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Title: Catchment geology preconditions spatio-temporal heterogeneity of ecosystem functioning in forested headwater streams

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Abstract

Catchment geology can affect water chemistry and groundwater influence, eventually affecting macroinvertebrate communities, but its effects on stream functions such as leaf decomposition have been scarcely investigated. To understand the effects of geology on leaf decomposition, we conducted leaf litter

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experiments in streams with volcanic and non-volcanic substrata using fine and coarse mesh bags. Volcanic spring-fed streams showed lower temperature in summer and higher temperature in winter (with temperature difference being more pronounced later in incubation) than non-volcanic streams. Macroinvertebrate communities captured inside coarse litter bags differed in the two stream types in both seasons, mainly because of shredder communities. Shredder abundance and biomass were higher in volcanic streams in both seasons. Geology-dependent temperature influenced microbe-mediated decomposition in both seasons, with total phosphorus as an additional driver in winter. Summer temperature was associated with an overall positive effect on the abundance of shredders, which affected invertebrate-mediated decomposition, but this was not evident in winter. Shredder activity in volcanic streams compensated for temperature-dependent microbial activity resulting in an overall balance in leaf decomposition. Spring-fed systems are valuable ecosystems, particularly for cold-adapted species. Thus, understanding these understudied ecosystems will significantly aid in their appropriate conservation.

Keywords: leaf decomposition, shredders, spring-fed streams, temperature, invertebrates

Statements and Declarations

The authors have no competing interests to declare that are relevant to the contents of this research article.

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Data Availability Statement

Data are present in the Supplementary Information and available from the corresponding author upon reasonable request.

Declarations

Conflict of interest

The authors have no competing interests to declare that are relevant to the contents of this research article.

Introduction

Aquatic communities and ecosystem functions are affected by abiotic factors such as water chemistry, temperature, and nutrient availability. Studies assessing the direct effects of physical and chemical characteristics of the river on different aquatic organisms and processes are extensive (see Boyero et al., 2011; Dallas & Ross-Gillespie, 2015; Chase et al., 2017), but few have considered the possible contribution of regional factors such as underlying geology (i.e., lithology of the substratum), which could indirectly affect aquatic processes through their influence on water quality. Underlying geology can dictate groundwater influence. Rivers with highly permeable underlying rocks would mean a stronger influence of groundwater to surface water (i.e., in spring-fed streams) than those with less permeable substratum (i.e., in run-off streams). A noticeable influence of groundwater to surface water is demonstrated in the relatively stable temperature regime of spring-fed streams, mainly due to the buffering effect of groundwater temperature to surface water temperature (Kaandorp et al., 2019).

Studies that relate geology and limnology are primarily in the field of hydrology, hydrogeology, and geomorphology (Younger, 1995; Mosher et al., 2010), and those that involve ecological components are mostly done on spring-fed rivers draining chalk and limestone aquifers (Berrie, 1992; Lusardi et al., 2021), with very few comparing rivers with different groundwater influence (Sear et al., 1999). Existing literature showed consistency in assessing spring-fed streams as relatively stable physical and chemical environments in terms of flow, temperature regime, and food availability compared to run-off streams, with variations in water quality resulting in different adaptations of invertebrate communities (see Death &

Winterbourn, 1995; Jin & Ward, 2007; Lusardi et al., 2016). In addition, few studies that investigated the effect of geology on aquatic components considered structural characteristics of macroinvertebrate communities such as invertebrate diversity and abundance (i.e., Barquin & Death, 2006; Olson, 2012; Carrie et al., 2015; Lusardi et al., 2016) but did not go further as to the effects of their observed differences on stream functions (but see Griffiths & Tiegs, 2016) such as ecosystem metabolism and leaf litter decomposition. The latter is the focus of this study.

In headwater streams, allochthonous organic matter in the form of plant litter fuels the aquatic food web (Vannote et al., 1980). Leaves are the main components of litterfall, amounting to as high as 73% of total annual litterfall during the autumn season (Abelho, 2001). Upon reaching the aquatic system, leaf litter undergoes decomposition and is either directly incorporated into the biomass of detritivores, metabolized to carbon dioxide, or transformed into other products such as dissolved organic matter and fine particulate organic matter (Wallace et al., 1995). Disentangling organic matter processing pathways and the major factors influencing them, including those of anthropogenic and natural origins, is essential for both aquatic biodiversity conservation and global carbon cycling. Organic matter exported in various forms is provided to downstream reaches to sustain productivity (Wipfli et al., 2007), and the emitted carbon dioxide can contribute substantial amounts to global carbon fluxes (Raymond et al., 2013). Decomposition processes integrate a myriad of biological, physical, and chemical processes in rivers, providing an important metric of river health assessment with a focus on functions (Young et al., 2008; Niyogi et al., 2013). Organisms (mainly fungi, bacteria, and macroinvertebrates) are the driving forces in aquatic decomposition; however, these organisms depend on the substrate and surrounding environment (Graça, 2001). Thus, intrinsic factors (i.e., leaf chemistry, macroinvertebrate preference) and extrinsic environmental factors (i.e., water quality, temperature, nutrient availability, seasonality) can play important roles in decomposition (Boyero et al., 2021a, b). Geology is a primary driver of variation in both factors via controls on water chemistry, nutrient content, channel geomorphology, and watershed hydrology, which elicit different responses from aquatic organisms, including benthic macroinvertebrates through adaptations in osmoregulation, feeding, habitat, and temperature regimes (Olson, 2012; Ishiyama et al., 2021; Lusardi et al., 2021).

This study examined if geology affects water quality and macroinvertebrate detritivores, indirectly resulting in spatial and temporal variations in leaf litter decomposition in forested headwater streams. To represent geological variation, we used two types of streams with different underlying geology: volcanic spring-fed streams (hereafter volcanic streams) and non-volcanic run-off streams (hereafter non-volcanic streams). We hypothesized that there would be a variation in surface water characteristics between the two stream types, with temperature being the most obvious difference (i.e., higher in non-volcanic streams during summer but lower during winter), resulting in variations in decomposition rates by affecting both microbial decomposition (leaf conditioning) and macroinvertebrate-mediated decomposition (biological shredding). Using fine mesh and coarse mesh leaf litter bags, we aimed to elucidate how microbe- and macroinvertebrate-mediated decomposition differ between stream types and determine the role of geology in the interplay of the factors affecting decomposition in two seasons (summer and winter). Specific predictions in both seasons were: 1) shredding invertebrates would be more abundant in volcanic streams because of the benign temperature that is optimal for the growth and development of shredders; 2) overall decomposition rate would be higher in volcanic streams because of the overriding importance of biological shredding relative to temperature-dependent microbial decomposition.

Materials and Methods

Study site

The study was conducted within 100-m long sections of ten forested streams in Furano, Central Hokkaido, Japan, encompassing an area of approximately 600 km^2 (Figure 1). All study sites are tributaries of the Sorachi River, which belongs to the Ishikari River drainage system, and are drained by similar-sized catchments. During the Quaternary Period, eruptions of the Daisetsu Mountain system covered the area from the northeast with pyroclastic flow deposits and formed surficial geology dominated by volcano-derived rock (Ikeda & Mukoyama, 1983; Nakamura, 2016). The study streams were chosen such that they differed in geological characteristics and were categorized into two types; volcanic and non-volcanic (five sites/streams each) according to the dominant underlying rock type based on the Seamless Digital Geological Map of Japan (Geological Survey of Japan, National Institute of Advanced Industrial Science and Technology). Volcanic stream types have underlying geology composed of Early Pleistocene nonalkaline pyroclastic flow volcanic rocks. In contrast, non-volcanic stream types have Early to Late Cretaceous accretionary complexes, metamorphic rocks, marine muddy turbidite, and late Pleistocene to Holocene marine and non-marine sediments in their respective watersheds. The mean (±standard deviation) percentage of the volcanic geological layer for each catchment (volcanic proportion) was 99.9 (± 2.0) for volcanic streams and 6.4 (± 12.80) for non-volcanic streams (Table S1.1).

