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Changes in macroinvertebrate community composition in two Norwegian glacier-fed rivers in response to rapid glacier retreat

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Briksdalsbreen (left) and Steindalsbreen (right), July 2022.

Preface

Finishing this thesis concludes my master's degree in Ecology at NMBU. I am grateful for all that I have learnt through six years of university education, especially in this past year when I was able to start scratching the surface of freshwater ecology.

Marianne Angård

Ås, 13 May 2023

Abstract

Glaciers are retreating globally in response to a warming climate, and the ecosystems of glacier-fed rivers are expected to change correspondingly. The macroinvertebrate community composition of glacier-fed rivers is shaped by the environmental constraints of the glacial meltwater input, which causes low temperatures and high substrate instability. An increase in biodiversity with decreasing glacial influence is therefore expected. This study, which is part of the international AASER25 project, aimed at identifying a possible upstream shift in benthic community composition, resulting in an increase in local biodiversity, in response to 25 years of glacial retreat in two contrasting Norwegian glacier-fed rivers. The study rivers, Dalelva and Leirungsåi, were sampled in July 2022 and the measured environmental parameters and macroinvertebrate diversity were compared to data sampled in the same rivers in 1997. Both source glaciers had retreated, and while discharge did not change during the 25 years, water temperature showed a marginally significant increase. Spot measurements of water temperature, turbidity and total P were higher, while conductivity was lower, in 2022 than in 1997. Alpha diversity, measured as richness and Shannon diversity, had increased, but the taxon compositions of the samples were more similar to each other in 2022 compared to 1997, suggesting a decrease in beta diversity. Shannon diversity correlated positively with spot measurements of temperature, conductivity, organic material, and pH, and negatively with turbidity and Pfankuch index. Coupled with the increased Shannon diversity since 1997, the correlations suggest changes in these environmental parameters as well. The results from this study show that there has in fact been a change in the macroinvertebrate community composition in the two study rivers, likely in response to glacial retreat and in line with what was expected. If the glacial meltwater input is reduced further, alpha diversity may continue to increase, while the beta diversity may be reduced, as the rivers become mainly snowmelt- or groundwater-fed.

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Introduction

Alpine streams

Rivers in alpine areas have three main sources of water: seasonal snow melt, glacial ice melt, and groundwater (Ward, 1994). Because these largely influence the hydrology of the streams and subsequently also their flora and fauna, alpine rivers are often categorized based on their main water source. A river just below a glacier will be dominated by glacial ice melt, before it gradually becomes snow- or groundwater-fed as the distance to the glacier margin increases and it is joined by non-glacial tributaries (Ward, 1994). Input of glacial melt water and eroded sediments in summer results in low water temperatures and unstable riverbeds, features that have a major impact on the benthic communities and creates a unique assemblage of specialised taxa (Milner & Petts, 1994). During winter, the river types may be more similar in physical properties, as well as in the macroinvertebrate community compositions, as they are mostly groundwater-fed at this time (Burgherr & Ward, 2001; Malard et al., 1999; Milner et al., 2001; Tockner et al., 1997).

Glacier-fed rivers are heterogeneous ecosystems due to their varying environmental conditions in both space and time (Brown et al., 2003; Smith et al., 2001). The melting regime of a glacier will influence the discharge, temperature, and suspended sediment load of the river, which may show large fluctuation during the summer melting period (Tockner et al., 1997; Ward, 1994). In addition to the gradual increase in water temperature and channel stability from glacier snout and downstream, tributaries may either enhance or reduce the glacial influence of a river, depending on its own source. Presence of lakes will have a warming and stabilizing effect on the downstream river, thereby reducing the effects of glacier meltwater input (Milner & Petts, 1994).

During the summer melting period, glacial rivers have high turbidity and generally low conductivity (Brown et al., 2003; Milner & Petts, 1994). Turbidity is a measure of water transparency, and cloudy water means more light is being scattered by sediment particles in the water, which gives higher turbidity values. Glacial rivers are generally more turbid than non-glacial rivers due to high eroded sediment loads which are released by the glacier (Brown et al., 2003; Ward, 1994). Conductivity measures the water's ability to conduct electrical currents and is connected to the amount of dissolved ions: more dissolved minerals in the water will give higher conductivity. Increased water temperatures will increase the conductivity. Large increases in conductivity in a water body may be an indicator of pollution

or changes in discharge, as the conductivity of undisturbed waters tends to be relatively stable (EPA, 2022).

The glacier melting regime also largely impact the nutrient balance of the glacial rivers. Mineral phosphorus (P) bound to eroded sediment particles can make the total P concentration relatively high in glacial rivers and lakes. Due to the high turbidity of glacial meltwater, and because soluble P is easily absorbed by sediment surfaces, most of the P found in glacial rivers is not dissolved but bound to mineral particles, and are therefore not bioavailable (Hodson et al., 2004; Lyche Solheim et al., 2020). Glacial rivers also have generally high total nitrogen (N) concentration compared to snowmelt-dominated rivers, with a gradual decline downstream (Warner et al., 2017). The high N concentration is likely due to atmospheric N accumulating in the glacier (Williams & Tonnessen, 2000) or leaching from surrounding tundra and exposed rock surface (Baron et al., 1994).

Macroinvertebrates

Milner and Petts (1994) proposed a conceptual model for predicting the composition of the macroinvertebrate communities of glacier-fed rivers. Due to the high level of stress and disturbance in these rivers, the benthic invertebrate species are almost entirely limited in their ability to colonise by the abiotic factors. High summer discharge and unstable river beds restrict dispersal of many taxa, and only cold water adapted species will be able to survive in the particularly low temperature of the streams with glacial input (Milner & Petts, 1994; Ward, 1994). Therefore, environmental variables such as water temperature and substrate stability, could be used to precisely predict the invertebrate taxa found in glacial rivers.

According to the model of Milner and Petts (1994), the invertebrate communities of glacier-fed rivers follow a gradual succession, from low-complexity communities with cold-water specialist taxa close to the glacier front, to more complex communities dominated by generalist species further downstream. The uppermost part of the glacial river, where the water temperature never exceeds 2°C, will be dominated by the subfamily Diamesinae in the non-biting midge family (Chironomidae). Diamesinae species are well adapted to the environment in rivers with high glacial influence, with flexible feeding strategies and high body-mass that increases further in particularly harsh conditions (Niedrist & Füreder, 2018). Other taxa which are less adapted to these extreme environments, such as the subfamily Orthocladiinae (Chironomidae) and black flies (Simuliidae), become present when the temperature increases to between 2°C and 4°C. When the water temperature exceeds 4°C, the

first mayflies (Ephemeroptera) and stoneflies (Plecoptera) are expected to be found, such as *Chloroperlidae*, *Nemouridae*, and *Baetidae*. Presence of lakes or inputs of non-glacial tributaries will speed up this process, while glacier-fed tributaries will slow it down and may also cause a set-back in the development of the benthic community (Milner & Petts, 1994).

The estimated diversity of macroinvertebrate communities will depend on which spatial level is measured (Cauvy-Fraunié et al., 2015). Biodiversity is commonly measured as alpha, beta and gamma diversity. The alpha diversity is the local-scale diversity within a community and is measured as the number of species within a reach. The beta diversity is the between-community diversity and is measured as the difference in number of species between reaches. Finally, the gamma diversity is the diversity at the regional scale, and is measured as the total number of species within a larger area, e.g. several rivers (Whittaker, 1972).

Impact of climate change

Because glacial rivers are heavily influenced by the glacier melting regime, these systems are expected to be substantially impacted by climate change (McGregor et al., 1995; Milner et al., 2009). Over the past decades, glacier retreat has accelerated globally (Hock et al., 2019), and in southern Norway a 10% glacial loss has been measured over the past 20 years, with the greatest loss being seen in areas with small glaciers (Andreassen et al., 2022). As glacier areas are reduced, the impact of ice melt on connected rivers also decreases and they gradually become more spring or snowmelt dominated, causing large changes to the physical habitat of the glacial rivers (Brown et al., 2007).

