insects alone, without enhancing biodiversity. In the present study, however, installation of CWD with branches retained organic matter of various sizes, resulting in an increase in diverse detritivores. Furthermore, the attraction of predators such as Perlodidae enhanced biodiversity through top-down regulation. Although biodiversity in the without-branches sections was lower than in

the with-branches sections, the presence of taxa unique to the without-branches sections also contributed to diversity at the reach scale.

The presence of branches enabled the local retention of substantial amounts of litter even during high-flow periods, when overall litter availability was limited. For assemblages characteristic of the with-branches sections during high-flow periods, not only POM retained on the riverbed but also litter directly trapped by CWD is likely to be important. Long-term retention of litter facilitates fungal colonization (Chung and Suberkropp 2008), which in turn may increase aquatic insects that feed on fungi. In addition, litter captured directly by branched CWD provides habitat not only for invertebrates inhabiting the riverbed but also for organisms such as adult Coleoptera, thereby contributing to the expansion of available habitats within the river ecosystem. Moreover, the study in forested wetlands have shown that woody debris supports not only aquatic invertebrates but also diverse non-aquatic arthropods, suggesting that its ecological role extends beyond the stream channel itself (Braccia and Batzer 2001).

Implications for maintaining healthy river environments

The presence of both CWD with branches and CWD without branches in rivers was shown to enhance benthic invertebrate diversity, highlighting the importance of environments where substrates, particularly gravel and POM, are locally concentrated. Supplementary surveys further suggested that CWD provides critical food resources and habitats, such as pools and perching sites, for fish, mammals, and birds, emphasizing its importance across the entire riparian ecosystem.

If the findings of this study are applied to freshwater conservation, it is necessary to retain or introduce diverse forms of CWD that reflect the variety of ways organisms utilize woody debris, particularly with respect to inundation depth and branch complexity considering human safety may yield substantial benefits. When applied to rivers overseas, which are often wider than those in Japan, such measures are expected to be particularly effective in tributaries.

In the supplementary mainstem survey, we identified meander bends adjacent to agricultural land, where the number of CWD pieces that had fallen vertically into the channel was lower than in other meander bends. Reduction in the extent of riparian forests due to agricultural development at meander bends is likely to constrain the sustained recruitment of CWD into river channels. Branched CWD represents relatively recently supplied woody material, highlighting the importance of continuous CWD input for maintaining its ecological functions. Therefore, conserving riparian forest buffers in parallel (Richardson et al. 2012) is essential to sustain long-term CWD recruitment.

Uno et al. (2026) emphasized the need to move beyond studies and conservation efforts focused solely on specific habitats and instead to integrate interactions among multiple habitats, riverine landscapes, and organisms. They further proposed clear conservation goals aimed at ensuring long-term ecosystem stability and sustainability through the restoration of natural river functions. In this context, integrated

conservation that includes river environments capable of sustaining continuous CWD recruitment is strongly recommended.

Declarations

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Data Availability

The datasets generated during the current study contain sensitive information related to specific sampling locations and habitats. Due to conservation considerations and the contextual nature of the data, they are not publicly available at this stage. However, the data are available from the corresponding author upon reasonable request, subject to appropriate ethical and conservation considerations.

Competing Interests

The authors declare that they have no competing interests.

Author Contributions

M.H. designed the study, conducted field surveys, performed data analyses, and wrote the manuscript.

Y.M. provided supervision and contributed to study design and interpretation of the results.

K.Y. conducted earlier field surveys and contributed data used in this study.

All authors reviewed and approved the final manuscript.

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Tables

Tables 1 to 3 are available in the Supplementary Files section.