According to the weather record at the Furano weather station of the Japan Meteorological Agency, approximately 20 km northwest of the study area, the mean annual temperature and annual precipitation (±standard deviation) for the period 2010 – 2021 were 6.98 (± 0.32) ˚C and 1060.09 (± 208.86) mm, respectively; mean monthly air temperature was highest in July (21.31 ˚C) and lowest in January (-8.25 ˚C). Higher resolution (1km x 1km) of mean annual precipitation and air temperature data obtained for each catchment using 30-year data (1980 – 2010) showed similar climatic characteristics between the two stream types (*P*=0.475 for mean annual precipitation and *P*=0.174 for mean annual temperature) (adjusted alpha = 0.008, see Statistical Analyses). Volcanic and non-volcanic streams recorded 1063.71 - 1292.58 mm and 1088.85 - 1580.80 mm mean annual precipitation, and 2.66 - 4.13 ˚C and 3.11 - 4.82 ˚C mean annual air temperature, respectively (Table S1.1). Selected volcanic and non-volcanic streams are similar in elevation (*P*=0.019) (Table S1.1), slope (*P*=0.034) (adjusted alpha = 0.008, see Statistical Analyses), and catchment size (*P*=0.897) (Table S1.2). High-resolution land-use and land cover maps used to calculate the proportion of forest type in the catchment using ArcGIS Pro (ESRI, version 2.4.0) showed that stream catchments were mainly composed of broadleaf forest and small percentages of needleleaf forest (Table S1.3). Overall, forest cover was high (92% in volcanic and 99% in non-volcanic streams), but there was a slight difference in forest cover between the two stream types due to the relatively lower broadleaf forest cover in one of the volcanic sites (P4) (Table S1.3).

Leaf decomposition experiment

Leaf litter packs were mimicked using 3.0 ± 0.1 g (mean dry weight ± standard errors) of *Alnus japonica* (Thunb.) Steud. (Japanese Alder) placed inside leaf litter bags (hereafter litter bags) with fine and coarse mesh nets (see Appendix S1). Fine mesh (257 x 266 μm) bags allow only microorganisms (bacteria and fungal conidia) to enter, while coarse mesh bags enable access to both microorganisms and macroinvertebrates. The coarse mesh bag is a hybrid of two net sizes (black net: 3.9 x 3.9 mm; green net: 1 x 1 cm), with the bottom portion (touching the riverbed) having black net only and the top portion having half green and half black net. The green part (facing upstream) accommodates larger shredders observed in the study sites during reconnaissance, and the black part (facing downstream) prevents the loss of fragmented alder leaves. Gholz et al. (2000) applied a similar principle of using two mesh sizes for leaf decomposition experiments. Two types of leaves were used to capture heterogeneous litter decomposition associated with leaf conditions: green and old senescent leaves during summer and old senescent and new senescent leaves during winter. Green leaves represent fresh leaves falling in summer due to wind or rain action. Old senescent leaves represent lateral input of remaining litter from the previous fall season while new senescent leaves represent both vertical and lateral input during the current fall season (see Appendix S2 for litter bag preparation).

Overall, 100 pairs of coarse and fine mesh bags were incubated each season (50 pairs in volcanic streams and 50 pairs in non-volcanic streams). Five replicates of four litter bags (factorial combinations of two mesh types and leaf types) were used for every stream, with each replicate tethered to a metal lever driven into the riverbed (20 bags in each stream per season). The distance between replicates within each stream was 10 to 25 m apart. Incubation of leaf litter was done in 2018 in two seasons, from 11th July to 3rd August during summer and 2nd November to 4th December during winter. December was chosen as the winter sampling period because this was the third coldest month (mean monthly air temperature for the period 2010 – 2021 at the Furano station: -4.84 ˚C) of the year after January and February (-7.15 ˚C) and the coldest snow-free month with road access to all the sites. The collection was done twice for each season, after approximately two- and three weeks of incubation during summer and after two- and four weeks during winter. Two replicates from each stream were retrieved during the first collection, and the remaining three replicates were retrieved during the second collection. Because this was the first time to perform a litter decomposition experiment on the sites, the speed of decomposition was only roughly estimated, and conditions such as lower water levels later in summer or heavy snow later in winter were anticipated. Thus, more replicates (three pairs) were left for the second collection to have a higher possibility of retrieving at least two pairs of litter bags.

Collection and processing of litter bags

Litter bag collection was done using laundry nets (0.4 mm × 0.4 mm mesh size) to avoid loss of both macroinvertebrates and remaining leaf litter which may be washed away upon moving the litter bags. Each pair of litter bags was enclosed in one laundry net while still underwater and raised slowly from the water, maintaining as little disturbance as possible. Some replicates were found slightly buried in deposited fine sediments. To quantify the extent of sediment burial, coarse litter bags were collected with the deposited sediment. Sediment did not penetrate in substantial amounts through the fine mesh and thus, was not quantified for the fine mesh bags. Collected litter bags were immediately placed inside a clean Ziploc bag and transported to the laboratory.

The remaining leaf litter was processed immediately upon reaching the laboratory. Contents of litter bags were washed and sorted, and the recovered *A. japonica* leaf litter was oven-dried at 60°C for seven days, weighed, combusted at 500 °C for 4 hours (FO310, Yamato Scientific Co., Ltd., Japan), and weighed again to obtain ash-free dry mass (AFDM). Macroinvertebrates were also recovered from the coarse litter bags and, upon reaching the laboratory, were immediately separated from remaining leaf litter and preserved in 75% Ethanol. All invertebrates, except for Nematoda, were counted and identified to family level using existing keys (Merritt & Cummins, 1996; Kawai & Tanida, 2005). Potential shredder families were determined according to the classification of Merritt & Cummins (1996) as "generally shredders". Some invertebrates, including all potential shredder families, were collected from the study sites and subjected to C and N stable isotope analyses along with potential primary food resources such as leaf litter (Figure S1) to confirm the invertebrate shredder families. Consequently, six families (Capniidae, Nemouridae, Lepidostomatidae, Limnephilidae, Tipulidae, Gammaridae) were considered shredders and examined in detail in relation to leaf litter decomposition. For all taxa, individuals were grouped into size classes by visual identification, and representatives were taken from each size class to measure the dry biomass of individuals from the respective season (Table S2). Average biomass per family per season was obtained and was multiplied by each individual count to obtain approximate total shredder biomass and total invertebrate biomass in each litter bag.

In coarse litter bags, the fine sediment removed from *A. japonica* and from other organic components (leaves and twigs), as well as sediments attached to invertebrates (i.e., in Limnephilidae cases), were collected, oven-dried at 60°C until fully dried and weighed with an analytical balance.

Estimation of physical and chemical parameters

For each site, one temperature logger (Hobo pendant temperature/light logger, UA-002-08, Onset Computer Corp., Massachusetts, USA) recording every 15 minutes was set up from the start of the litter bag incubation period until the collection of the last set of litter bags. Two types of temperature data were used for subsequent analyses. For comparing stream types (in Table 1), the average temperature was obtained by getting the mean value of all sites per day for each stream type. For structural equation modeling (SEM) analyses (see Statistical analyses), the average temperature used was the mean temperature for each site for every incubation period. Electrical conductivity (EC) and pH were recorded in each stream during set-up and every litter bag collection using a handheld EC/pH meter (WM 32EP, DKK-TOA Co., Tokyo, Japan). Water samples were collected using 250-mL acid-washed polyethylene bottles once from each site for each season. The collected water was filtered through a 0.5μm filter paper (GC-50 Advantec, Tokyo, Japan) and subjected to an ion analyzer (IA-300, DKK-TOA Corp., Tokyo, Japan) to determine chloride (Cl^-), phosphate (PO_4^{3-}), sulfate (SO_4^{2-}), nitrite (NO_2^-) and nitrate (NO_3^-) concentration. Nitrite and phosphate were below the detection limit (0.05 mg/L) in all cases and thus were no longer reported hereafter. An unfiltered portion was subjected to digestion using the colorimetric method and eventually to spectrophotometry (UV-1280, Shimadzu Corp., Japan) to obtain total nitrogen (TN) and total phosphorus (TP) concentration using a method described in Rahman et al. (2021). Winter water samples were obtained in November 2018, while for the summer data, water samples were obtained in August 2019.