The macroinvertebrate community may show a fast response to hydrological changes due to climate warming. While the alpine landscape can create barriers for dispersal between rivers (Cauvy-Fraunié et al., 2015), macroinvertebrates can show fast dispersal within a river by drift of larvae or flight of adult individuals (Brittain & Eikeland, 1988; Lencioni et al., 2006; Milner, 1994). When the glacier influence is reduced, the gradual development of macroinvertebrate communities is therefore expected to shift upstream the river. Biodiversity is expected to increase in the upper parts of the river (alpha diversity), as cold-water specialist taxa are replaced by generalist taxa moving upstream (Brown et al., 2018; Milner & Petts, 1994). However, this will also lead to a decrease in abundance of the cold-water specialist taxa. When the glacial input is minimal, the specialist taxa is expected to disappear completely due to competition exclusion, resulting in a reduced biodiversity at a regional

scale (gamma diversity). Rare species specialized to glacier-fed rivers are therefore especially vulnerable to climate change (Brown et al., 2007; Milner et al., 2009).

Because of their low complexity and high sensitivity to changes in hydrology, macroinvertebrate communities in alpine river systems are well suited to be used as indicators of climate change (Milner et al., 2009). Accurate monitoring of long-term changes in the physical properties of glacial streams can be both difficult and expensive, as they are highly variable in space and time (Smith et al., 2001; Tockner et al., 1997). Analysing the macroinvertebrate community can therefore be a good alternative, as the species composition will reflect the general environment of the river and will therefore indicate physical changes in the ecosystem. Furthermore, as the alpine ecosystems usually have low anthropogenic influence, it is possible to exclude the impacts of other human activity and investigate the individual effects of climate change (Milner et al., 2009).

The AASER project

The EU-funded project Arctic and Alpine Stream Ecosystem Research (AASER), which ran from 1996 to 1999, investigated how macroinvertebrate communities varied according to environmental factors in glacier-fed rivers across an altitudinal and climatic gradient (Brittain & Milner, 2001a). The project aimed at validating the conceptual model of Milner & Petts (1994) and proposed that the knowledge can be used to predict future changes to macroinvertebrate species composition in glacier-fed rivers in response to climate change. AASER investigated several rivers across Europe, including rivers in the Pyrenees, the Alps, Iceland, Norway, and Svalbard. The resulting articles from the AASER study were published in a special issue of the journal Freshwater Biology (Brittain & Milner, 2001b).

The two Norwegian rivers included in AASER, Dalelva and Leirungsåi, were sampled in 1996 and 1997, and the results were presented in Brittain *et al*. (2001). They found that environmental variables connected to water temperature and channel stability were the most important in explaining the macroinvertebrate communities, especially during the summer period of high discharge. Leirungsåi showed a greater heterogeneity in environmental variables than Dalelva, which was explained by the large altitudinal range and variation in riparian vegetation of Leirungsåi, and the addition of glacial tributaries in Dalelva, which kept the glacial influence high. Furthermore, Diamesinae dominated closest to the glacier front in both rivers, with a gradual shift to more Orthocladiinae downstream. This change happened further upstream in Leirungsåi than in Dalelva due to the non-glacial tributaries in Leirungsåi.

In both rivers, lakes were shown to significantly affect the benthic invertebrate community composition.

This study is part of AASER25, a new investigation of the original AASER project's glacier-fed rivers after 25 years. Since the original study was done, climate warming has caused substantial declines in glacier covers globally, likely followed by environmental change in glacier-fed rivers. The goal of AASER25 is to investigate if there have in fact been changes to the macroinvertebrate communities during the past 25 years and whether this can be associated with a changed environment caused by decreased glacial influence, as predicted in the original study. The altitudinal gradient across Europe sampled in AASER was used as a space-for-time gradient to study the different successional stages of the benthic communities. Large declines in glacier cover within the study region since then have made it possible to re-examine the same rivers to evaluate their response to climate change.

Research aims

This study aimed at identifying how glacial retreat during the past 25 years has influenced the macroinvertebrate community composition of two Norwegian glacier-fed rivers. It is hypothesised that reduced glacier cover has resulted in increased temperature and channel stability, which in turn is likely to have caused the macroinvertebrate community composition to shift upstream the river, resulting in an increase in local biodiversity. To test this hypothesis, the specific aims of this study were (1) to investigate if and how the glacial extent in the catchment area and the environment in the study rivers (temperature and discharge) have changed during the past 25 years, (2) to quantify possible changes in temperature, Pfankuch index, turbidity, conductivity, total N, and total P over the past 25 years and how these variables, including organic material and pH, vary downstream in the study rivers, (3) to investigate if and how the macroinvertebrate richness and Shannon diversity in the study rivers have changed during the past 25 years, and how they vary downstream, and (4) to explore if any of the environmental variables (temperature, Pfankuch index, turbidity, conductivity, total N, total P, organic material, and pH) were correlated with the Shannon diversity, as this would indicate if the changes in the diversity, if any, can be connected to environmental changes.

Methods

Study area

The two glacier-fed rivers included in this study were Dalelva and Leirungsåi (Fig. 1), the same rivers which were studied in the original AASER project. These rivers were originally chosen because they represent contrasting climates: while Dalelva is situated in a coastal area of western Norway, dominated by a wetter oceanic climate, Leirungsåi is located in the central inland mountain area of Jotunheimen with a dryer continental climate.

Dalelva (Fig. 1, 3, 4) originates from Briksdalsbreen, a glacial arm of the larger Jostedalsbreen icecap. The oceanic climate gives high annual precipitation and a relatively low annual temperature range with mild winters. In contrast to the global tendency of decreasing glaciers during the past 100 years, Briksdalsbreen had an unexpected advance in the 1990s due to higher winter precipitation (Brittain et al., 2001). The glacier has since undergone a massive loss of ice and has retreated by about 1000 m between 1997 and 2022. The reaches sampled in 2022 in Dalelva spanned an altitudinal range from 350 m to 40 m a.s.l. and were situated between 450 m to 6 km from the glacier front. The width of the river varied from ca. 9 m to 20 m (Table 1).

In 1996/97 the glacier snout reached down into and covered a proglacial lake. Therefore, the first sampling reach was chosen just below this lake. The riparian vegetation below the lake was then, as now, dominated by birch and alder. In 2022, the glacier had retreated far beyond this lake, causing the uppermost part of the river to run over an area of bare rock, before it runs into the glacial lake. Further downstream, Dalelva also runs through the lakes Oldevannet and Floen, before running out into the fjord Nordfjord. The bedrock around Dalelva is mainly made up of gneiss and covered by moraine material (Brittain et al., 2001).

The glacial source of Leirungsåi is Steindalsbreen (Fig. 1, 2), a cirque glacier which has steadily decreased by ca. 9 m/yr since the 19th century (Brittain et al., 2001). The continental climate gives moderate annual precipitation and relatively large annual temperature range, with cold winters and warm summers. Since 1997, Steindalsbreen has retreated about 300 m, and a proglacial lake has formed in front of it. In 2022, the sampled reaches in Leirungsåi were distributed from 264 m to 23 km from the glacial snout, ranging from 1550 m to 970 m a.s.l (Table 1). Most of the reaches are situated above the treeline, with riparian vegetation varying from absent to lichen and grass, to dense willows, and finally dense birch forest in the lowest reaches. The width of the river varies between ca. 1 m to 10 m, and it runs through the

two lakes Øvre Leirungen and Gjende. The area surrounding the river is covered by moraine deposits, and the bedrock consists mainly of gabbro and gneiss (Brittain et al., 2001).

Table 1 River reaches sampled in Dalelva (BRI) and Leirungsåi (LEI) in 2022.

