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

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23
24 **Abstract**

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

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

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

41 **Statements and Declarations**

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

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53

54 **Data Availability Statement**

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

57 **Declarations**

58 **Conflict of interest**

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

60

61 **Introduction**

62 Aquatic communities and ecosystem functions are affected by abiotic factors such as water chemistry,
63 temperature, and nutrient availability. Studies assessing the direct effects of physical and chemical
64 characteristics of the river on different aquatic organisms and processes are extensive (see Boyero et al.,
65 2011; Dallas & Ross-Gillespie, 2015; Chase et al., 2017), but few have considered the possible contribution
66 of regional factors such as underlying geology (i.e., lithology of the substratum), which could indirectly
67 affect aquatic processes through their influence on water quality. Underlying geology can dictate
68 groundwater influence. Rivers with highly permeable underlying rocks would mean a stronger influence of
69 groundwater to surface water (i.e., in spring-fed streams) than those with less permeable substratum (i.e.,
70 in run-off streams). A noticeable influence of groundwater to surface water is demonstrated in the relatively
71 stable temperature regime of spring-fed streams, mainly due to the buffering effect of groundwater
72 temperature to surface water temperature (Kaandorp et al., 2019).

73 Studies that relate geology and limnology are primarily in the field of hydrology, hydrogeology,
74 and geomorphology (Younger, 1995; Mosher et al., 2010), and those that involve ecological components
75 are mostly done on spring-fed rivers draining chalk and limestone aquifers (Berrie, 1992; Lusardi et al.,
76 2021), with very few comparing rivers with different groundwater influence (Sear et al., 1999). Existing
77 literature showed consistency in assessing spring-fed streams as relatively stable physical and chemical
78 environments in terms of flow, temperature regime, and food availability compared to run-off streams, with
79 variations in water quality resulting in different adaptations of invertebrate communities (see Death &

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

86 In headwater streams, allochthonous organic matter in the form of plant litter fuels the aquatic
87 food web (Vannote et al., 1980). Leaves are the main components of litterfall, amounting to as high as 73%
88 of total annual litterfall during the autumn season (Abelho, 2001). Upon reaching the aquatic system, leaf
89 litter undergoes decomposition and is either directly incorporated into the biomass of detritivores,
90 metabolized to carbon dioxide, or transformed into other products such as dissolved organic matter and fine
91 particulate organic matter (Wallace et al., 1995). Disentangling organic matter processing pathways and
92 the major factors influencing them, including those of anthropogenic and natural origins, is essential for
93 both aquatic biodiversity conservation and global carbon cycling. Organic matter exported in various forms
94 is provided to downstream reaches to sustain productivity (Wipfli et al., 2007), and the emitted carbon
95 dioxide can contribute substantial amounts to global carbon fluxes (Raymond et al., 2013). Decomposition
96 processes integrate a myriad of biological, physical, and chemical processes in rivers, providing an
97 important metric of river health assessment with a focus on functions (Young et al., 2008; Niyogi et al.,
98 2013). Organisms (mainly fungi, bacteria, and macroinvertebrates) are the driving forces in aquatic
99 decomposition; however, these organisms depend on the substrate and surrounding environment (Graça,
100 2001). Thus, intrinsic factors (i.e., leaf chemistry, macroinvertebrate preference) and extrinsic
101 environmental factors (i.e., water quality, temperature, nutrient availability, seasonality) can play important
102 roles in decomposition (Boyero et al., 2021a, b). Geology is a primary driver of variation in both factors
103 via controls on water chemistry, nutrient content, channel geomorphology, and watershed hydrology, which
104 elicit different responses from aquatic organisms, including benthic macroinvertebrates through adaptations
105 in osmoregulation, feeding, habitat, and temperature regimes (Olson, 2012; Ishiyama et al., 2021; Lusardi
106 et al., 2021).

107 This study examined if geology affects water quality and macroinvertebrate detritivores, indirectly

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

122

123 **Materials and Methods**

124 *Study site*

125 The study was conducted within 100-m long sections of ten forested streams in Furano, Central Hokkaido,
126 Japan, encompassing an area of approximately 600 km² (Figure 1). All study sites are tributaries of the
127 Sorachi River, which belongs to the Ishikari River drainage system, and are drained by similar-sized
128 catchments. During the Quaternary Period, eruptions of the Daisetsu Mountain system covered the area
129 from the northeast with pyroclastic flow deposits and formed surficial geology dominated by volcano-
130 derived rock (Ikeda & Mukoyama, 1983; Nakamura, 2016). The study streams were chosen such that they
131 differed in geological characteristics and were categorized into two types; volcanic and non-volcanic (five
132 sites/streams each) according to the dominant underlying rock type based on the Seamless Digital
133 Geological Map of Japan (Geological Survey of Japan, National Institute of Advanced Industrial Science
134 and Technology). Volcanic stream types have underlying geology composed of Early Pleistocene non-

135 alkaline pyroclastic flow volcanic rocks. In contrast, non-volcanic stream types have Early to Late
136 Cretaceous accretionary complexes, metamorphic rocks, marine muddy turbidite, and late Pleistocene to
137 Holocene marine and non-marine sediments in their respective watersheds. The mean (\pm standard deviation)
138 percentage of the volcanic geological layer for each catchment (volcanic proportion) was 99.9 (\pm 2.0) for
139 volcanic streams and 6.4 (\pm 12.80) for non-volcanic streams (Table S1.1).