During litter bag collection, water depth was measured thrice for every replicate, with the 1st measurement immediate to the left side of the 1st bag, the 2nd measurement in-between the 2nd and 3rd bags, and the 3rd measurement immediate to the right side of the 4th bag. At the same time, flow velocity (Propeller-based Velocity Meter, CR-11, Cosmo-Riken Inc., Tokyo, Japan) on top of litter bags was also recorded by taking three points (in between every bag) for each replicate. Flow velocity measurements were consistently taken at approximately 60% of the depth relative to the water surface.

Estimation of decomposition rates

Decomposition rates were estimated for every litter bag collected at the second collection according to their treatment types (n=12 for each stream per season) by employing the exponential decay model (Fig. S2):

$$AFDM_r = e^{-kt}$$

where:

$AFDM_r$ (remaining AFDM) = final AFDM (g) / initial AFDM (g)

t = incubation duration (days)

k = breakdown rate coefficient

To fit the model, $AFDM_r$ obtained for leaf bags at the first collection was processed to provide mean values that corresponded to each combination of mesh type and leaf type (mean $AFDM_r$ at the first collection). The initial $AFDM_r$, which was assumed to be 100, the mean $AFDM_r$ at the first collection, and $AFDM_r$ at the second collection were used in non-linear least square regression (nls function in R software; see Statistical analyses below) with the corresponding t to obtain a total of 12 k values (six each for fine k and coarse k) for each stream. Fine k represents largely microbial decomposition process (hereafter microbe k), whereas coarse k represents microbial and macroinvertebrate shredder activities (hereafter overall k).

Decomposition rate due to shredder activity only (invertebrate k) was also approximated. To obtain the approximate value of final AFDM if only detritivore consumption happened (i.e., excluding the contribution of microbes), the lost AFDM due to microorganism (fine mesh) decomposition was added to the remaining AFDM obtained for coarse mesh samples. In instances where approximate final AFDM due to macroinvertebrates only exceeds the initial AFDM (fine mesh decomposition was greater compared to that in the coarse-mesh bags because of slight differences in leaf mass at the beginning), the value of initial AFDM was adopted as the final AFDM, so that contribution due to macroinvertebrates is approximated as zero and is considered irrelevant. In total, 18 *k* values (six replicates for each type of *k*) were estimated for each stream in each season.

Statistical analyses

General characteristics of the watershed (elevation, forest cover, slope, catchment area, annual mean temperature, annual mean precipitation) and physical and chemical characteristics of streams (temperature, ions, TN, TP, EC, pH, discharge) were compared between stream types per season using Generalized Linear Mixed Models (GLMMs) with the main effect of stream type and random factor of river identity (or river identity and sampling occasion/incubation day for EC, pH, and temperature) and with Gaussian error distribution. Because multiple comparisons (disjunction testing) (Rubin 2021) were done within these two data sets, alpha was adjusted using the Holm's Sequential Bonferroni Procedure to control for Type I error (Abdi, 2010). Adjusted alpha for general watershed characteristics and physicochemical data are P=0.008 and P=0.006, respectively.

The taxonomic richness and Shannon-Weiner diversity index of the entire community and abundance and biomass of shredders were compared between stream types and seasons. GLMMs were developed with the main effects of stream types and seasons and their interaction, and random factors of leaf type, river identity, and sampling occasion and with the following error distributions: Poisson for taxonomic richness, negative binomial for shredder abundance, and Gaussian for diversity index and shredder biomass). The same analyses were conducted for overall *k*, microbe *k*, and invertebrate *k* with Gaussian error distribution. Permutational multivariate analysis of variance (PERMANOVA) was used to test the compositional differences of invertebrates between stream types. For this analysis, $\log_{10}$-transformed abundance and raw biomass of family-level macroinvertebrates were used. Moreover, similarity percentages analysis (SIMPER) (Clarke, 1993) was used to determine the percentage contribution of shredder taxa to the average dissimilarity between communities in the two stream types.

To identify the drivers through which geological differences in catchments affect decomposition rates directly and indirectly, structural equation modeling (SEM) was adopted, with microbe *k* and invertebrate *k* as response variables. The modeling was performed in three cases in each season: one for microbe *k* and two for invertebrate *k,* which used either shredder abundance or biomass as one of the factors. There were 60 data points for each type of *k* in each season. Physical and chemical data available only at the stream scale (e.g., volcanic proportion) were assigned to all data points in corresponding streams. In the analyses for microbe *k* and invertebrate *k*, volcanic proportion, temperature, and other local environmental factors (local flow velocity for microbe *k*, and both local flow velocity and sediment deposited on coarse litter bags for invertebrate *k*) that can affect decomposition rates were included as direct or indirect factors. Nitrate and TN, which are known factors that affect leaf decomposition, were not included in the SEM analyses due to the lack of significant difference in nitrate and TN between the stream types for both seasons (as stated in the results). On the other hand, discharge and TP were included in the SEM models even though they did not show significant differences between the stream types because of their relatively higher values in one of the stream types in a certain season. The a priori path structures were decided using existing knowledge about invertebrates and physical and chemical environments (Allan et al., 2021). For the invertebrate *k* analyses, we initially did not include direct pathways from volcanic proportion to the invertebrate abundance or biomass and invertebrate *k* as unknown effects in our hypothetical SEMs. However, these relationships appeared as important latent relationships in all cases without which the model did not become statistically significant. This was because there were other potentially important factors, such as temporal variability of flow and water quality in the study periods. Furthermore, factors directly related to geology, such as rock type, erodibility of underlying rocks and substrate lithology, can also influence invertebrates (see Shearer & Young, 2011 and Nitzu et al., 2018). Thus, direct pathways from volcanic proportion to invertebrate abundance/biomass were eventually included to represent these possible direct effects. The Piecewise SEM framework was adopted, and each relationship was constructed using generalized linear models with Gaussian error distribution (Lefcheck, 2016; Miller et al., 2018). Variables were $\log_{10}$-transformed and scaled when appropriate. Type of leaf and location of subsite were included as random factors.

All statistical analyses were performed using R version 4.0.1 (R Core Team, 2020) using ‘glmmTMB’, ‘lme4’, ‘vegan’, ‘ADONIS’, and ‘piecewiseSEM’ packages. The statistical significance level for analyses was set at 0.05. For piecewise SEM, Fisher’s C statistics ($p>0.05$) was used to determine the model's goodness of fit.

Results

Stream-type difference reflected through water temperature was more evident in summer than in winter, with volcanic and non-volcanic streams ranging from 9.10 – 10.86 °C and 13.63 – 16.14 °C, respectively, during summer incubation and 4.28 – 6.06 °C and 3.63 – 4.87 °C, respectively, during winter incubation (Table S3.1). In summer, volcanic streams recorded significantly lower water temperature while in winter, temperature was significantly higher in volcanic than non-volcanic streams (Figure 2, Table 1). Based on this result, water temperature was considered as a possible factor affecting *k* in the SEM analyses later. Although not statistically significant, discharge in summer was relatively higher in non-volcanic streams (0.432 ± 0.198 m^3/s) than volcanic streams (0.209 ± 0.048 m^3/s), and TP concentration in winter was relatively higher in volcanic (0.025 ± 0.009 mg/L) than non-volcanic streams (0.015 ± 0.004 mg/L) (Table S3.1 and S3.2). The pattern observed in TP was due to a decrease in TP concentration in non-volcanic streams during winter while the concentration in volcanic streams remained similar in the two seasons.