Station	Altitude (m a.s.l)	Slope (m m^{-1})	Main channel width (m)	Distance to glacier (km) 2022	Catchment glacier cover (%) 2022
BRI0	350	NA	10	0.45	78.82
BRI1	340	0.034	19	1.1	71.41
BRI2	300	0.016	9	2.0	66.82
BRI3	180	0.070	15	3.0	63.70
BRI4	70	0.021	26	3.6	54.79
BRI5	40	0.006	20	6.0	57.42
BRI7	150	0.068	9	NA	20.92
LEI1	1550	0.080	4	0.26	29.24
LEI2	1380	0.034	21	1.9	16.53
LEI3	1270	0.008	15	4.2	14.18
LEI4	1150	0.106	20	7.9	13.79
LEI5	1100	0.007	35	11.3	7.87
LEI6	986	0.051	20	15.3	7.04
LEI7	970	0.001	50	23.3	8.20
LEI8	1250	0.044	13	NA	0.00
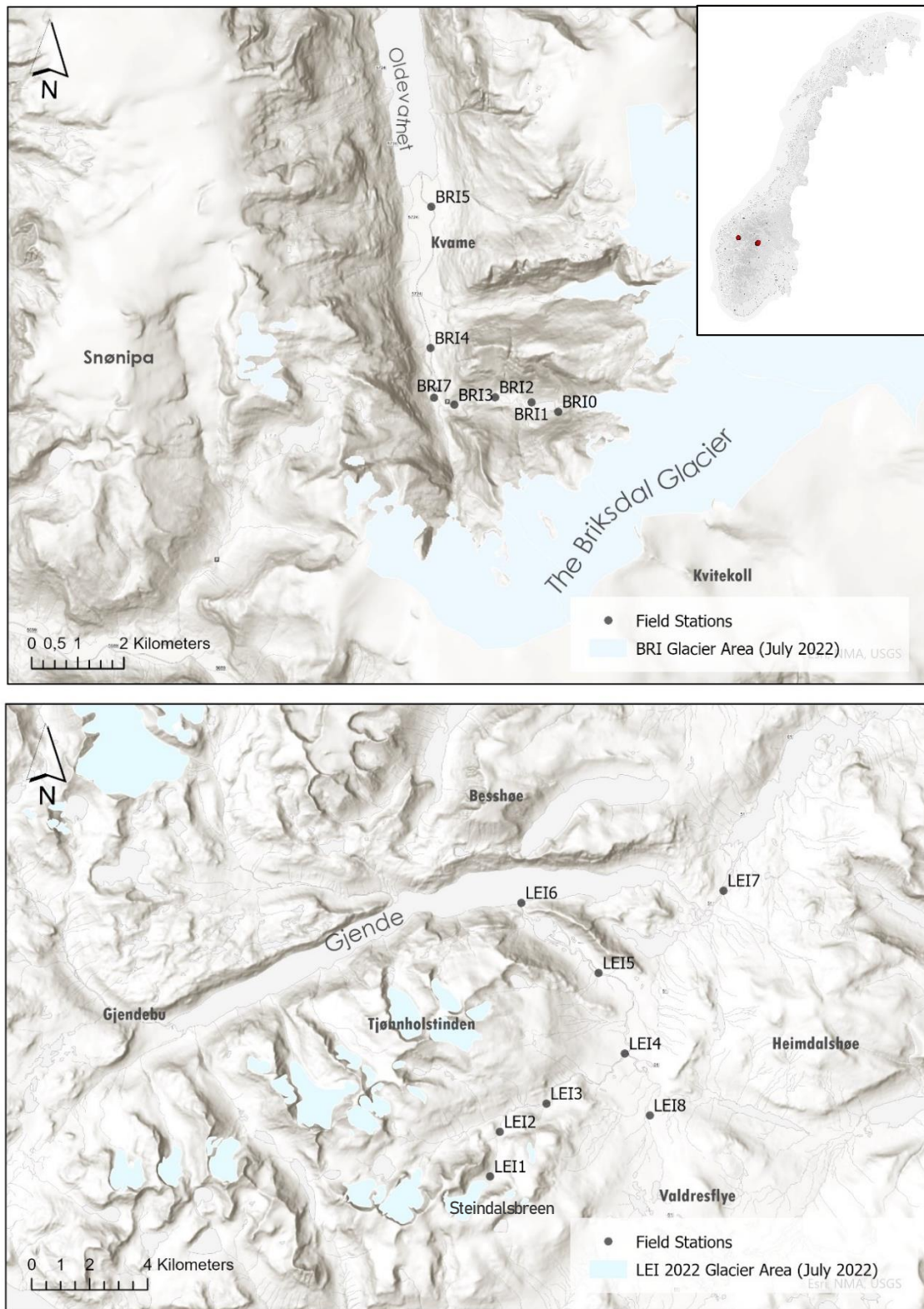
Fig. 1 Maps of the study rivers, Dalelva in Briksdalen in western Norway (top), and Leirungsåi in Jotunheimen in central Norway (bottom). In the map in the top right corner, the locations of Dalelva (left point) and Leirungsåi (right point) are marked with red points. All the field stations are marked with black points and glacial area is marked in light blue. Station BRI6 (not sampled in 2022) was located below lake Oldevatnet in Dalelva (area not included in map).

Fig. 2 Steindalsbreen, the glacial source of Leirungsåi, close to LEI1, taken in July 1996 (left) and 21 July 2022 (right).

Fig. 3 Dalelva by BRI4, in July 1996 (left) and 18 July 2022 (right). The glacier Melkevollbreen, another glacial arm connected to Jostedalsbreen icecap, can be seen in the background.

Fig. 4 Dalelva by BRI1, in July 1996 (left) and 19 July 2022 (right). Briksdalsbreen can be seen in the background in the picture from 1996, when it was reaching down into the proglacial lake.

Sampling sites

This thesis is part of the AASER25 project, with the main goal to re-investigate the study sites from the original AASER project to detect any possible changes to the macroinvertebrate communities after 25 years of glacial retreat. Therefore, the methods used for sampling the reaches closely followed the protocol from 1996/97 (Brittain et al., 2001), in order to obtain comparable results.

Data was collected during one sampling period 18-23 July 2022. The locations of the original 15 m long reaches were found using maps and photographs. Each reach was sampled once, and all measurements from a station were taken at the same time. In 1996 and 1997, data collection was done during three periods each year: spring (May-June), summer (July-August-September), and autumn (September-October). The summer sampling was done in mid-late July for both rivers in 1997 (15-29 July), and for Leirungsåi in 1996 (30-31 July and 1 August). However, summer sampling of invertebrates in Briksdalen in 1996 had to be postponed to 12-13 September due to particularly high discharge in July that year.

Some changes were made in the stations sampled in 2022 compared to the original stations. At BRI1, a side channel, approximately 3-4 m wide, was sampled due to high flow in the main channel. LEI1 was sampled 50-100 m upstream the previous location because the channel had shifted since 1997 and the water flow was too high for sampling at the previous location. A new station, BRI0, was added upstream the glacial lake below Briksdalsbreen (Fig. 1), an area completely covered by the glacier 25 years ago and much closer to the current glacier snout than BRI1. At this new reach, the river formed a braided fan with many side channels, varying in width between ca. 1 m and 10 m. The original BRI6 was not sampled as it was considered not to be relevant due to its location below the large lake Oldevatnet, which causes the glacial influence to be minimal. As in 1996/97, in order to separate the effects of the glaciers itself from general climate related effects, a non-glacial tributary (LEI8) or one with considerably less glacial influence (BRI7) was also sampled. LEI8 was located at more or less the same altitude as LEI3, but with no glacial influence. BRI7 was located altitudinally between BRI3 and BRI4.

Environmental parameters

In 2022, temperature, pH, and electrical conductivity were measured using a Hach probe HQ40D, and they were all measured once at each station. In 1996/97, temperature and conductivity were measured twice at each reach in every sampling period, once before and once after the invertebrates were sampled. pH was not measured in 1996/97. The turbidity in 2022 was measured using an Oakton T-100 turbidity meter and was measured twice and at the same time at each station. In 1996/97 however, turbidity was measured by taking water samples at the reaches and analysing them in a laboratory, finding minimum and maximum turbidity. Two water samples were taken at each station in 2022 and analysed for total N and total P concentrations using a Skalar SAN++ autoanalyzer. Double water samples were also taken in at each station in every sampling period in 1996/97 and analysed in a laboratory. The

Pfankuch index (Pfankuch, 1975) was used in both the old and the new sampling to classify stream stability. This index was estimated by summing classification values of the following components: rock angularity, bed-surface brightness, particle consolidation, percent stable bed, scouring and deposition, and aquatic vegetation (Appendix 4).