140 According to the weather record at the Furano weather station of the Japan Meteorological Agency,
141 approximately 20 km northwest of the study area, the mean annual temperature and annual precipitation
142 (\pm standard deviation) for the period 2010 – 2021 were 6.98 (\pm 0.32) °C and 1060.09 (\pm 208.86) mm,
143 respectively; mean monthly air temperature was highest in July (21.31 °C) and lowest in January (-8.25 °C).
144 Higher resolution (1km x 1km) of mean annual precipitation and air temperature data obtained for each
145 catchment using 30-year data (1980 – 2010) showed similar climatic characteristics between the two stream
146 types ($P=0.475$ for mean annual precipitation and $P=0.174$ for mean annual temperature) (adjusted alpha =
147 0.008, see Statistical Analyses). Volcanic and non-volcanic streams recorded 1063.71 - 1292.58 mm and
148 1088.85 - 1580.80 mm mean annual precipitation, and 2.66 - 4.13 °C and 3.11 - 4.82 °C mean annual air
149 temperature, respectively (Table S1.1). Selected volcanic and non-volcanic streams are similar in elevation
150 ($P=0.019$) (Table S1.1), slope ($P=0.034$) (adjusted alpha = 0.008, see Statistical Analyses), and catchment
151 size ($P=0.897$) (Table S1.2). High-resolution land-use and land cover maps used to calculate the proportion
152 of forest type in the catchment using ArcGIS Pro (ESRI, version 2.4.0) showed that stream catchments
153 were mainly composed of broadleaf forest and small percentages of needleleaf forest (Table S1.3). Overall,
154 forest cover was high (92% in volcanic and 99% in non-volcanic streams), but there was a slight difference
155 in forest cover between the two stream types due to the relatively lower broadleaf forest cover in one of the
156 volcanic sites (P4) (Table S1.3).

157

158

159 *Leaf decomposition experiment*

160

161 Leaf litter packs were mimicked using 3.0 ± 0.1 g (mean dry weight \pm standard errors) of *Alnus japonica*
162 (Thunb.) Steud. (Japanese Alder) placed inside leaf litter bags (hereafter litter bags) with fine and coarse
163 mesh nets (see Appendix S1). Fine mesh (257 x 266 μ m) bags allow only microorganisms (bacteria and

164 fungal conidia) to enter, while coarse mesh bags enable access to both microorganisms and
165 macroinvertebrates. The coarse mesh bag is a hybrid of two net sizes (black net: 3.9 x 3.9 mm; green net:
166 1 x 1 cm), with the bottom portion (touching the riverbed) having black net only and the top portion having
167 half green and half black net. The green part (facing upstream) accommodates larger shredders observed in
168 the study sites during reconnaissance, and the black part (facing downstream) prevents the loss of
169 fragmented alder leaves. Gholz et al. (2000) applied a similar principle of using two mesh sizes for leaf
170 decomposition experiments. Two types of leaves were used to capture heterogeneous litter decomposition
171 associated with leaf conditions: green and old senescent leaves during summer and old senescent and new
172 senescent leaves during winter. Green leaves represent fresh leaves falling in summer due to wind or rain
173 action. Old senescent leaves represent lateral input of remaining litter from the previous fall season while
174 new senescent leaves represent both vertical and lateral input during the current fall season (see Appendix
175 S2 for litter bag preparation).

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

192

193 *Collection and processing of litter bags*

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

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

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

222

223 *Estimation of physical and chemical parameters*

224 For each site, one temperature logger (Hobo pendant temperature/light logger, UA-002-08, Onset Computer
225 Corp., Massachusetts, USA) recording every 15 minutes was set up from the start of the litter bag incubation
226 period until the collection of the last set of litter bags. Two types of temperature data were used for
227 subsequent analyses. For comparing stream types (in Table 1), the average temperature was obtained by
228 getting the mean value of all sites per day for each stream type. For structural equation modeling (SEM)
229 analyses (see Statistical analyses), the average temperature used was the mean temperature for each site for
230 every incubation period. Electrical conductivity (EC) and pH were recorded in each stream during set-up
231 and every litter bag collection using a handheld EC/pH meter (WM 32EP, DKK-TOA Co., Tokyo, Japan).
232 Water samples were collected using 250-mL acid-washed polyethylene bottles once from each site for each
233 season. The collected water was filtered through a 0.5µm filter paper (GC-50 Advantec, Tokyo, Japan) and
234 subjected to an ion analyzer (IA-300, DKK-TOA Corp., Tokyo, Japan) to determine chloride (Cl⁻),
235 phosphate (PO₄³⁻), sulfate (SO₄²⁻), nitrite (NO₂⁻) and nitrate (NO₃⁻) concentration. Nitrite and phosphate
236 were below the detection limit (0.05 mg/L) in all cases and thus were no longer reported hereafter. An
237 unfiltered portion was subjected to digestion using the colorimetric method and eventually to
238 spectrophotometry (UV-1280, Shimadzu Corp., Japan) to obtain total nitrogen (TN) and total phosphorus
239 (TP) concentration using a method described in Rahman et al. (2021). Winter water samples were obtained
240 in November 2018, while for the summer data, water samples were obtained in August 2019.