A total of 18,938 macroinvertebrate individuals (7,013 in summer and 11,925 in winter) were collected from the coarse litter bags. In eight fine litter bags, an average of four early instars Chironomidae (17 individuals at the most) per bag were found, which were 0.57-7.69% of the Chironomidae abundance in their paired coarse bag. Because of the small body size and lower abundance compared to those found in the coarse litter bags, the presence of Chironomidae larvae in the fine mesh bags was assumed to have no substantial contribution to decomposition and was not included in the analyses. Community differences between river types and seasons were observed in diversity indices and shredder community structure. Taxonomic richness and Shannon-Weiner index were higher in volcanic streams in summer (Table 2 a, b; Figure 3 a, b). Detritivores comprised 68.9 and 80.8% of the abundance and biomass of all samples, respectively, with some variations between seasons and river types (Figure S3). Shredder abundance was higher in volcanic streams in summer (Table 2 c, Figure 3 c). Shredder biomass was higher in winter compared to summer, and volcanic streams exhibited higher values in both seasons (Table 2 d, Figure 3 d). The results of SIMPER indicated that shredder taxa were among the most critical groups in distinguishing river-type communities (Table 3).

Decomposition rate exhibited various responses to seasons and river types depending on the type of *k,* with all cases having statistically significant interactions between two factors (Table 4, Figure 4). Overall, *k* seasonally fluctuated in nonvolcanic streams, whereas volcanic streams showed relatively stable values. Microbe *k* was higher in summer and decreased in winter in non-volcanic streams, whereas the decreasing trend in volcanic streams was statistically insignificant. These seasonal trends in microbe *k* were consistent with those in overall *k,* although the degree of the change was lesser in the latter. Damped seasonal contrasts in overall *k* were explained by the trends in invertebrate *k*, which offset the seasonal changes in microbe *k*. The invertebrate *k* was lowest in non-volcanic streams in summer and was relatively higher in volcanic streams in both seasons.

All SEM exhibited acceptable levels of goodness of fit (Fisher's C statistics, $p>0.09$ in all cases). Temperature was the most important environmental factor by which surface geology affected microbe *k* in both seasons (summer: standard coefficient (coef) = 0.48, $r^2 = 0.24$; winter: coef = 0.47, $r^2 = 0.48$) (Figure 5 a, d). These pathways were directionally contrasting, with colder water in volcanic streams (coef = -0.96, $r^2 = 0.93$) limiting the microbe *k* in summer and warmer water in volcanic streams (coef = 0.67, $r^2 = 0.45$) promoting the microbe *k* in winter (Figure 5 a, d). In addition to temperature, relatively higher TP levels associated with volcanic geology (coef = 0.68, $r^2 = 0.45$) also contributed to an increased microbe *k* in winter (coef = 0.26, $r^2 = 0.48$). Indirect effects of surface geology affecting invertebrate *k* via shredding invertebrates were apparent in three out of four cases (except for biomass in summer) (Figure 5 b, e, f). In summer, the colder temperature in volcanic streams was associated with positive overall effects on shredder abundance (coef = -1.45, $r^2 = 0.37$) and thus invertebrate *k* (coef = 0.28, $r^2 = 0.28$) (Figure 5 b); unknown direct pathways were also detected for geology-invertebrate *k* relations (coef = 0.29 for abundance and 0.34 for biomass). In winter, both abundance (coef = 0.29) and biomass (coef = 0.36) adequately explained the variation in invertebrate *k* ($r^2 = 0.45$ for abundance and 0.46 for biomass), although temperature-mediated effects of surface geology on invertebrate *k* were undetected. The detected effects of surface geology on invertebrate *k* via measured environmental factors included indirect effects of flow velocity through its direct effect on abundance (coef = -0.38, $r^2 = 0.21$) and biomass (coef = -0.28, $r^2 = 0.33$) in winter; unknown direct pathways were also detected for geology-shredder relations (abundance: coef = 0.68, $r^2 = 0.21$; biomass: coef = 0.79, $r^2 = 0.33$).

Discussion

Spatial heterogeneity in surface geological characteristics at the landscape level and its effects on physical properties of riverine ecosystems such as catchment hydrology have been well recognized (McDonnell et al., 2007; Olson, 2012; Kaandorp et al. 2019). Despite the known effects of flow regime and catchment hydrology on biota (Leland & Porter, 2000; Newton et al., 2008; Wenger et al., 2011; Lusardi et al., 2021), our understanding of catchment-geology controls on ecosystem functioning remained limited. By using leaf litter decomposition as a measure of key ecosystem functioning in forested headwater streams, our findings supported the hypothesis that catchment geology mediates decomposer community structures, leading to variations in ecosystem functioning. However, our specific prediction was partially unsupported because the overall decomposition rate in coarse litter bags was not significantly higher in shredder-abundant volcanic streams but was more seasonally stable than in non-volcanic streams.

The observed physical environmental gradients across study streams can be attributed to geological characteristics of the surficial deposits because other factors that could dictate water temperature, such as climatic characteristics, were shown to be similar between the two stream types. Although there was a slight difference in overall forest cover due to one volcanic site (P4) with a lower cover, this did not affect the observed temperature regime characteristic of the volcanic sites. Specifically, although P4 showed a slightly higher temperature than other volcanic streams during summer, it was still lower than the non-volcanic streams. This could also highlight the importance of underlying geology in relation to the effects of forest cover on water temperature in headwaters. Moreover, the thermal regimes of the two stream types are similar to those observed in other studies (particularly in the middle of summer and beginning of winter) (i.e., Jin & Ward, 2007; Lusardi et al., 2021) which reported difference in temperature pattern of streams due to variation in substrata. Geology was found to be a strong predictor of stream water temperature. Pyroclastic flow volcanic rocks found in the underlying geology of volcanic streams were mainly pumice deposits characterized by high porosity, with large pores connected by small channels (Bernard et al., 2007). High groundwater input allows a stable temperature regime due to the strong interaction of groundwater with surface water (Kaandorp et al., 2019). In volcanic streams, the stability of groundwater temperature would result in colder summer temperatures and warmer winter temperatures than non-volcanic streams (Crisp & Le Cren, 1970). As observed in our study sites, the temperature is colder in volcanic sites than in non-volcanic sites during summer and the expected shifting of the pattern was also observed during winter, with volcanic streams having warmer water than non-volcanic streams especially in the latter part of incubation. This contrast may be more pronounced later in winter because water temperature in non-volcanic streams would have been more strongly affected by colder temperatures in the middle of winter (i.e., January).

The structure of macroinvertebrate communities was distinctive in relation to the geological characteristics of the contributing catchments. Variations in macroinvertebrate community composition between streams having different groundwater influences have been reported by several studies on benthic invertebrates (i.e., Barquin & Death, 2006; Lusardi et al., 2016). It has been noted that the relative stability of the spring-fed system enables the provision of good quality and quantity of food resources. Interestingly, invertebrate shredders appear to be particularly responsive to geological differences. Volcanic spring-fed rivers were observed to have higher retention of large woody debris (Barquin & Death, 2004; Lusardi et al., 2021), which, in addition to stable flow, could contribute to the possible retention of leaf litter, thereby increasing the food availability for shredders.

An important limiting factor of community structure highlighted in this study is water temperature in summer. In aquatic insects, the temperature regime can be the most important factor influencing growth in areas where food is not limited. Because of this, the emergence of terrestrial form can be significantly affected (Watanabe et al., 1999; Bayoh & Lindsay, 2003; Jin & Ward, 2007). High temperatures hasten physiological development and might shorten the available time for organisms to accumulate the required nutrients needed for complex processes such as eclosion and emergence to the adult stage of some species (Lassiter et al., 1994). These direct limiting effects of temperature can be detrimental for shredders. The majority of the shredders collected in the study area are from the orders Plecoptera and Trichoptera, which are evolutionarily adapted to cold waters (Balian et al., 2008) – the same reason that there are more shredders in temperate areas compared to the tropics (Irons et al., 1994; Boyero et al., 2011). Thus, higher water temperature in non-volcanic streams in summer could limit the abundance and diversity of invertebrate communities.