Long-term temperature and discharge data from monitoring stations at both rivers were obtained from the Norwegian Water Resource and Energy Directorate (NVE, 2023b). The temperature data was measured by the monitoring stations 'Leirungsåi 1270 m.a.s.l.' (close to LEI3) and 'Oldenelva by Olden Kirke' (close to BRI6), and the discharge data was measured by the stations 'Nedre Sjodalsvatn' (downstream of the lake Gjende) and 'Nordre Oldevatn' (between the lake Oldevatnet and BRI6). Monitoring of temperature data started in 1996 for both rivers, and discharge was monitored from 1987 in Dalelva and 1981 in Leirungsåi. Both temperature and discharge data were included from monitoring start until 2022.

Data on glacier area and river catchment area were obtained from NEVINA database from NVE (NVE, 2023a) and the Global Land Ice Measurements from Space (GLIMS) database (GLIMS, 2018). Differences in catchment glacier covers between 1997 and 2022 were calculated by subtracting the catchment glacier covers in 2022 from those in 1997. Catchment glacier covers in 2022 and 1997 were calculated by dividing glacier areas by catchment area. Glacier areas in July 2022 were estimated using manual delineation of glacier extent from satellite images and GLIMS outlines. Glacier areas in Leirungsåi the 1990s were estimated using 1997 GLIMS outlines, but because GLIMS outlines were not available for Dalelva at the time, glacial extents in Dalelva were estimated from 1999 Landsat satellite images and 2006 GLIMS outlines. Catchment areas in July 2022 were estimated using catchment shapefiles from NEVINA (NVE, 2023a) uploaded into GIS. Catchment areas in 1997 were calculated automatically on NEVINA.

The distances from the glacier snouts to the stations were estimated using GLIMS data in QGIS. The distances were drawn following the river meanders and drawing straight lines through any lakes present. For some of station, another glacier than Briksdalsbreen/Steindalsbreen was the closest glacier – BRI4 (Melkevollbreen), BRI5 (Brenndalsbreen), LEI4 and LEI5 (Steinflybrean), and LEI6 and LEI7 (Unnamed glacier). However, to get the same type of data as was calculated in 1997, the distances from glacier snout were calculated from Briksdalsbreen/Steindalsbreen.

Biological sampling

The same method for invertebrate sampling was used in 2022 as in 1996/97 (Brittain et al., 2001). Kick samples were taken by holding a 250-µm net to the river bottom and kicking an area of approximately 30cm × 30cm for 30 second upstream of the net, causing the macroinvertebrates to loosen and flow into the net. Five kick samples were taken per station at different spots. The samples were first emptied into a tray for quick inspection. Large stones were removed from the samples before the rest was placed in plastic bags with 96% ethanol.

In the laboratory, the macroinvertebrates were picked out of the samples and stored in 70% ethanol for later identification. In samples with very high numbers of invertebrates, sub-sampling was used by evenly spreading out the sample in a tray, dividing the tray into four equally large areas, and thereafter picking only one of these parts. After the macroinvertebrates were identified and counted, the numbers were multiplied by four to get an estimate of total number in the sample.

The material left after picking the samples was stored in plastic bags with 96% ethanol. The material was later rinsed with water in a 450 mm net, placed in aluminium containers and dried in a drying oven at 70°C for four days to ensure that all the water had evaporated. Afterwards, ceramic containers were filled with dried material from the samples, weighed, and placed in a muffle furnace at 550°C for three hours. After combustion, the samples were cooled down to room temperature and reweighed to find the ash free dry weight, which represents the weight for organic material.

Invertebrate identification

The macroinvertebrates were identified to the same taxonomic level as in 1996/97 using the following literature: Dobson et al. (2012); Engblom (1996); Lillehammer (1988); Lindegaard (1997); Rinne and Wiberg-Larsen (2018); Solem and Gullefors (1996). The highest resolution identification was made for Plecoptera, Trichoptera, and Ephemeroptera, which were identified to species where possible. In samples with more than 50 Chironomids, 50 individuals were picked at random and identified to sub-family or tribe. This was used to estimate the total number of each taxonomic group within the sample.

Statistical analyses

In order to get most comparable results, data from 2022, which was sampled in mid-late July, was only compared with data sampled in mid-late July 1997. The 1996 summer kick-sampling in Dalelva was postponed to September due to particularly high discharge in July that year. Data from 1996 were therefore excluded in this analysis because it would be inaccurate to compare samples from July and September, as the invertebrate taxon composition in the rivers is likely to change in this period (Brown et al., 2006). One exception from this was LEI4, where neither macroinvertebrate data nor samples from July 1997 were found, meaning that these samples were likely lost before they were identified. Data from July 1996 was therefore used for LEI4. Statistical analyses were conducted using R studio software version 2023.03.0 (Posit team, 2023). A 95% significance level was used for all statistical analyses.

Temperature and discharge

The long-term trends in discharge and temperature were estimated by fitting linear models using the *lm* function in the 'stats' package (R Core Team, 2020), with annual mean summer discharge (July and August) or temperature (June, July, and August) as response variable and year as the explanatory variable. Data was included from all years which had been recorded by the monitoring stations, meaning that the discharge data were included from 1987 for Dalelva and 1981 for Leirungsåi, and temperature data were included from the 1996 for both rivers. There were some outliers in the summer temperature data from Dalelva from 2021 and 2022, measuring temperatures between 20° and 25°C, lasting for around 7 days each year. This was likely because the logger was out of the water when data was collected, and consequently measuring the air temperature. This type of outliers is regularly controlled for and removed by NVE, but this has likely not been done yet for the previous two years. Temperature data from 2021 and 2022 was therefore not included in the analysis of long-term temperature trend in Dalelva.

Other environmental variables

Possible changes in the spot measurements of the environmental variables (i.e., temperature, Pfankuch index, turbidity, conductivity, total N, total P) was investigated using paired samples t-tests. The t-tests, which were conducted using the *t.test* function in the 'stats' package (R Core Team, 2020), compared each environmental variable in each station between 1997 and 2022. BRI0 and BRI6 were not included in this analysis, as they were only measured one year each. Before running the t-tests, normality of the differences was tested by

applying a Shapiro-Wilk test using the function *shapiro.test* in the 'stats' package. If the p-value from the test was less than the significance level (< 0.05), the difference was significantly different from a normal distribution, and the data would have to be transformed. This was the case for turbidity, which had to be log-transformed to get a normal distribution. Control stations were removed when comparing.

Conductivity had one outlier, LEI7 in 2022, which was clearly higher than the other data. LEI7 could possibly have been polluted from two tourist cabins/camping sites upstream the station (Gjendesheim and Maurvangen), which may explain the high conductivity. Because of this, LEI7 was removed before running the paired samples t-test for conductivity. For variables with more than one measurement per station, the mean of the two measures were used in the analysis. Some of the turbidity data from 1997 was missing, so instead of calculating the mean of the measured minimum and maximum values, the available data were used, meaning only minimum turbidity values were used for Dalelva and only maximum values were used for Leirungsåi. All the environmental variables were plotted per station per year to visualize the differences.

Macroinvertebrates

Biodiversity was measured by calculating the alpha diversities as taxon richness and Shannon diversity per sample. Taxon richness was calculated as the sum of all taxonomic groups registered in a sample. The Shannon diversity index (Shannon, 1948) was calculated as the negative sum of the relative abundances of the taxa in a sample multiplied by the natural logarithm of the same relative abundances, written as the formula:

$$H = -\sum p_i \times \ln(p_i)$$

where *H* is the Shannon diversity and p_i is the proportion of the community which is made up of taxon *i*. Shannon diversity was used because it both emphasizes rare species and takes evenness into account.

To test if there was an increase in biodiversity downstream the rivers, linear regression models were made using the *lm* function in the 'stats' package (R Core Team, 2020), with mean Shannon diversity as response variable and distance to glacier snout (km) as explanatory variable for both 2022 and 1997. The distance to the glacier snout had to be log-transformed (ln(distance +1)) to get normally distributed residuals. To see if there had been an overall change between the years, paired samples t-test was used on mean Shannon diversity

and richness per station to compare each station in 1997 with the same station in 2022. The t-tests were again conducted using the *t.test* function in the 'stats' package. Control stations (BRI7, LEI8) were removed in the comparisons, and BRI0 and BRI6 were not included as they had only been sampled one year each.