Figures

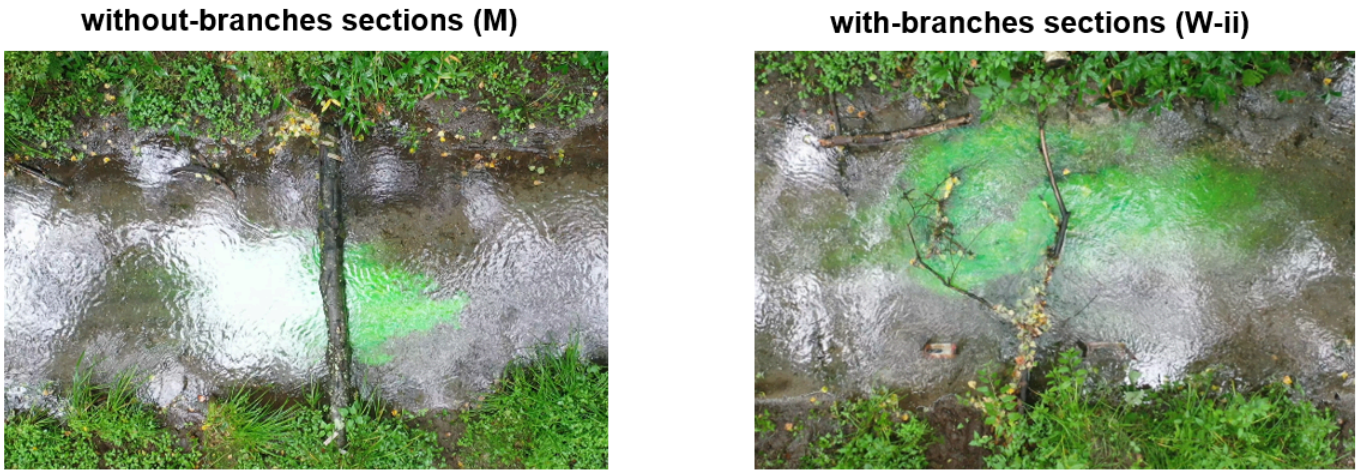


Figure 1

The Birunai Creek, a tributary flowing through the Birunai Research Forest in Teshikaga Town, eastern Hokkaido, Japan (modified from the Geospatial Information Authority of Japan map, 2025)

The main study reach consisted of these three sections: coarse woody debris without branches sections (blue outlines) installed in 2021, CWD with branches sections (green outlines) installed in 2023, and a control section (gray outlines). Aerial photographs of the main study reach were taken during the flood season in 2024 from an altitude of 100 m using an unmanned aerial vehicle (photographs by Yokokura).