It was also possible that the physical and chemical environment influenced by geology indirectly affected invertebrates via mediation of food quality through leaf litter conditioning. This pathway was visualized by dividing k into several constituents together with SEM analyses. It is noticeable that microbe-mediated decomposition follows the temperature pattern. This trend was expected since the positive effect of temperature on microbial activity has already been established in both laboratory and field settings. Temperature has a positive effect on microbial mass and enzymatic activity (Ferreira & Chauvet, 2011; Ferreira et al., 2015), explaining about 40% of variations in microbe-mediated decomposition (Boyero et al., 2011). During decomposition, microorganisms use cellulases (e.g., β-glucosidase) to degrade cellulose fibers through cellulolysis. Temperature was reported to have the strongest interaction with substrate chemistry and cellulolytic activities compared to other water quality parameters and was shown to cause higher decomposition efficiency and cellulase activity, giving it a leading role as a predictor of decomposition rates (Fenoy et al., 2016). Ultimately, temperature can positively affect the leaf conditioning process of microorganisms, which is crucial for the palatability of leaf litter for shredder invertebrates. However, in this study, summer temperature did not probably lead to positive effects on shredder invertebrates through litter conditioning, as evidenced by the lower abundance and biomass of shredders in the warmer non-volcanic streams. In contrast, temperature positively affected microbe k in winter, suggesting possible positive effects of volcanic geology on shredders via increased food resource quality in this season. Furthermore, microbial processes and production in winter might have been stimulated by the relatively higher concentration of phosphorus in volcanic streams, as observed in the positive pathway from geology to TP and microbe k in the SEM plot (Fig. 5). This illustrates the effect of phosphorus-stimulated food quality on leaf decomposition (Gulis et al., 2006; Ardon et al., 2020). The TP concentration in volcanic streams was similar in the two seasons and was relatively higher than in non-volcanic streams during winter, probably due to the different sources of TP for each stream type. In contrast with volcanic streams, which are highly influenced by groundwater, non-volcanic streams are highly affected by contributions from surface runoff, which are lower during winter. Volcanic streams can have high phosphorus levels because groundwater can move through the young volcanic rocks rich in phosphorus. This may also be brought about by the weathering of rock materials associated with volcanic deposits (e.g., Timperley & Vigor-Brown, 1985). Substantial contribution of volcanic geology to phosphorus load has also been documented elsewhere (Felitsyn, 2002; Domagalski & Saleh, 2015; Records et al., 2016). Although there was no significant difference in TP between stream types, the noticeable decrease in TP concentration in non-volcanic streams during winter showed substantial contribution to the microbe-mediated decomposition SEM, highlighting the importance of stability of TP concentration in the leaf decomposition in volcanic streams.

The significant contribution of invertebrates to macroinvertebrate-mediated decomposition, particularly in volcanic areas, can be attributed to the presence of more shredders in the relatively temperature-stable volcanic streams. However, this causal pathway was not reflected as the overarching effect of geology on shredders and invertebrate *k* when examined separately for each season in the SEM plot. First, temperature-mediated effects of geology on invertebrate *k* were not detected in winter. Second, the TP-mediated effect of geology on invertebrate *k*, which was expected from the phosphorus-stimulated food quality hypothesis above, was not observed in winter. Also, direct pathways from geology to invertebrate abundance and biomass unexplained by the measured environmental variables were rather substantial as seen in the values of R^2 and standard coefficients. A plausible explanation for the above-mentioned discrepancies in seasonal patterns and the unexpected extent of the direct effects of geology on invertebrate-related response variables would be the temporal mismatch between the recorded biota response and the environmental parameters used in the analyses. Most shredder taxa are considered to have univoltine to semivoltine life cycles (personal observations based on body size frequency distribution and emergent adults in the study sites, JNN), being potentially susceptible to any seasonal environmental filters. Moreover, there is inherent complexity in the response of different shredder invertebrate species to environmental factors according to their life history strategies (i.e., some species undergo aestivation, some undergo winter diapause, while others migrate to warmer areas in the river to prepare for winter) which might be entirely different with the other species under the same family. In our case, as mentioned earlier, the summer water temperature may strongly limit macroinvertebrate communities, including shredders, while community structure could have little association with the same environmental variable measured in different seasons. For the same reason, positive effects of phosphorus-stimulated food quality may affect other properties of the community, such as individual growth rate or survival rates, which may not be detected as strong associations between TP and shredders in winter.

Recognizing the effects of geology on the structural and functional characteristics of streams is essential due to the observed influence of geology on both biotic and abiotic components of the stream. Leaf decomposition provides the primary energy source for the aquatic food web, which is further linked with the terrestrial food web in headwater streams, making it an important component of complex aquatic-terrestrial relationships. This highlights the importance of quantifying and understanding factors that could affect the decomposition process. Although the results of this study were able to pinpoint temperature as one of the vital factors in the geology-leaf decomposition connection, the robustness of data and accuracy of the conclusion can still be improved by adding more environmental factors to the analyses and conducting manipulative experiments to elucidate causal relationships. Because summer conditions or winter conditions each by themselves or in combination across two seasons can create bottlenecks in the invertebrate community (i.e., temperature and velocity limiting shredder abundance and biomass) as well as associated ecosystem functioning (i.e., temperature and/or TP influencing microbe decomposition), future studies would need to have a design to empirically disentangle them.

Conclusions

This study established a strong conclusion regarding the differences in volcanic and non-volcanic systems in terms of macroinvertebrate community structure and functional attributes such as leaf litter decomposition, which is vital in continuing aquatic ecosystem processes. Importantly, temporally stable functioning was maintained by shredding invertebrate activity that balanced well with temperature-dependent microbial activity in volcanic streams. Implications of temperature as a strong factor influencing decomposition call attention to the prospected increase in global atmospheric temperature. There is a growing threat to the survival of cold-adapted aquatic organisms as increasing temperature and broader temperature fluctuations limit their distribution and survival. As thermally and functionally stable systems, volcanic spring-fed systems can be valuable, and identification and conservation of these systems, including invertebrate diversity, is important in this age of increasing global atmospheric temperature.

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Tables

Table 1 Results of GLMMs testing for the effect of stream type on physical and chemical variables. *p*-values shown for the two seasons were produced for the Wald Z-statistic. The significance level determined by Holm-Bonferroni Sequential Procedure requires a *p*-value of 0.006 after alpha adjustment. Bold letters denote statistical significance. The sample size for each analysis is n=10 except for EC (summer=40, winter=60), pH (summer=30, winter=60), and temperature (summer=44, winter=58).

Water Quality	EC (mS/m)	pH	Cl^- (mg/L)	NO_3^- (mg/L)	SO_4^{2-} (mg/L)	TP (mg/L)	TN (mg/L)	Discharge (m^3/s)	Temperature (ºC)

Parameter									
Summer	0.153	0.568	0.243	0.327	0.953	0.493	0.354	0.014	**p<0.006**
Winter	0.145	0.745	0.0234	0.234	0.279	0.019	0.264	0.204	**p<0.006**

Table 2 Results of GLMMs testing of the effects of stream types related to geological characteristics (G), season (S), and their interactions on the taxonomic richness (a), Shannon-Wiener diversity index (b), shredder abundance (c), and shredder biomass (d) in coarse litter bags. P-values were produced in GLMM for the Wald Z-statistic. Bold letters indicate statistical significance. SD represents standard deviations.