Analysis of Variance (ANOVA) and Tukey's Honest Significant Difference (HSD) test were used to further investigate for differences between the two rivers (without controls), and for differences between the control stations (BRI7, LEI8) and the glacier-influenced stations in similar altitude (BRI3, LEI3). The ANOVAs, which were conducted using the *aov* function in the 'stats' package (R Core Team, 2020), had the alpha diversity (richness or Shannon diversity) as response variable, and year and river as interacting explanatory variable. Tukey's HSD test, conducted using the *TukeyHSD* function in the 'stats' package, was run to see which groups were significantly different from each other. Also here, the normality of the differences was tested by applying a Shapiro-Wilk test in the 'stats' package.

Non-metric multi-dimensional scaling (NMDS), with Bray-Curtis dissimilarity which considered both taxa presence/absence and density, was used to further illustrate any change in taxonomic variation between the years. The NMDS was conducted using the *metaMDS* function in the 'vegan' package (Oksanen et al., 2022). The function *goodness* in the same package was used to test the goodness of fit for the individual samples.

Modelling
Generalized linear mixed models (GLMMs) were used to investigate which environmental factors that may have influenced the macroinvertebrate community. In the GLMMs, which were run using the *lme* function in the 'nlme' package (Pinheiro et al., 2020), Shannon diversity index was used as response variable, year was used as random effect and the different environmental factors were used as fixed effects. One model was made per environmental variable. Turbidity was log-transformed also here. Since organic material and pH was measured only in 2022, they were instead included in linear models, using the *lm* function in the 'stats' package, with Shannon diversity as response variable and each environmental factor as predictor variable.

Results

Glacial catchment and river changes

Dalelva generally had higher glacial influence than Leirungsåi, and the largest decrease in catchment glacial cover was seen in the lower Briksdalen stations and the upper Leirungsåi stations (Fig. 5). Briksdalsbreen had the largest retreat of the two glaciers with about 1000 m from 1997 to 2022, while Steindalsbreen had retreated about 305 m during the same period (Fig. A1).
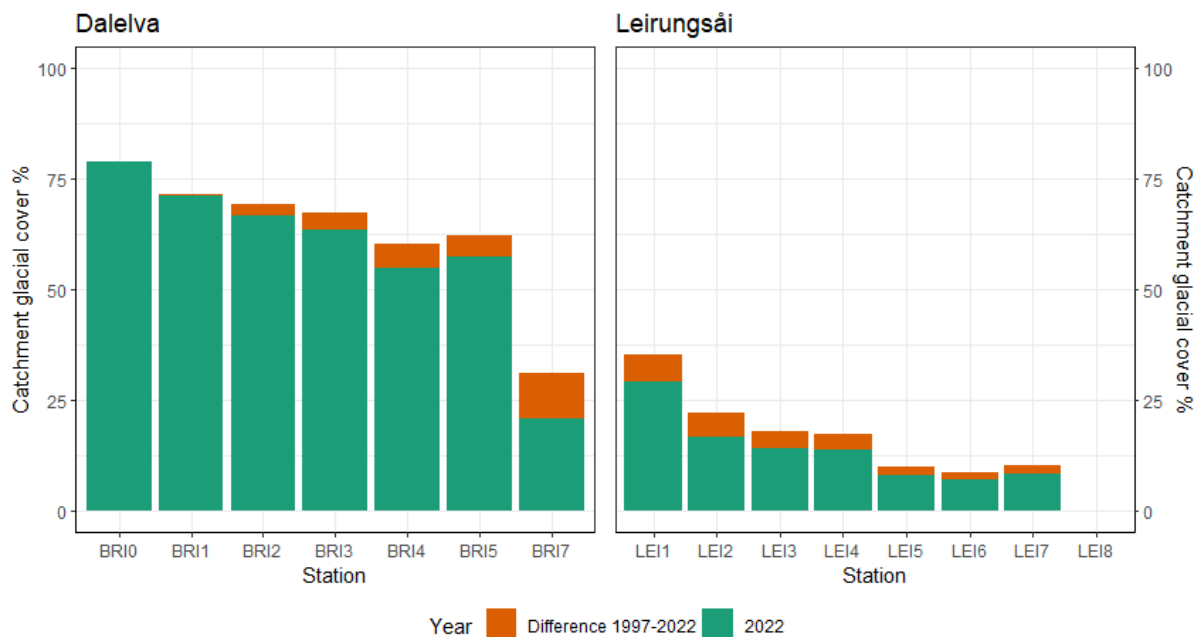
Fig. 5 Catchment glacial cover in percent per station in Dalelva (left) and Leirungsåi (right) in 2022 (green) and decrease in catchment glacial cover per station between 1997 and 2022 (orange).

Over the past 25 years, there was no trend in mean summer discharge for neither Dalelva (slope $\beta = 0.079$; $p = 0.450$) nor Leirungsåi ($\beta = 0.092$; $p = 0.389$; Fig. 6, table A1). There was however a marginally significant trend of increasing temperatures in both Dalelva ($\beta = 0.027$; $p = 0.093$) and Leirungsåi ($\beta = 0.039$; $p = 0.076$; Fig. 7, table A1).
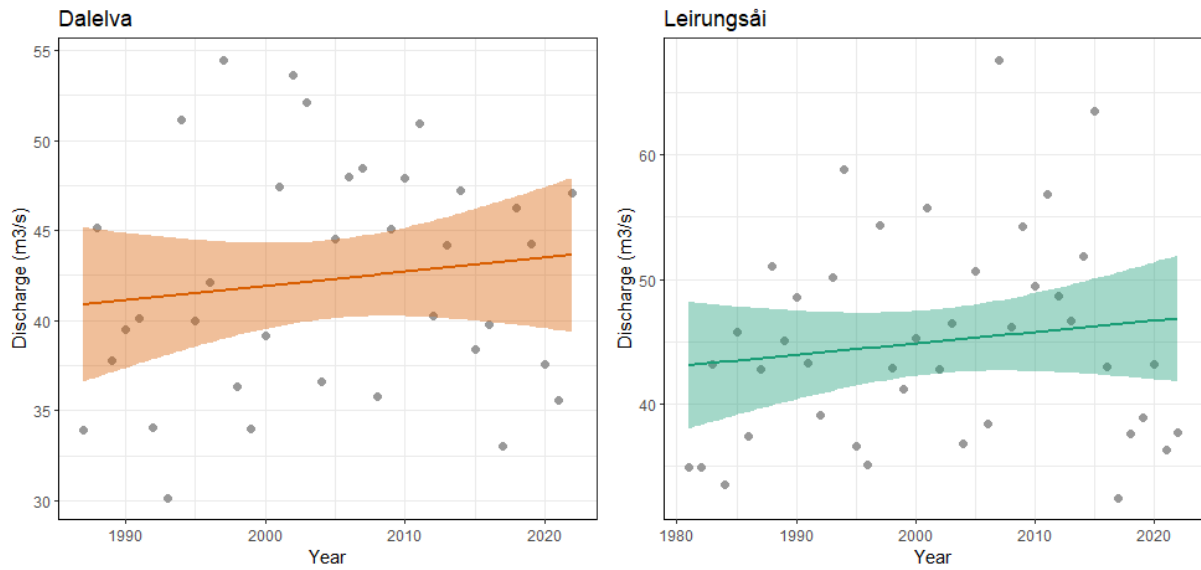
Fig. 6 Mean summer discharge (m³s⁻¹) in Dalelva between 1987 and 2022 (left), and in Leirungsåi between 1981 and 2022 (right). The points represent the mean summer (July and August) discharge per year. The lines represent the linear models for discharge as a function of year per river, and the bands around the lines represent the 95% confidence intervals.
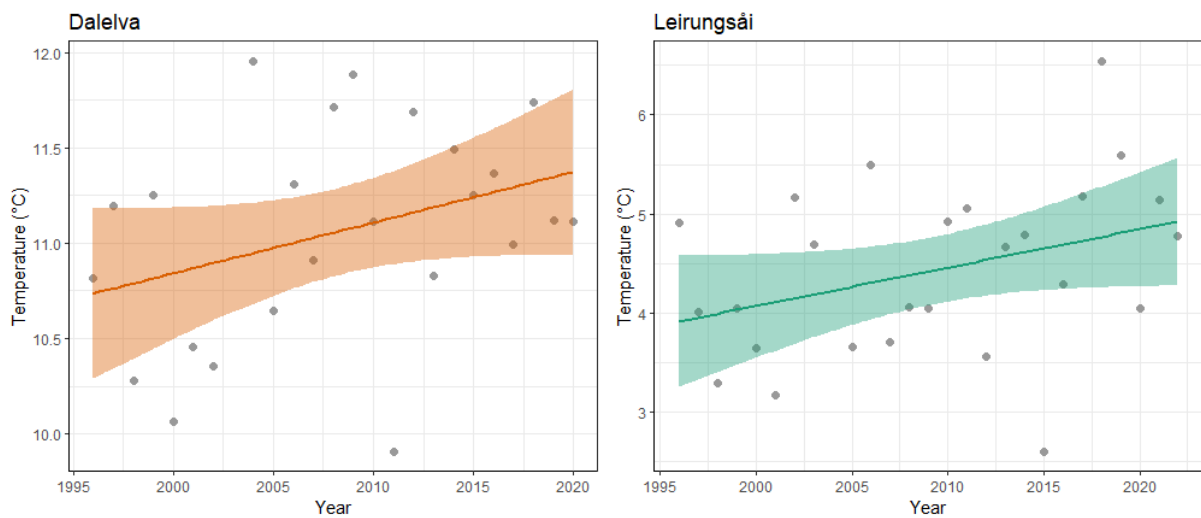
Fig. 7 Mean summer temperature (°C) in Dalelva between 1996 and 2020 (left), and in Leirungsåi between 1996 and 2022 (right). The points represent the mean summer (June, July, and August) temperature per year. The lines represent the linear models for temperature as a function of year per river, and the bands around the lines represent the 95% confidence intervals.