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

246 consistently taken at approximately 60% of the depth relative to the water surface.

247

248 *Estimation of decomposition rates*

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

251
$$AFDM_r = e^{-kt}$$

252

253 where:

254
$$AFDM_r \text{ (remaining AFDM)} = \text{final AFDM (g)} / \text{initial AFDM (g)}$$

255
$$t = \text{incubation duration (days)}$$

256
$$k = \text{breakdown rate coefficient}$$

257

258 To fit the model, $AFDM_r$ obtained for leaf bags at the first collection was processed to provide
259 mean values that corresponded to each combination of mesh type and leaf type (mean $AFDM_r$ at the first
260 collection). The initial $AFDM_r$, which was assumed to be 100, the mean $AFDM_r$ at the first collection, and
261 $AFDM_r$ at the second collection were used in non-linear least square regression (nls function in R software;
262 see Statistical analyses below) with the corresponding t to obtain a total of 12 k values (six each for fine k
263 and coarse k) for each stream. Fine k represents largely microbial decomposition process (hereafter microbe
264 k), whereas coarse k represents microbial and macroinvertebrate shredder activities (hereafter overall k).

265 Decomposition rate due to shredder activity only (invertebrate k) was also approximated. To obtain
266 the approximate value of final AFDM if only detritivore consumption happened (i.e., excluding the
267 contribution of microbes), the lost AFDM due to microorganism (fine mesh) decomposition was added to
268 the remaining AFDM obtained for coarse mesh samples. In instances where approximate final AFDM due
269 to macroinvertebrates only exceeds the initial AFDM (fine mesh decomposition was greater compared to
270 that in the coarse-mesh bags because of slight differences in leaf mass at the beginning), the value of initial
271 AFDM was adopted as the final AFDM, so that contribution due to macroinvertebrates is approximated as

272 zero and is considered irrelevant. In total, 18 k values (six replicates for each type of k) were estimated for
273 each stream in each season.

274

275 *Statistical analyses*

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

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

296 To identify the drivers through which geological differences in catchments affect decomposition
297 rates directly and indirectly, structural equation modeling (SEM) was adopted, with microbe k and
298 invertebrate k as response variables. The modeling was performed in three cases in each season: one for

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

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

327

328 **Results**

329 Stream-type difference reflected through water temperature was more evident in summer than in winter,
330 with volcanic and non-volcanic streams ranging from 9.10 – 10.86 °C and 13.63 – 16.14 °C, respectively,
331 during summer incubation and 4.28 – 6.06 °C and 3.63 – 4.87 °C, respectively, during winter incubation
332 (Table S3.1). In summer, volcanic streams recorded significantly lower water temperature while in winter,
333 temperature was significantly higher in volcanic than non-volcanic streams (Figure 2, Table 1). Based on
334 this result, water temperature was considered as a possible factor affecting *k* in the SEM analyses later.
335 Although not statistically significant, discharge in summer was relatively higher in non-volcanic streams
336 (0.432 ± 0.198 m³/s) than volcanic streams (0.209 ± 0.048 m³/s), and TP concentration in winter was
337 relatively higher in volcanic (0.025 ± 0.009 mg/L) than non-volcanic streams (0.015 ± 0.004 mg/L) (Table
338 S3.1 and S3.2). The pattern observed in TP was due to a decrease in TP concentration in non-volcanic
339 streams during winter while the concentration in volcanic streams remained similar in the two seasons.

340 A total of 18,938 macroinvertebrate individuals (7,013 in summer and 11,925 in winter) were
341 collected from the coarse litter bags. In eight fine litter bags, an average of four early instars Chironomidae
342 (17 individuals at the most) per bag were found, which were 0.57-7.69% of the Chironomidae abundance
343 in their paired coarse bag. Because of the small body size and lower abundance compared to those found
344 in the coarse litter bags, the presence of Chironomidae larvae in the fine mesh bags was assumed to have
345 no substantial contribution to decomposition and was not included in the analyses. Community differences
346 between river types and seasons were observed in diversity indices and shredder community structure.
347 Taxonomic richness and Shannon-Weiner index were higher in volcanic streams in summer (Table 2 a, b;
348 Figure 3 a, b). Detritivores comprised 68.9 and 80.8% of the abundance and biomass of all samples,
349 respectively, with some variations between seasons and river types (Figure S3). Shredder abundance was
350 higher in volcanic streams in summer (Table 2 c, Figure 3 c). Shredder biomass was higher in winter
351 compared to summer, and volcanic streams exhibited higher values in both seasons (Table 2 d, Figure 3 d).
352 The results of SIMPER indicated that shredder taxa were among the most critical groups in distinguishing
353 river-type communities (Table 3).