(a) Coefficients	Estimates	SD	*p*-value
Intercept	1.583	0.108	**<0.001**
G (volcanic relative to non-volcanic)	0.530	0.147	**<0.001**
S (winter relative to summer)	0.480	0.081	**<0.001**
G x S	-0.215	0.104	**0.038**

(b) Coefficients	Estimates	SD	*p*-value
Intercept	1.280	0.161	**<0.001**
G (volcanic relative to non-volcanic)	0.878	0.192	**<0.001**
S (winter relative to summer)	0.643	0.170	**<0.001**
G x S	-0.483	0.167	**0.004**

(c) Coefficients	Estimates	SD	*p*-value
Intercept	1.824	0.231	**<0.001**
G (volcanic relative to non-volcanic)	0.853	0.320	**0.008**
S (winter relative to summer)	1.397	0.199	**<0.001**
G x S	-0.356	0.265	0.180

(d) Coefficients	Estimates	SD	*p*-value
Intercept	1.021	0.283	**<0.001**
G (volcanic relative to non-volcanic)	1.501	0.400	**<0.001**
S (winter relative to summer)	1.224	0.400	**0.002**
G x S	-0.647	0.565	0.252

Table 3 Results of SIMPER analyses with abundance (a) and biomass (b) showing overall dissimilarity between communities of the two stream types, average contribution of ten most important taxa to overall dissimilarity, and their cumulative contribution.

(a) Summer			Winter		
Overall dissimilarity	62.8%		Overall dissimilarity	51.4%	
Contributory taxa	Average contribution (%)	Cumulative contribution (%)	Contributory taxa	Average contribution (%)	Cumulative contribution (%)
Leptophlebiidae	7.9	12.6	Ephemerellidae	5.6	10.8
Chironomidae	7.8	25.0	Lepidostomatidae[†]	4.6	19.7
Nemouridae[†]	6.9	35.9	Leptophlebiidae	4.3	27.9
Perlodidae	6.0	45.5	Capniidae[†]	4.2	36.1
Ephemerellidae	5.3	53.9	Chironomidae	4.0	43.9
Tipulidae[†]	3.7	59.8	Nemouridae[†]	3.8	51.3
Lepidostomatidae[†]	3.5	65.4	Perlodidae	3.3	57.7
Chloroperlidae	3.4	70.8	Chloroperlidae	2.8	63.2
Limnephilidae[†]	2.9	75.4	Limnephilidae[†]	2.5	68.0
Uenoidae	2.2	78.8	Baetidae	2.1	72.2

[†] shredder invertebrates

(b) Summer			Winter		
Overall dissimilarity	68.23%		Overall dissimilarity	77.70%	
Contributory taxa	Average contribution (%)	Cumulative contribution (%)	Contributory taxa	Average contribution (%)	Cumulative contribution (%)
Tipulidae†	10.8	15.8	Ephemerellidae	16.0	20.6
Limnephilidae†	7.8	27.2	Lepidostomatidae†	13.1	37.5
Chironomidae	7.6	38.4	Limnephilidae†	12.8	53.9
Uenoidae	6.1	47.4	Perlodidae	12.0	69.3
Rhyacophilidae	5.5	55.5	Capniidae†	5.0	75.7
Ephemerellidae	4.9	62.7	Tipulidae†	5.0	82.1
Nemouridae†	4.0	68.6	Chironomidae	1.8	84.5
Perlodidae	3.9	74.3	Nemouridae†	1.8	86.7
Lepidostomatidae†	3.6	79.5	Chloroperlidae	1.6	88.7
Leptophlebiidae	3.4	84.5	Gammaridae†	1.5	90.7

†shredder invertebrates

Table 4 Results of GLMMs testing of the effects of stream types related to geological characteristics (G), season (S), and their interactions on overall (a), microbial (b), and invertebrate (c) decomposition rates (*k*) of leaf litter. *p*-values were produced in GLMM for the Wald Z-statistic. Bold letters indicate statistical significance. SD represents standard deviations.

(a) Coefficients	Estimates	SD	*p*-value
Intercept	-3.687	0.2017	**<0.001**
G (volcanic relative to non-volcanic)	0.0483	0.1722	0.779
S (winter relative to summer)	-0.6046	0.2466	**0.014**
G ×S	0.285	0.135	**0.035**

(b) Coefficients	Estimates	SD	*p*-value
Intercept	-3.6691	0.1485	**<0.001**
G (volcanic relative to non-volcanic)	-0.3713	0.0775	**<0.001**
S (winter relative to summer)	-1.0229	0.2022	**<0.001**
G ×S	0.5336	0.0748	**<0.001**

(c) Coefficients	Estimates	SD	*p*-value
Intercept	-6.756	0.407	**<0.001**
G (volcanic relative to non-volcanic)	1.371	0.407	**<0.001**
S (winter relative to summer)	1.201	0.494	**0.015**
G ×S	-1.086	0.398	**0.006**

Figure Captions

Fig. 1 Study sites in headwater watersheds of the Sorachi River, a tributary of the Ishikari River in Furano, Central Hokkaido, Japan. Symbols denote the site locations and their catchments are indicated by solid lines. The five volcanic sites are represented by open circles with site names accompanied by asterisks, while open triangles represent the five non-volcanic sites. Map colors correspond to different rock types in the area.

Fig. 2 Daily average temperature of the two stream types during summer (top) and winter (bottom) obtained from temperature loggers measuring continuously at 15-minute intervals. Data shown are only for time periods where all temperature loggers were able to record at the same time. Mean value was obtained from simultaneous temperature readings of different sites for each stream type (n=4 for summer volcanic, one site was not included due to logger malfunction; n=5 for summer non-volcanic; n=5 for winter volcanic; n=5 for winter non-volcanic). Solid lines represent volcanic stream type and dashed lines represent non-volcanic stream type.

Fig. 3 Boxplots showing taxonomic richness (a) and Shannon-Weiner diversity index (b) of the entire invertebrate community and the abundance (c) and biomass (d) of shredder invertebrates in two seasons (summer and winter) in the two stream types (non-volcanic and volcanic). Alphabetical letters indicate the results of multiple comparisons among groups after GLMMs testing of effects of season, stream type, and their interactions. For taxonomic richness, diversity index, and abundance, four groups were compared; groups accompanied by the same letter are statistically indistinguishable. For biomass, group comparisons were conducted for two main factors (season and stream type); unbracketed capital letters indicate statistically different groups between seasons, while bracketed capital letters indicate different groups between stream types across two seasons.

Fig. 4 Boxplots showing decomposition rate (*k*) for overall decomposition (a), microbe-mediated decomposition (b), and invertebrate-mediated decomposition (c) observed within each litter bag in two seasons (summer and winter) in the two stream types (non-volcanic and volcanic). Alphabetical letters indicate the results of multiple comparisons among groups after GLMMs testing for effects of season, stream type, and their interactions. In all cases, four groups were compared with each other; groups accompanied by the same letters are statistically indistinguishable.

Fig. 5 Graphical summary of results of SEM analyses in two seasons (summer and winter) for effects of geology on microbe *k* via environmental variables (a, d), effects of geology on invertebrate *k* via environmental variables, and shredder invertebrate abundance (b, e), and effects of geology on invertebrate *k* via environmental variables and shredder invertebrate biomass (c, f). Only statistically significant pathways are shown as arrows with positive effects in red and negative effects in blue. Standardized coefficients of the effects are listed in boldface beside corresponding arrows. R-squared values (in normal typeface) are shown for significantly explained response variables. Abbreviations: geo for volcanic proportion; temp for temperature; disc for flow discharge; vel for local flow velocity; sed for the total amount of sediment on coarse litter bag; abun for abundance; mass for biomass; and TP for total phosphorus.