<u>Other environmental variables</u>

Spot measurements of water temperature (mean difference (M) = 1.98; $p < 0.001$), turbidity (M = 2.57; $p < 0.001$) and total P (M = 0.072; $p < 0.001$) were significantly higher in 2022 compared to 1997, while conductivity measurements were significantly lower in 2022 than in 1997 (M = -1.18; $p = 0.005$). There was no significant difference in neither Pfankuch index nor total N concentration between the two sampling periods (table A2). All measurements of the environmental variables from 1997 and 2022 are presented in Fig. 8. Organic material and pH, which were only measured in 2022, are presented in Fig. 9.
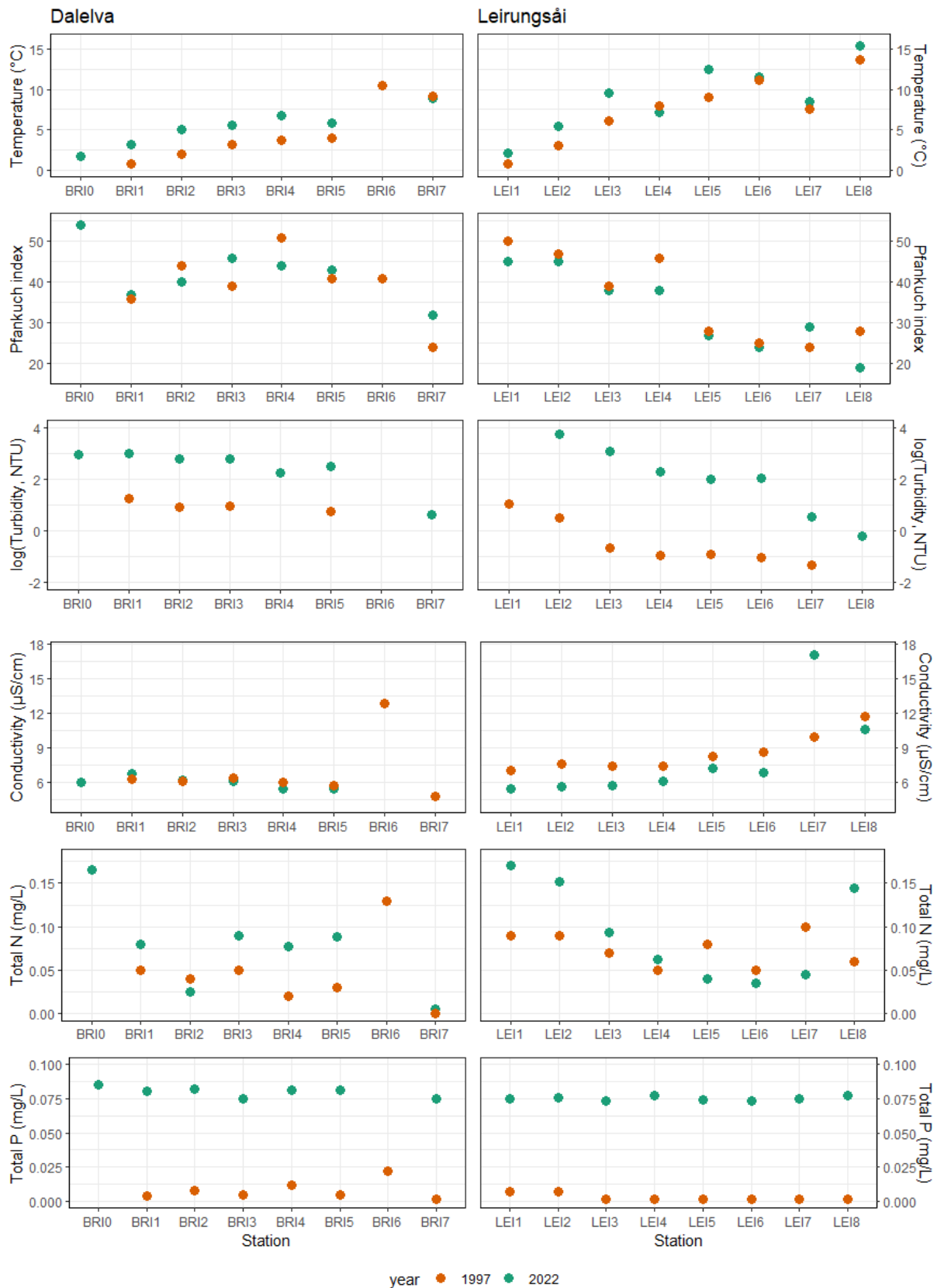
Fig. 8 Environmental variables measured in 1997 (orange) and 2022 (green): temperature (°C), Pfankuch index, log-transformed turbidity (NTU), conductivity (µS/cm), total N (mg/L) and total P (mg/L).
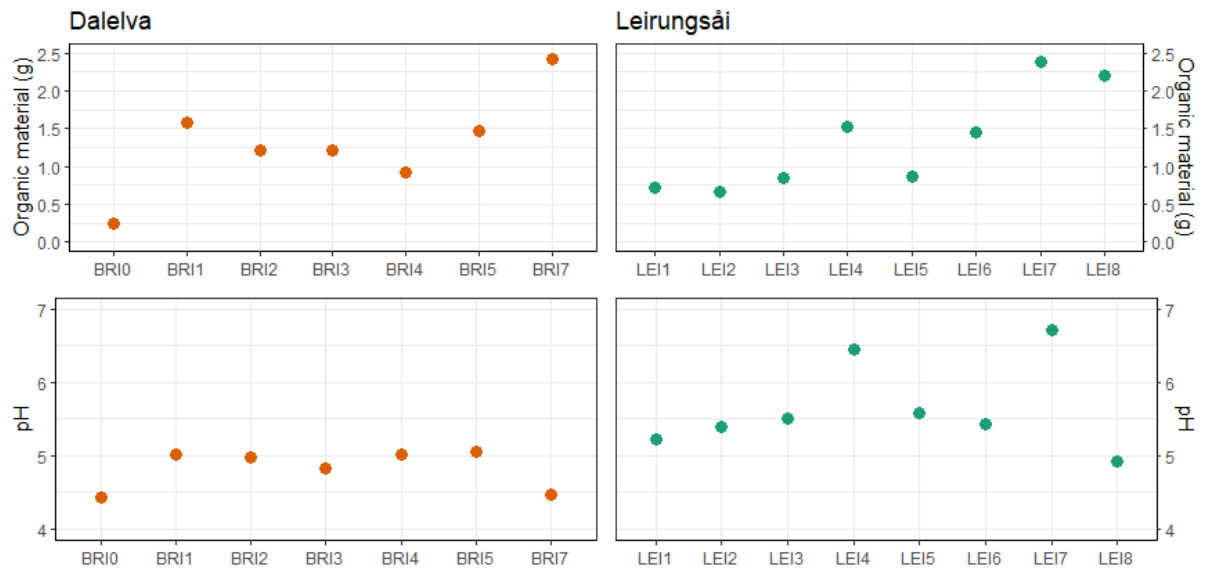
Fig. 9 Organic material (g) and pH measured in 2022 in Dalelva (left) and Leirungsåi (right).