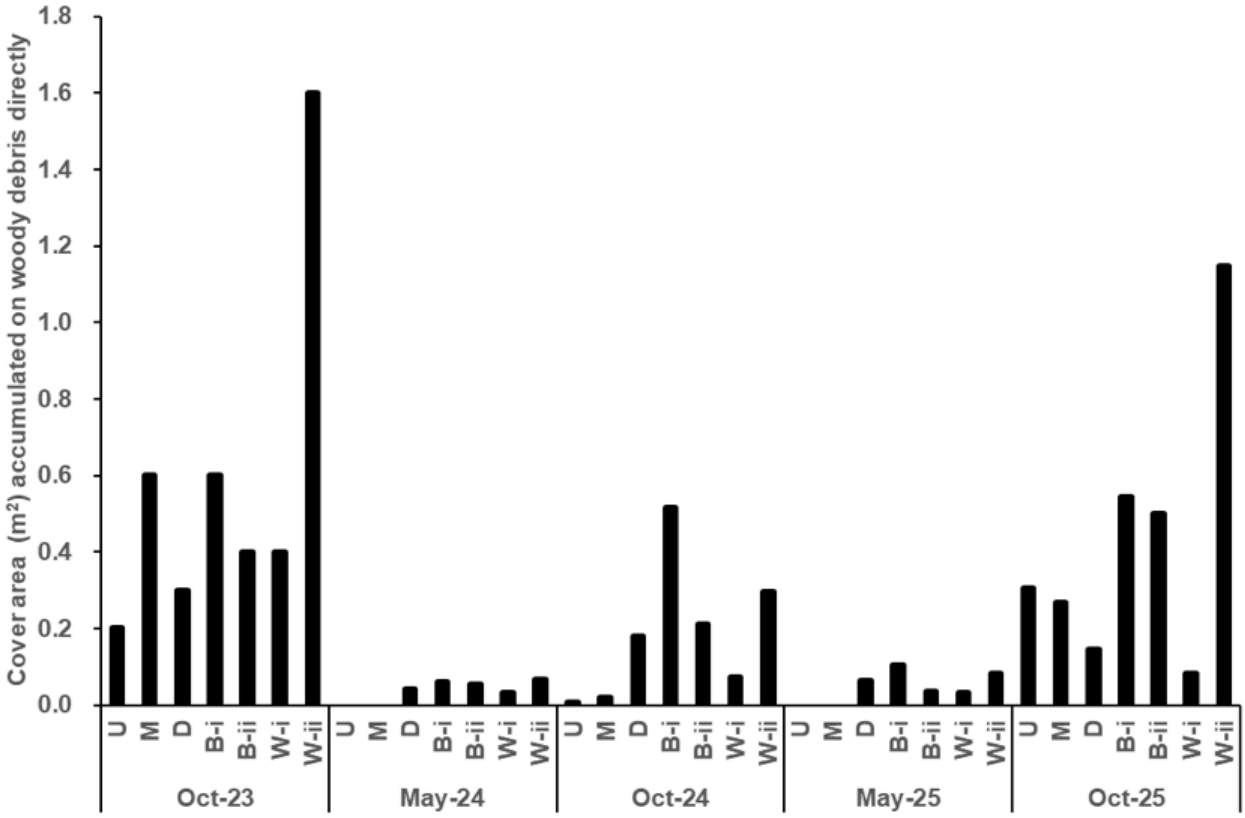


Figure 2

Installation of branched woody debris and placement of measurement points

Panel A shows the installation of woody debris, and B presents a schematic diagram of the installed transects and measurement points. The red square in A indicates the measurement area of a single section. In schematic C, black circles at the intersections of transects parallel to the flow (a–c) and perpendicular to the flow (1–6) indicate environmental measurement points, whereas white circles indicate biological sampling points.