354 Decomposition rate exhibited various responses to seasons and river types depending on the type

355 of k , with all cases having statistically significant interactions between two factors (Table 4, Figure 4).
356 Overall, k seasonally fluctuated in nonvolcanic streams, whereas volcanic streams showed relatively stable
357 values. Microbe k was higher in summer and decreased in winter in non-volcanic streams, whereas the
358 decreasing trend in volcanic streams was statistically insignificant. These seasonal trends in microbe k were
359 consistent with those in overall k , although the degree of the change was lesser in the latter. Damped
360 seasonal contrasts in overall k were explained by the trends in invertebrate k , which offset the seasonal
361 changes in microbe k . The invertebrate k was lowest in non-volcanic streams in summer and was relatively
362 higher in volcanic streams in both seasons.

363 All SEM exhibited acceptable levels of goodness of fit (Fisher's C statistics, $p > 0.09$ in all cases).
364 Temperature was the most important environmental factor by which surface geology affected microbe k in
365 both seasons (summer: standard coefficient (coef) = 0.48, $r^2 = 0.24$; winter: coef = 0.47, $r^2 = 0.48$) (Figure
366 5 a, d). These pathways were directionally contrasting, with colder water in volcanic streams (coef = -0.96,
367 $r^2 = 0.93$) limiting the microbe k in summer and warmer water in volcanic streams (coef = 0.67, $r^2 = 0.45$)
368 promoting the microbe k in winter (Figure 5 a, d). In addition to temperature, relatively higher TP levels
369 associated with volcanic geology (coef = 0.68, $r^2 = 0.45$) also contributed to an increased microbe k in
370 winter (coef = 0.26, $r^2 = 0.48$). Indirect effects of surface geology affecting invertebrate k via shredding
371 invertebrates were apparent in three out of four cases (except for biomass in summer) (Figure 5 b, e, f). In
372 summer, the colder temperature in volcanic streams was associated with positive overall effects on shredder
373 abundance (coef = -1.45, $r^2 = 0.37$) and thus invertebrate k (coef = 0.28, $r^2 = 0.28$) (Figure 5 b); unknown
374 direct pathways were also detected for geology-invertebrate k relations (coef = 0.29 for abundance and 0.34
375 for biomass). In winter, both abundance (coef = 0.29) and biomass (coef = 0.36) adequately explained the
376 variation in invertebrate k ($r^2 = 0.45$ for abundance and 0.46 for biomass), although temperature-mediated
377 effects of surface geology on invertebrate k were undetected. The detected effects of surface geology on
378 invertebrate k via measured environmental factors included indirect effects of flow velocity through its
379 direct effect on abundance (coef = -0.38, $r^2 = 0.21$) and biomass (coef = -0.28, $r^2 = 0.33$) in winter; unknown
380 direct pathways were also detected for geology-shredder relations (abundance: coef = 0.68, $r^2 = 0.21$;
381 biomass: coef = 0.79, $r^2 = 0.33$).

382

383 **Discussion**

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

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

411 volcanic sites than in non-volcanic sites during summer and the expected shifting of the pattern was also
412 observed during winter, with volcanic streams having warmer water than non-volcanic streams especially
413 in the latter part of incubation. This contrast may be more pronounced later in winter because water
414 temperature in non-volcanic streams would have been more strongly affected by colder temperatures in the
415 middle of winter (i.e., January).

416 The structure of macroinvertebrate communities was distinctive in relation to the geological
417 characteristics of the contributing catchments. Variations in macroinvertebrate community composition
418 between streams having different groundwater influences have been reported by several studies on benthic
419 invertebrates (i.e., Barquin & Death, 2006; Lusardi et al., 2016). It has been noted that the relative stability
420 of the spring-fed system enables the provision of good quality and quantity of food resources. Interestingly,
421 invertebrate shredders appear to be particularly responsive to geological differences. Volcanic spring-fed
422 rivers were observed to have higher retention of large woody debris (Barquin & Death, 2004; Lusardi et al.,
423 2021), which, in addition to stable flow, could contribute to the possible retention of leaf litter, thereby
424 increasing the food availability for shredders.

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

437 It was also possible that the physical and chemical environment influenced by geology indirectly

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

467 concentration in non-volcanic streams during winter showed substantial contribution to the microbe-
468 mediated decomposition SEM, highlighting the importance of stability of TP concentration in the leaf
469 decomposition in volcanic streams.

470

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

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

507

508 **Conclusions**

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

519

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688 **Tables**

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

Water	EC	pH	Cl ⁻	NO ₃ ⁻	SO ₄ ²⁻	TP	TN	Discharge	Temperature
Quality	(mS/m)		(mg/L)	(mg/L)	(mg/L)	(mg/L)	(mg/L)	(m ³ /s)	(°C)

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

694

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

(a) Coefficients	Estimates	SD	<i>p</i> -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

699

(b) Coefficients	Estimates	SD	<i>p</i> -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

700

(c) Coefficients	Estimates	SD	<i>p</i> -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

701

(d) Coefficients	Estimates	SD	<i>p</i> -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

702

703 **Table 3** Results of SIMPER analyses with abundance (a) and biomass (b) showing overall dissimilarity
704 between communities of the two stream types, average contribution of ten most important taxa to overall
705 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