Macroinvertebrate community

Richness

Taxon richness showed an increasing trend downstream both rivers in both years (Fig. 10). However, the trend did not seem linear for Dalelva in 1997, where the number of taxa was stably low, around two taxa, at most of the stations (BRI1-BRI5), before it increased to a mean richness of 12.2 taxa at the most downstream station (BRI6). The difference in richness between 1997 and 2022 increased downstream in both rivers. The differences in mean richness between 1997 and 2022 ranged from 3.4 (BRI1) to 8.2 (BRI5) in Dalelva and from 1.6 (LEI2) to 9.4 (LEI7) in Leirungsåi (Fig. 10; Table A4).

Fig. 10 Taxon richness per station compared between 1997 and 2022, with median values (horizontal lines), 50% interquartile range (IQR, coloured boxes), 1.5 * IQR (whiskers) and data outside the 1.5 * IQR (black points).

The t-test showed an overall increase in richness from 1997 to 2022 (mean difference (M) = 5.8, p < 0.001). When running the ANOVA which compared richness per river per year, the Shapiro-Wilk test revealed that the data did not meet the assumption of normally distributed residuals. This model could therefore not be used. The other ANOVAs, which compared the non-glacial control stations (BRI7, LEI8) with the glacial stations at similar altitude (BRI3, LEI3), showed that there was a significant increase in taxon richness from 1997 to 2022 in Dalelva at BRI3 (p < 0.001), but not at the control BRI7 (Fig. A2, table A5). The opposite was seen in Leirungsåi, where richness at the control LEI8 increased significantly from 1997

to 2022 (p = 0.002), but not at LEI3 (p = 0.163; Fig. A2, table A6). Richness at the control stations (BRI7, LEI8) was significantly higher compared to the glacier-influenced stations at similar altitude (BRI3, LEI3) in both 1997 and 2022 (p < 0.001 for all; Fig. A2, table A5-A6).

Shannon diversity

Shannon diversity increased significantly with increasing distance to glacier margin in both 1997 (slope β = 0.333, p < 0.001) and 2022 (β = 0.305, p < 0.001; Fig. 12, table A3). One exception from this was in Dalelva in 1997, where the Shannon diversity was decreasing from BRI1 to BRI3 and then increased again from BRI4 to BRI6 (Fig. 11).

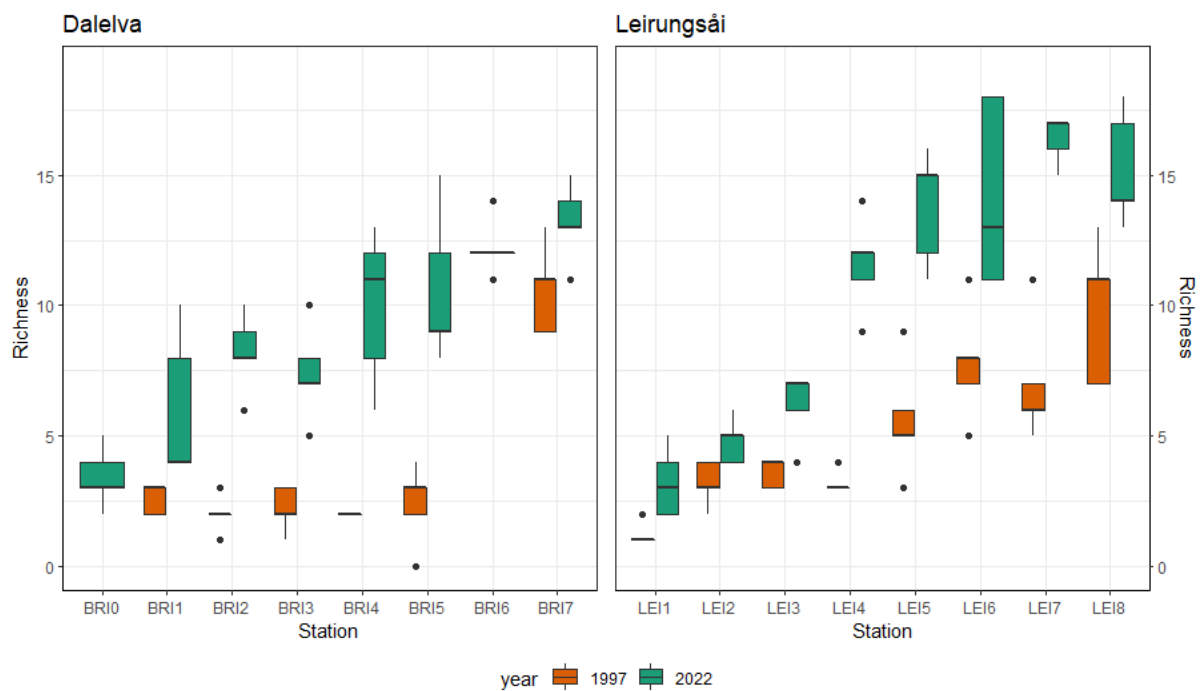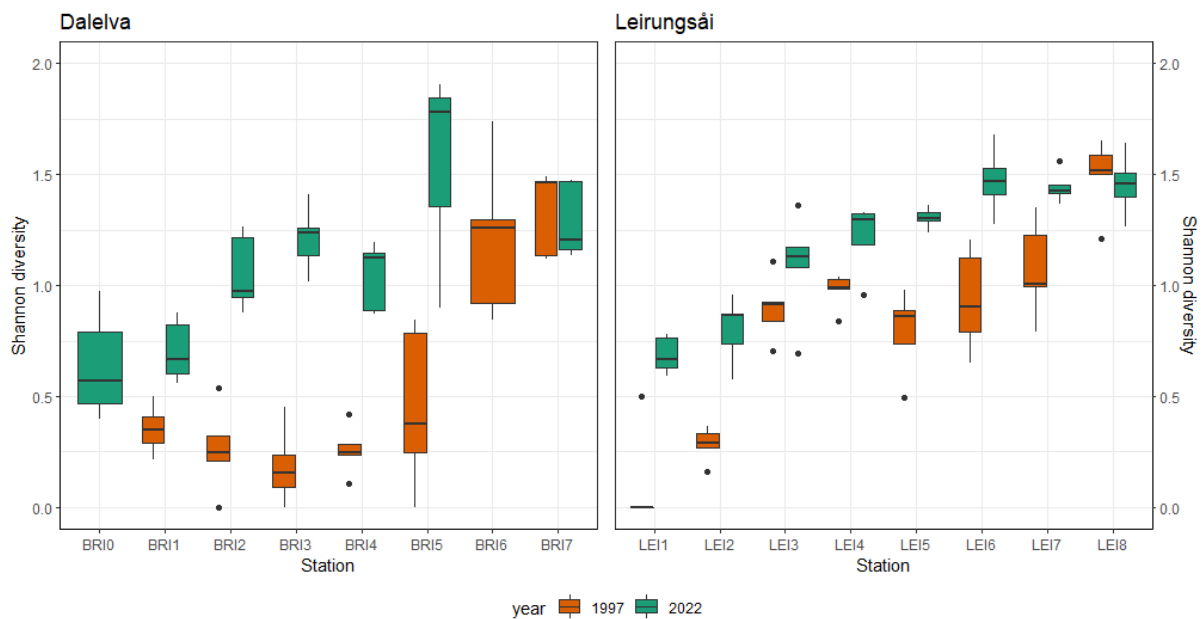**Fig. 11** Shannon diversity per station in both rivers, compared between 1997 and 2022, with median values (horizontal lines), 50% interquartile range (IQR, coloured boxes), 1.5 * IQR (whiskers) and data outside the 1.5 * IQR (black points).