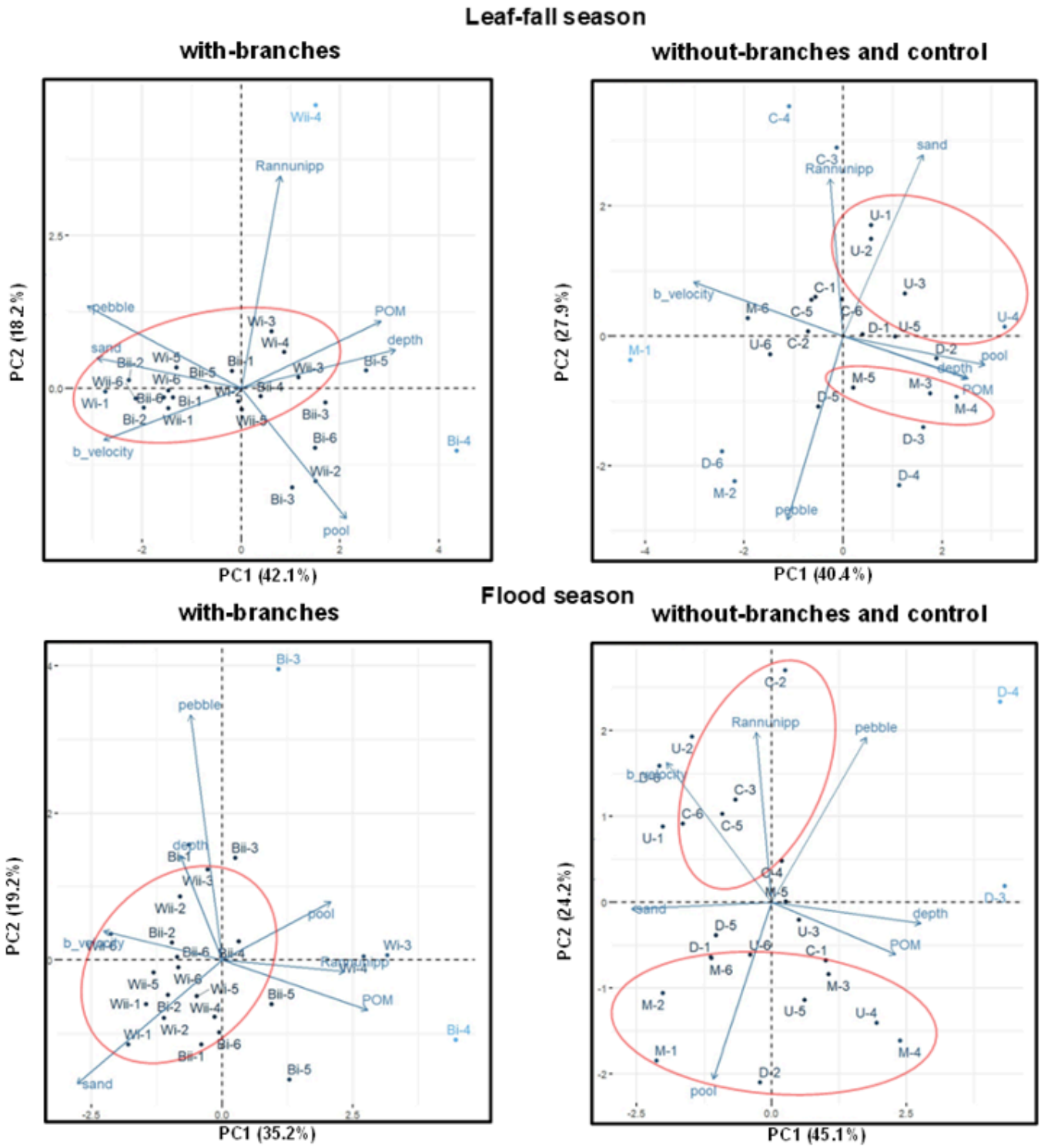


Figure 3

TWINSPAN classification of benthic invertebrates in with-branches and without-branches sections

The resulting benthic invertebrate groups are distinguished by numbers. Taxa are arranged in order of indicator strength and are shown at the family level. Measurement areas aggregated for each benthic invertebrate group are listed on the right side of the figure. Positions are indicated for each section name as areas upstream of the woody debris (u; total abundance from transects 1–3) or downstream of the

woody debris (d; total abundance from transects 4–6). Ev. indicates eigenvalues. Functional feeding groups are shown in Table 3. See Table 2 for details.