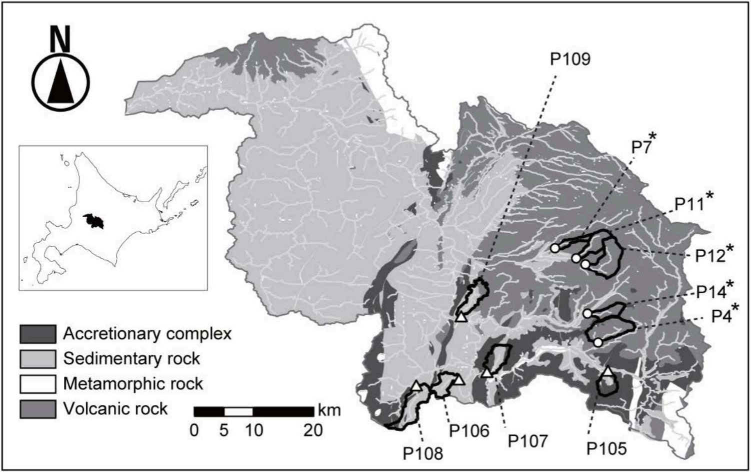
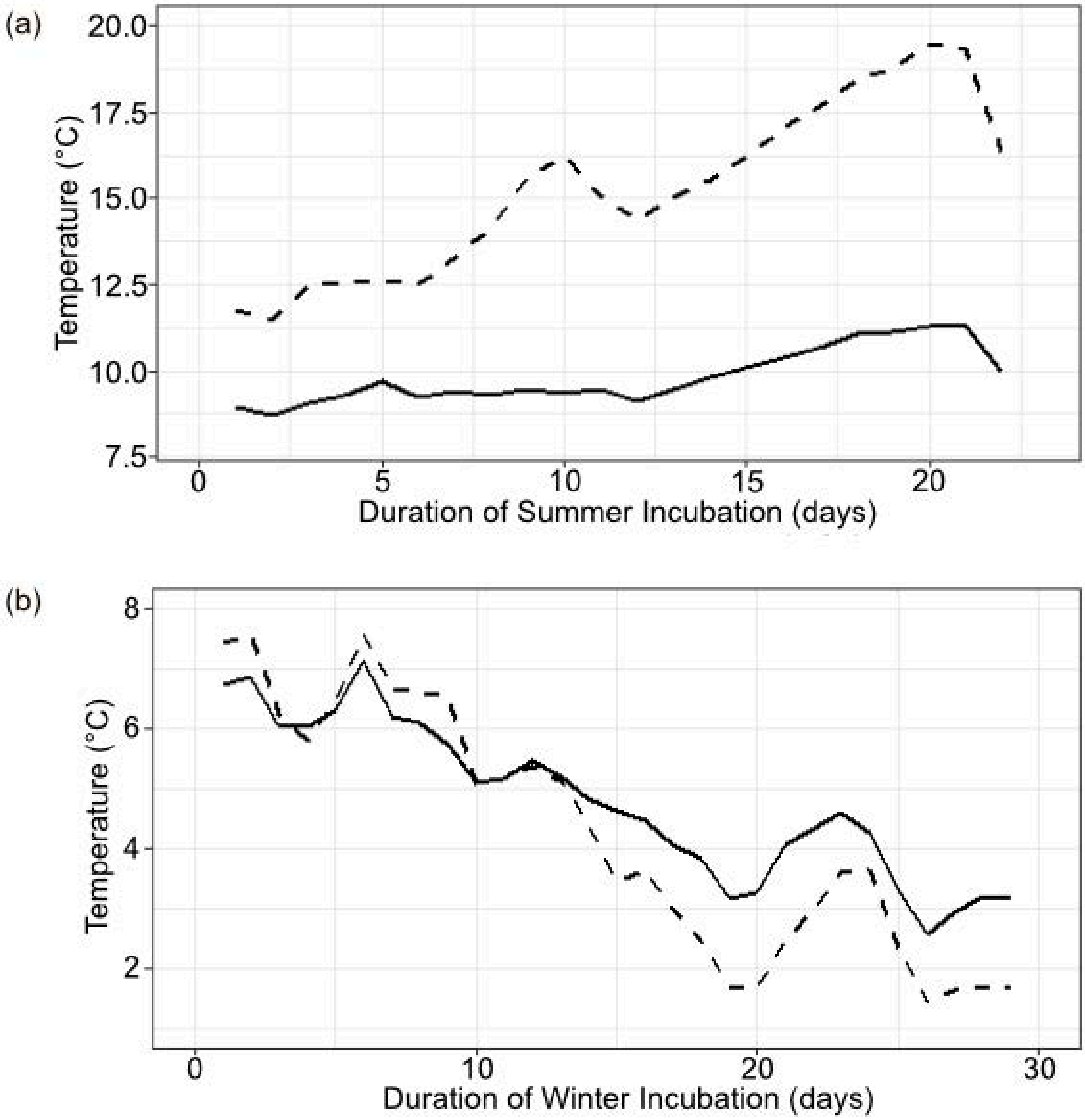
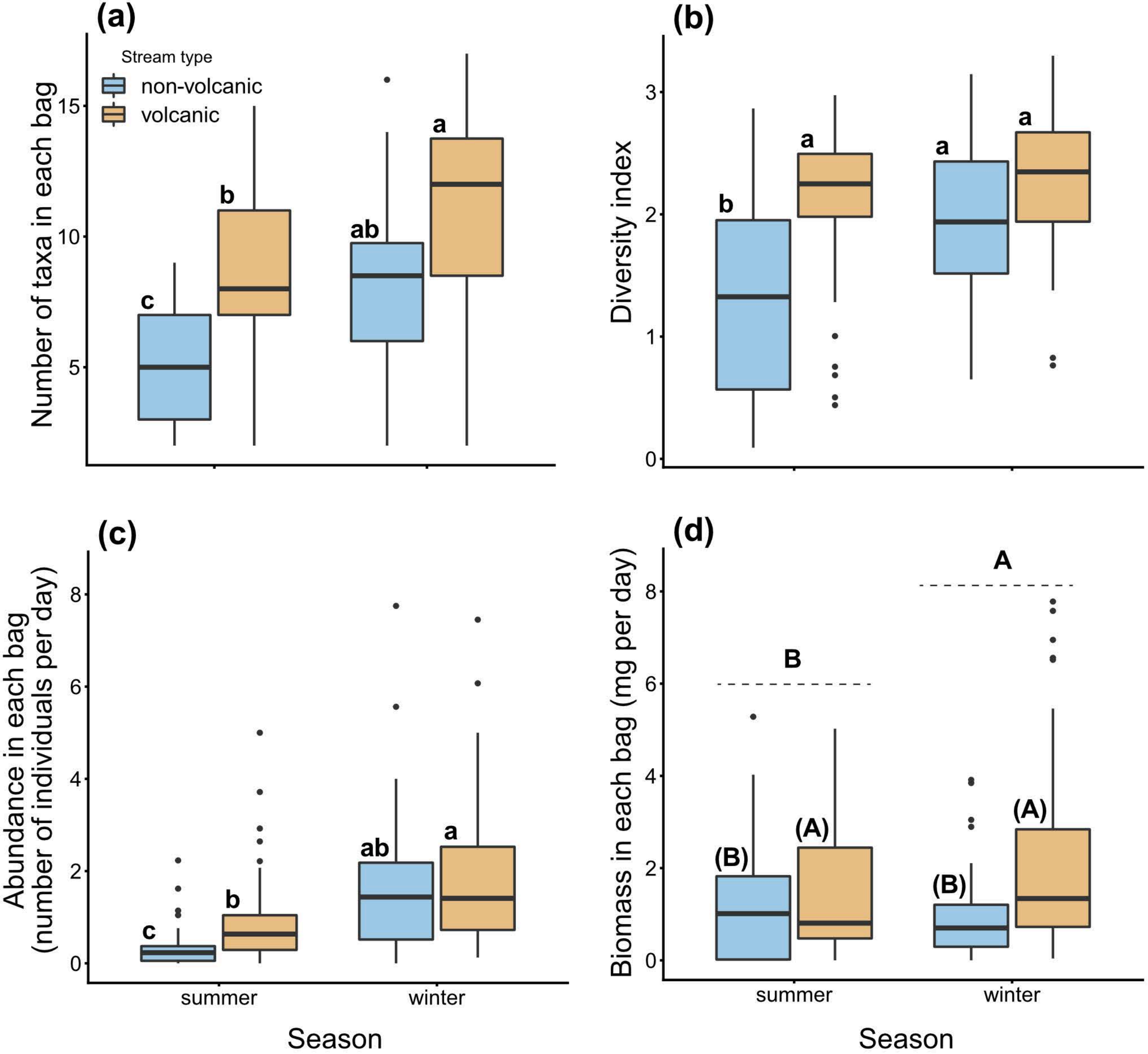
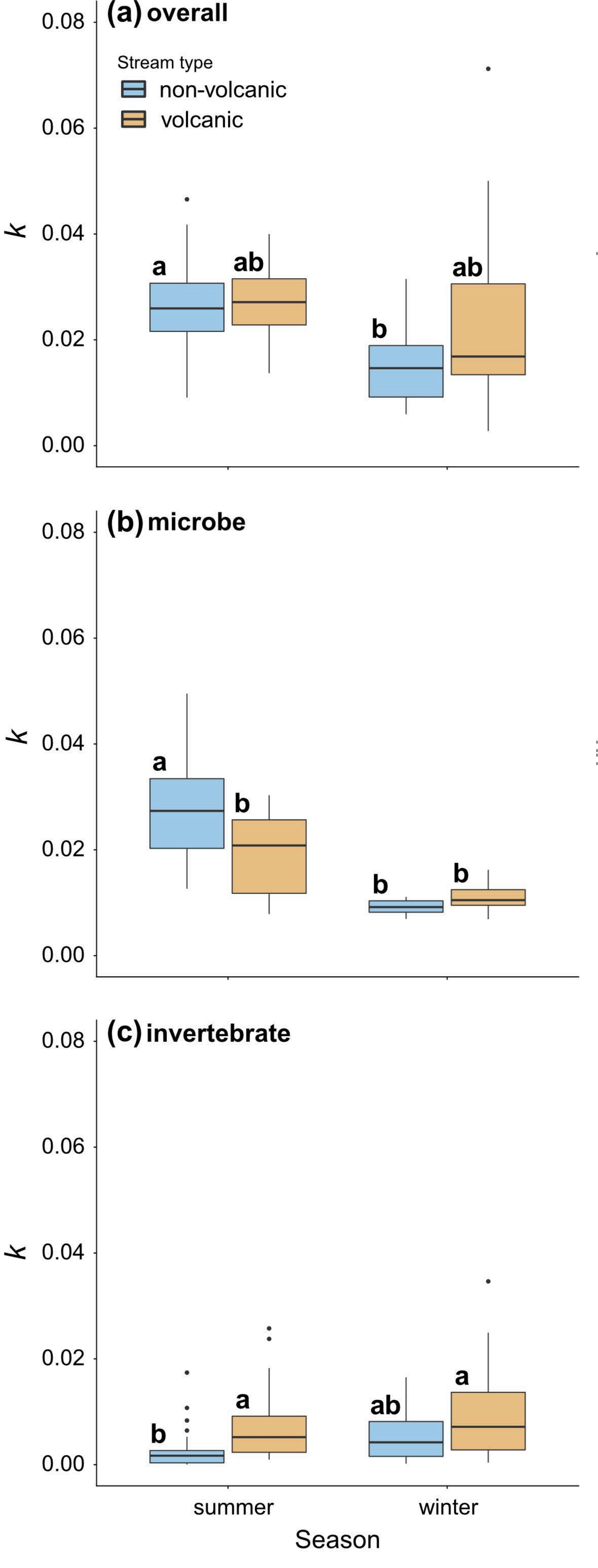