706

(b) Summer			Winter		
Overall dissimilarity	68.23%		Overall dissimilarity	77.70%	
	Average contribution (%)	Cumulative contribution (%)		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

707

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

(a) Coefficients	Estimates	SD	<i>p</i> -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

712

(b) Coefficients	Estimates	SD	<i>p</i> -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

713

(c) Coefficients	Estimates	SD	<i>p</i> -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

714

715

716 **Figure Captions**

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

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

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

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

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

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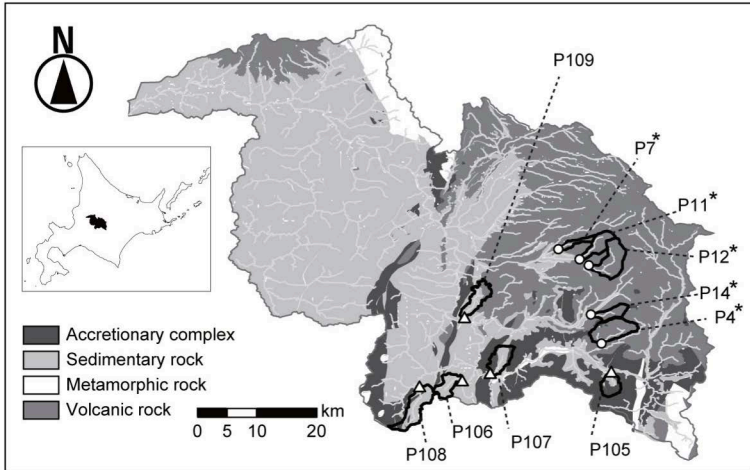
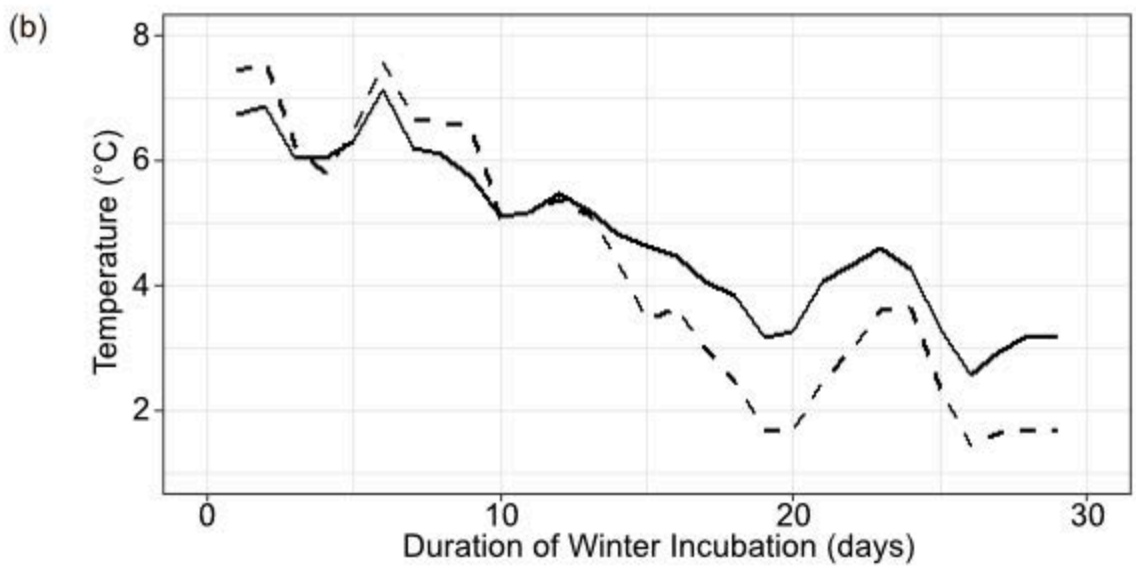
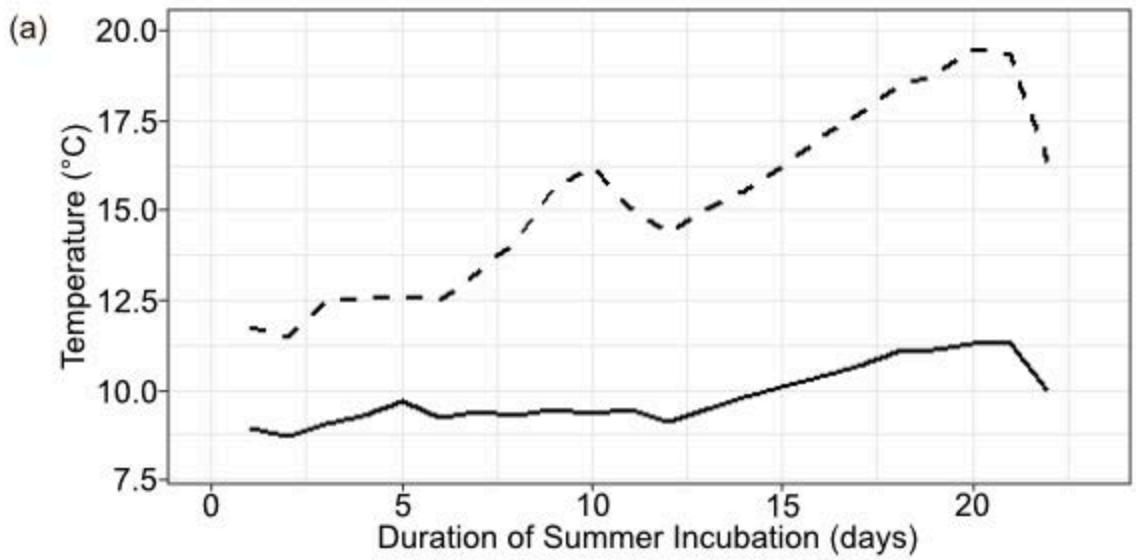
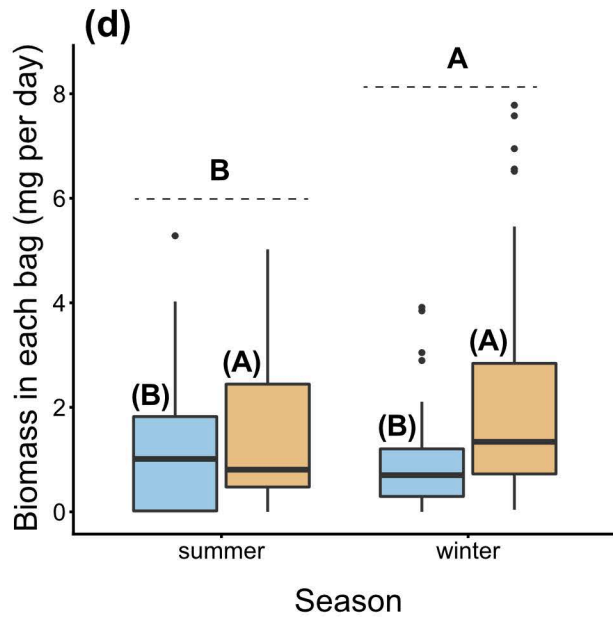
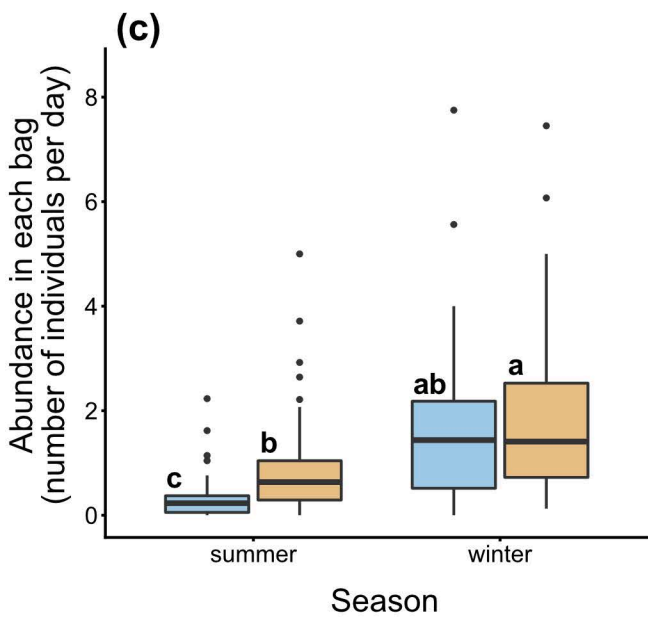
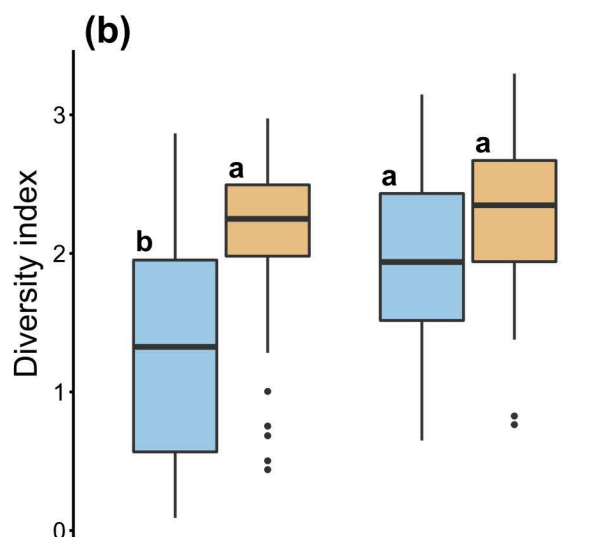
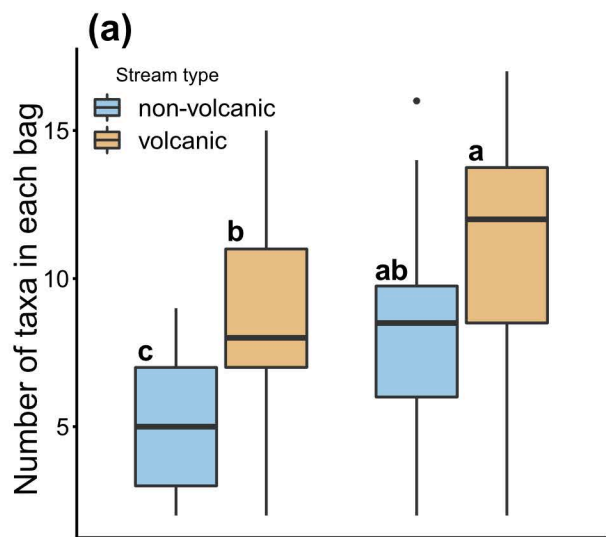
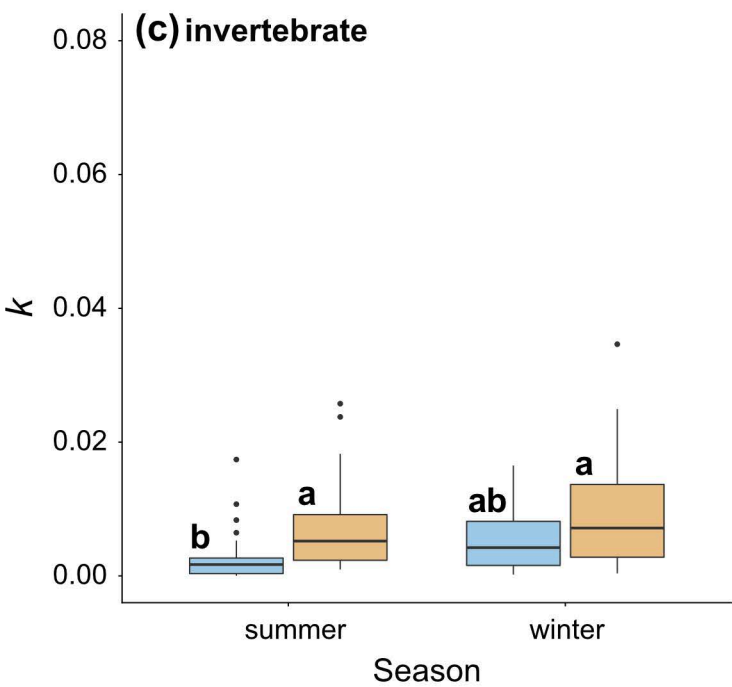
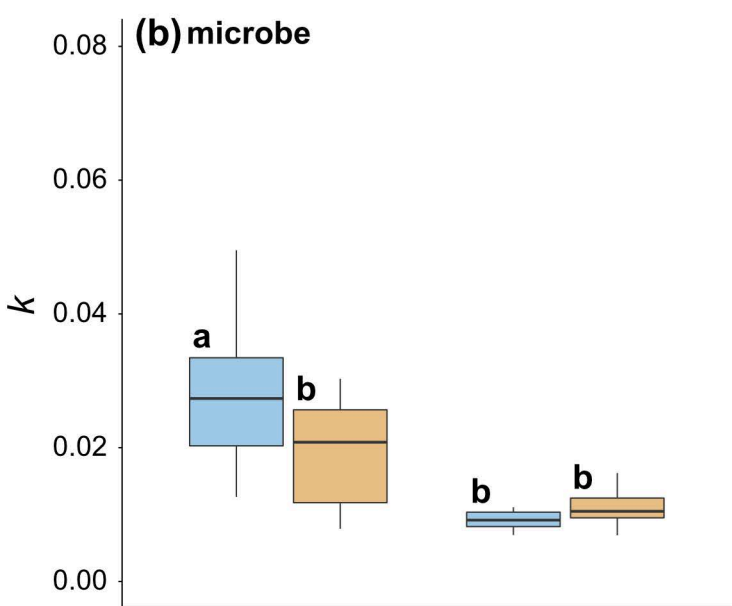
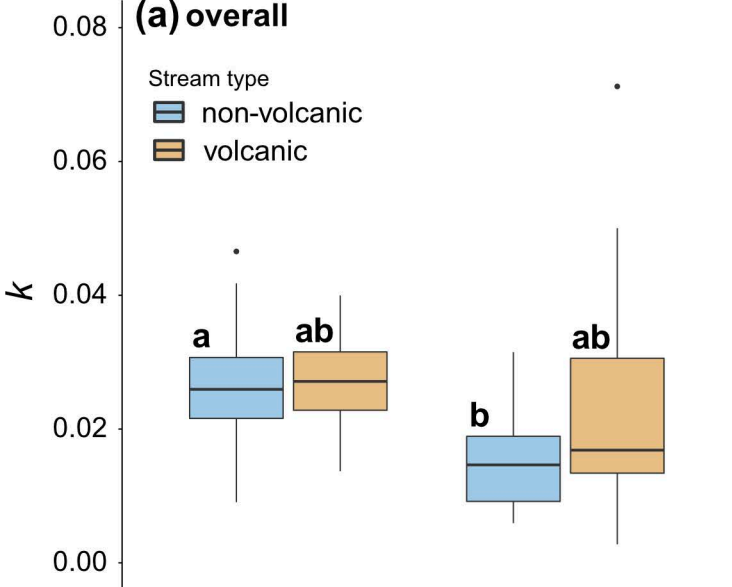