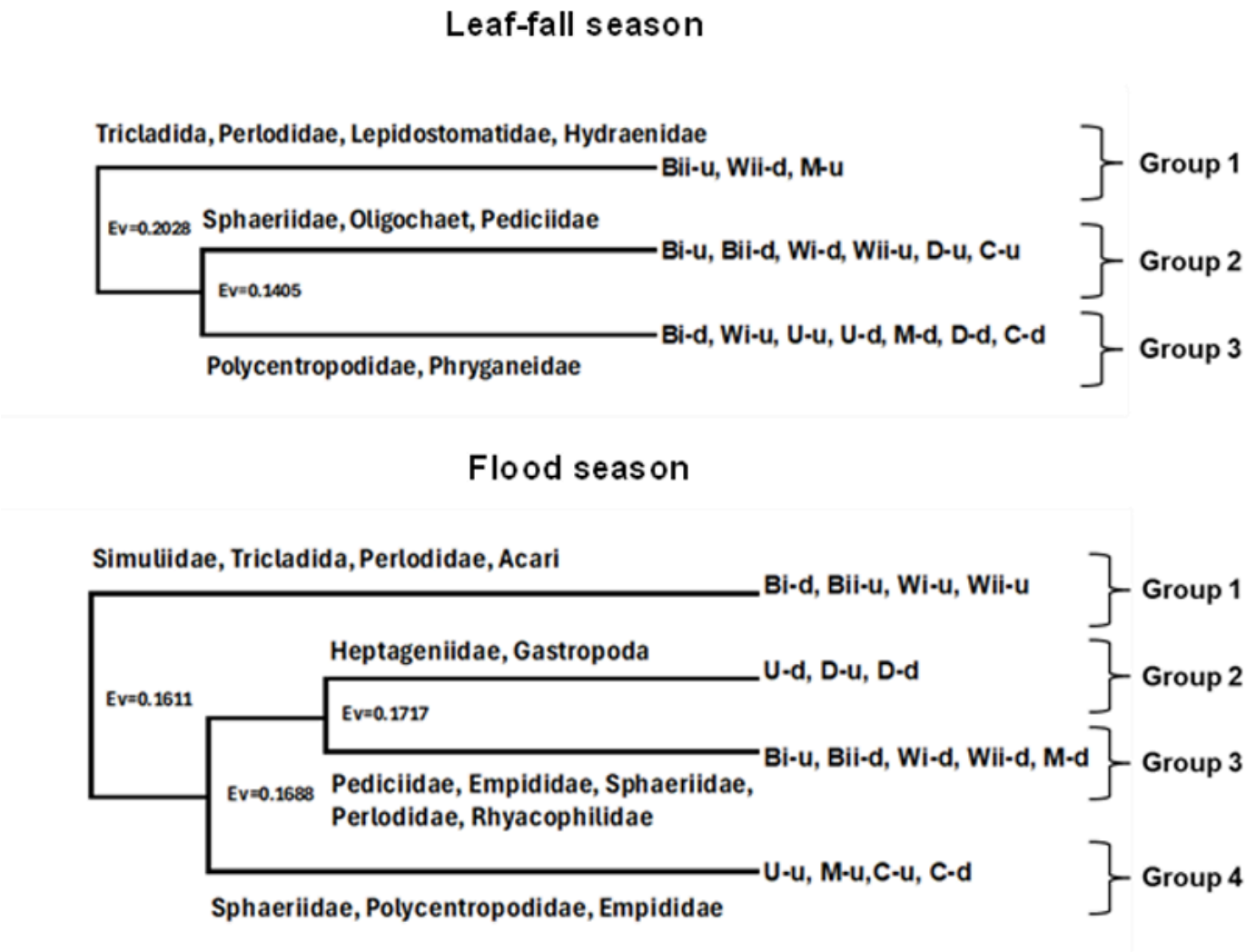


Figure 4

Results of PCA of environmental factors

Each plot represents a measurement transect within the study sections, including both CWD sections and the control section, with positions indicated as *section name–transect name* for transects perpendicular to the flow. Red circles highlight transects with aggregated or characteristic conditions.

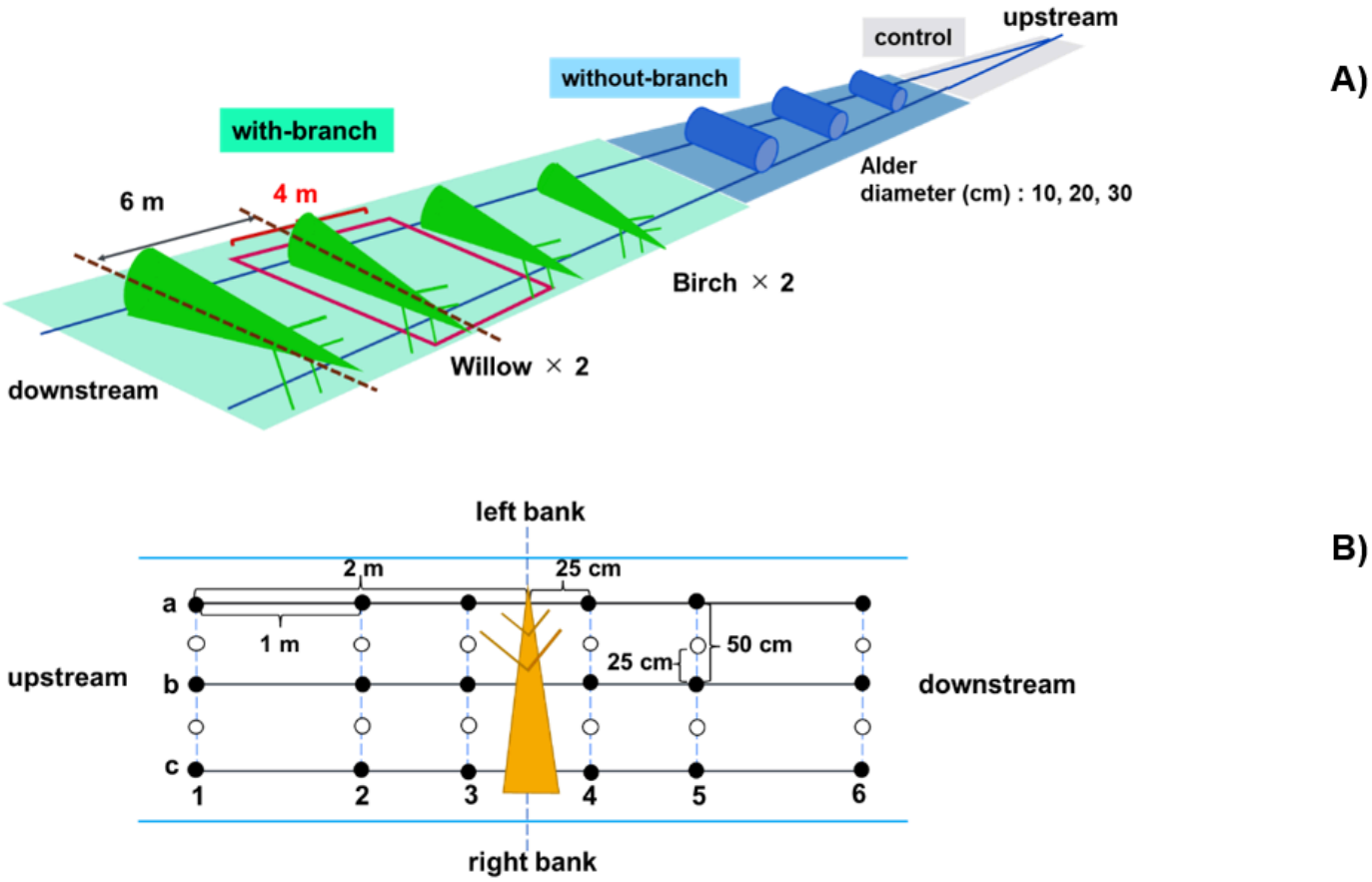


Figure 5

Temporal changes in accumulated cover area (m²) on woody debris from the leaf-fall season of 2023 to the leaf-fall season of 2025