Fig. 1 Tolod et al. 2022


(a)
Temperature (°C)
20.0
17.5
15.0
12.5
10.0
7.5
0
5
10
15
20
Duration of Summer Incubation (days)
(b)
Temperature (°C)
8
6
4
2
0
10
20
30
Duration of Winter Incubation (days)


(a)
Stream type
non-volcanic
volcanic
Number of taxa in each bag
5
10
15
c
b
ab
a
(b)
Diversity index
0
1
2
3
b
a
a
a
(c)
Abundance in each bag
(number of individuals per day)
0
2
4
6
8
c
b
ab
a
summer
winter
Season
(d)
Biomass in each bag (mg per day)
0
2
4
6
8
B
A
(B)
(A)
(B)
(A)
summer
winter
Season


(a) overall
(b) microbe
(c) invertebrate
Stream type
non-volcanic
volcanic
k
0.00
0.02
0.04
0.06
0.08
a
ab
b
ab
a
b
b
b
b
a
ab
a
summer
winter
Season

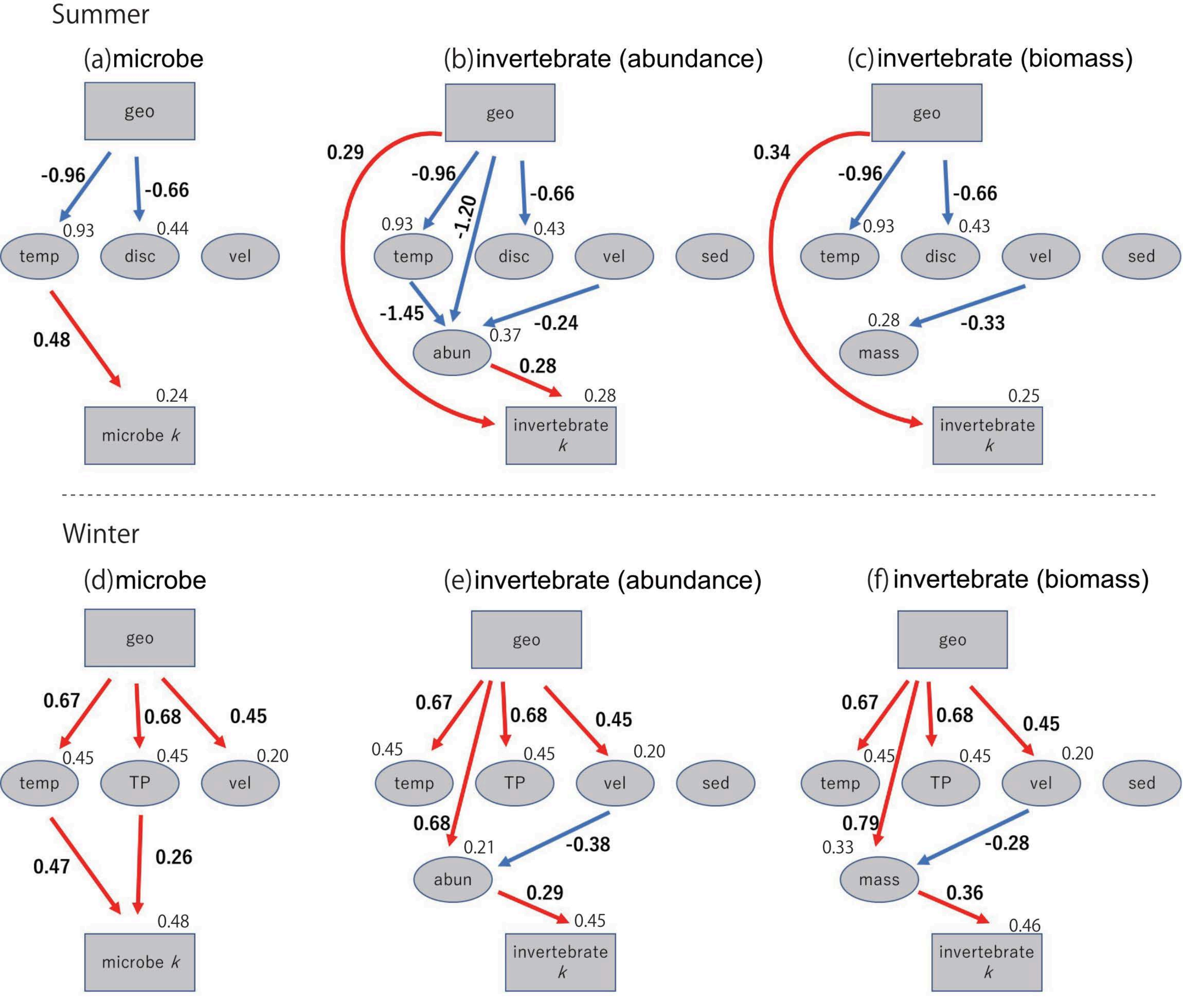


Fig. 5 Tolod et al. 2022