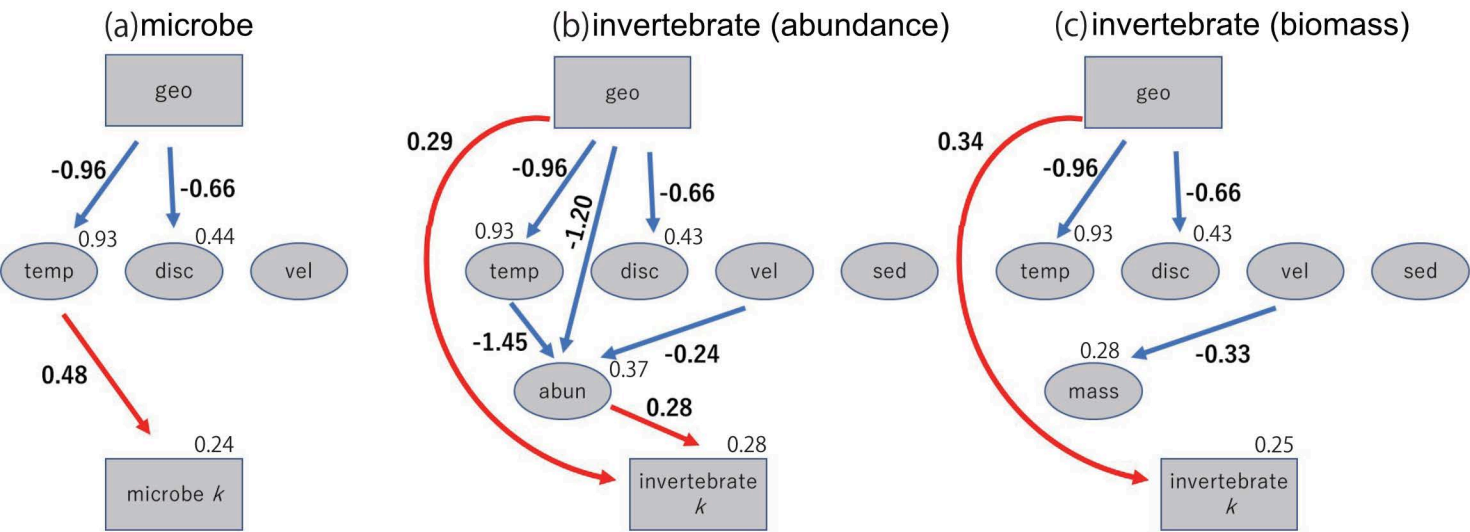
Fig. 1 Tolod et al. 2022







Summer



Winter

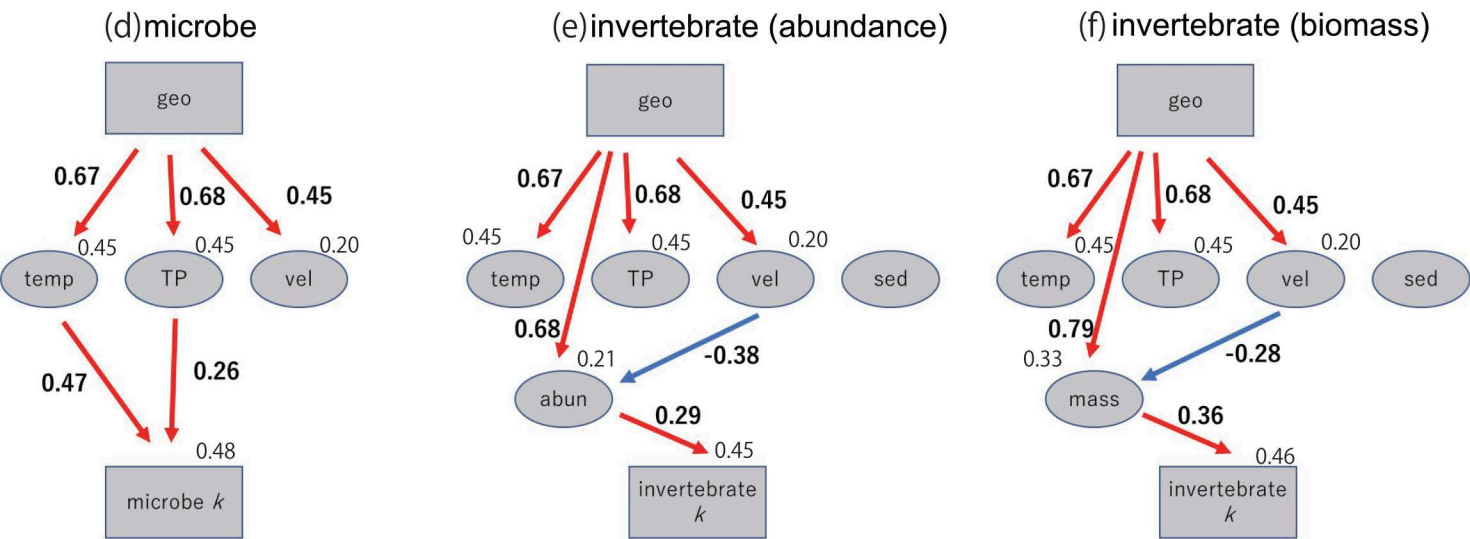


Fig. 5 Tolod et al. 2022