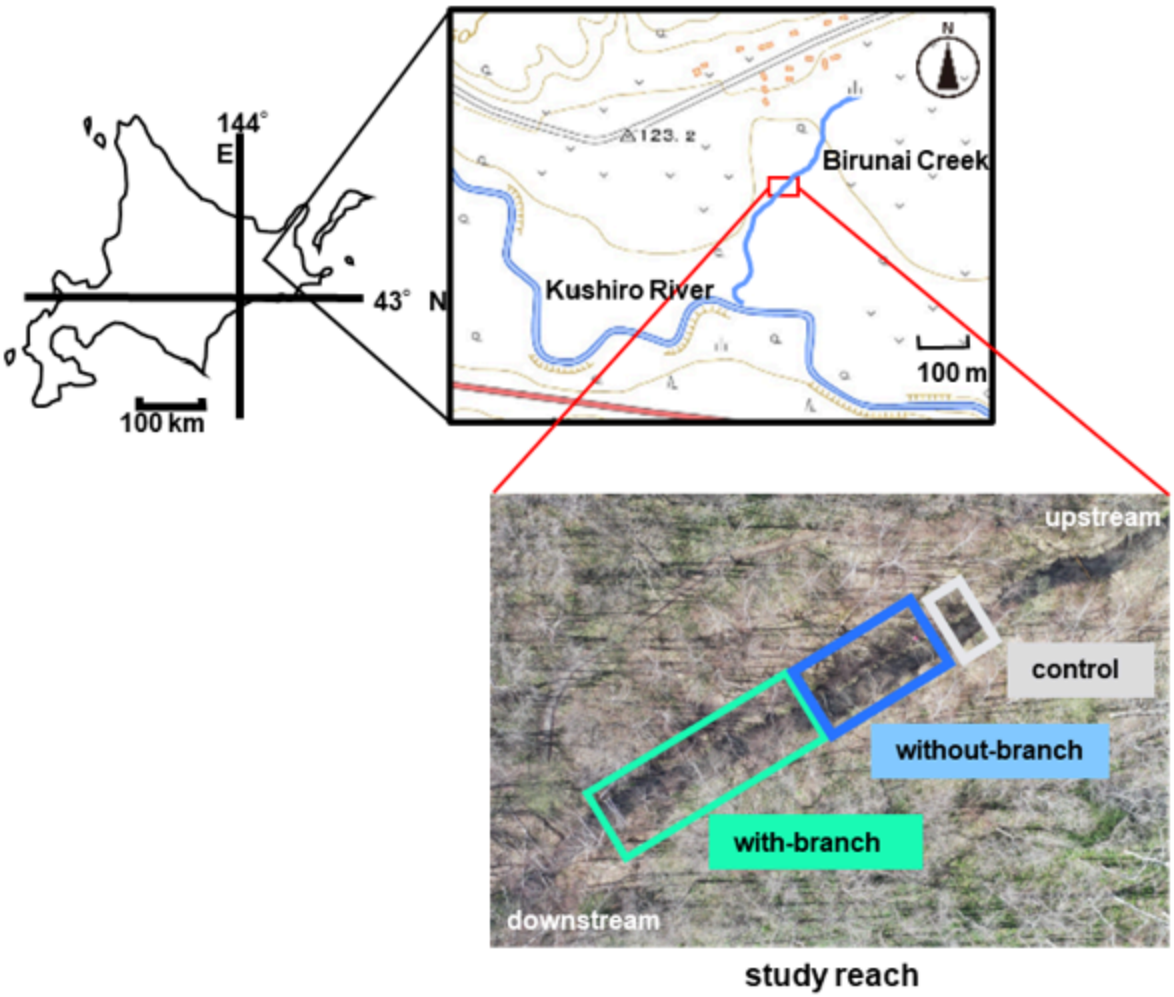


Figure 6

Dye transport around woody debris

In all images, the left side indicates upstream and the right side indicates downstream.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- Tables.docx