The t-test showed an overall increase in Shannon diversity from 1997 to 2022 (M = 0.585, p < 0.001). The ANOVA showed that Shannon diversity was significantly higher in 2022 than in 1997 in both Dalelva (p < 0.001) and Leirungsåi (p < 0.001). While Shannon diversity was significantly higher in Leirungsåi than in Dalelva in 1997 (p < 0.001), they were of similar values in 2022 (Fig. A3, table A7). In Dalelva, Shannon diversity did not increase at the control station BRI7 between 1997 and 2022, while the glacial station at similar altitude BRI3 showed a significant increase (p < 0.001). The Shannon diversity at BRI3 and BRI7 were significantly different in 1997 (p < 0.001), but there was no difference between these two stations in 2022 (Fig. A3, table A8). In Leirungsåi, Shannon diversity did not change significantly from 1997 to 2022 for neither LEI3 nor LEI8, but the two stations were

significantly different from each other in both 1997 (p < 0.001) and 2022 (p = 0.024; Fig. A3, table A9).
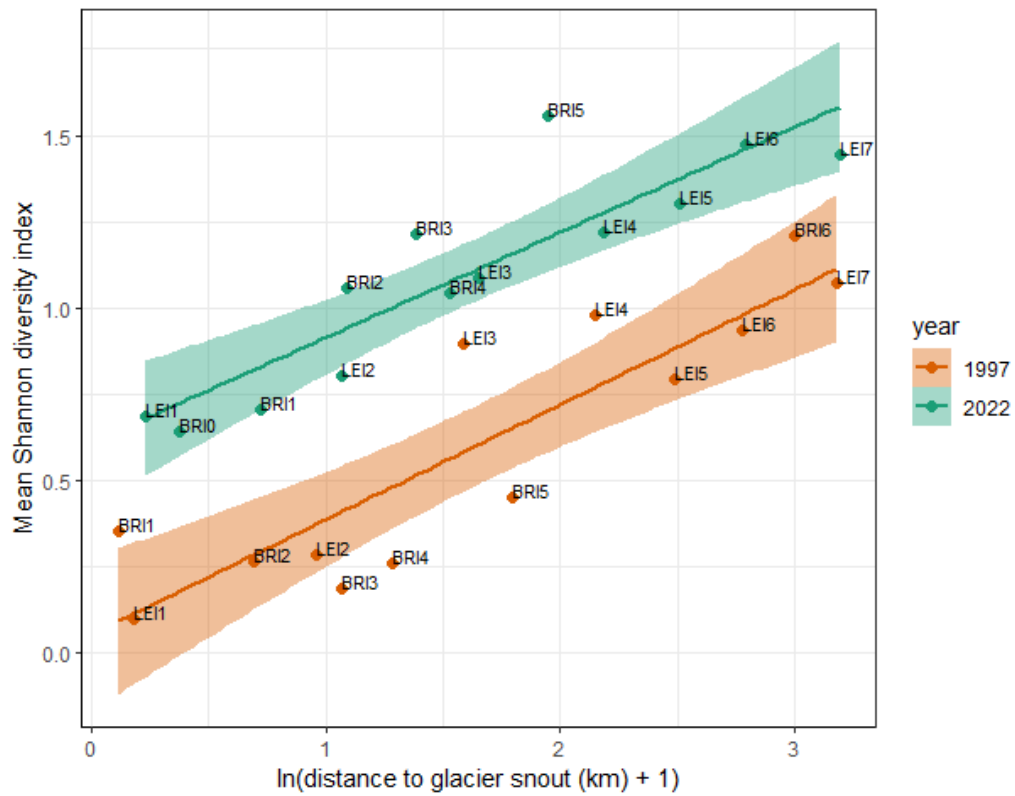
Fig. 12 Linear models of mean Shannon diversity index per station as a function of log-transformed distance to glacier snout (km; ln(distance + 1)) for 1997 (orange) and 2022 (green). The points represent the mean Shannon diversity per station, solid lines are the fitted linear models, and the bands around them represent the 95% confidence intervals.

The NMDS plots in Fig. 13 show that samples were generally more similar to each other in 2022 than they were in 1997. In Dalelva, the samples were centred more to the middle of the plot in 2022 than in 1997, moving away from the taxa at top and far right side of the plot. In Leirungsåi, the samples were moving mainly downward and right in 2022 compared to 1997. The polygons representing samples from 1997 and 2022 are heavily overlapping, meaning that the macroinvertebrate communities in 2022 have not changed greatly since 1997.
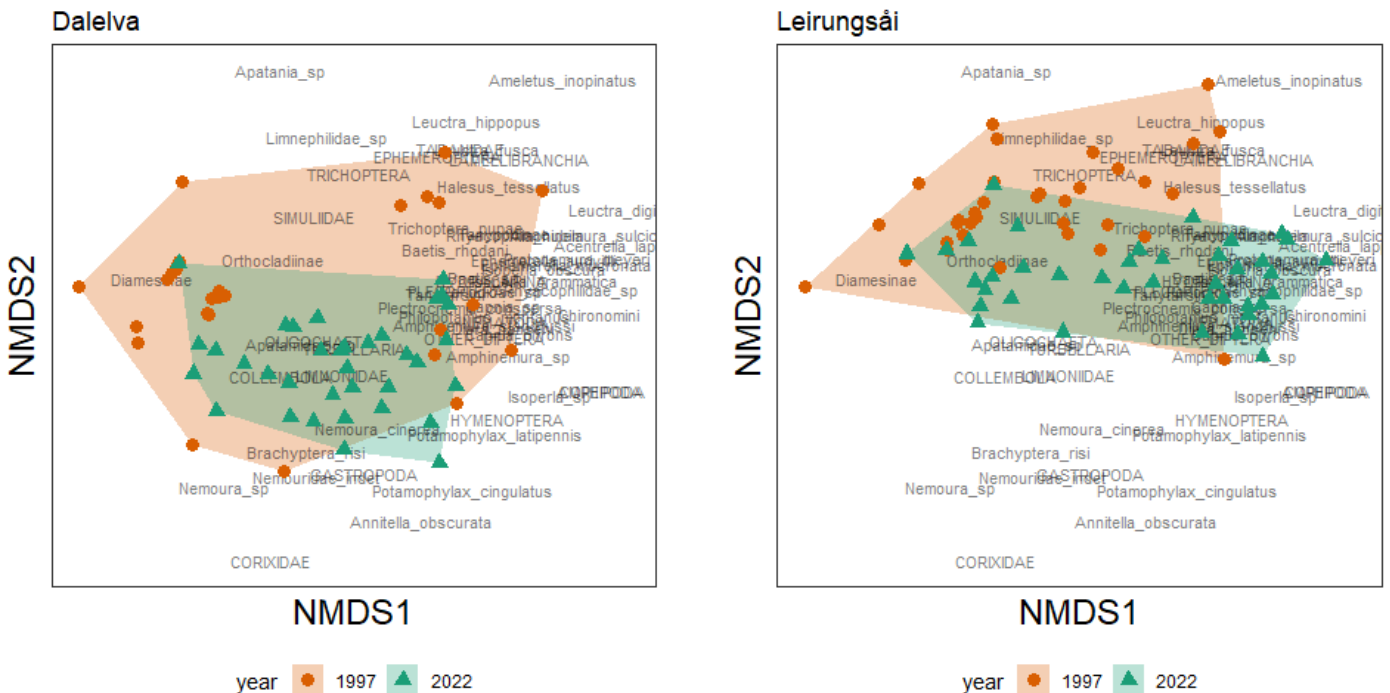
Fig. 13 NMDS plots showing the diversity in the samples, which are represented by the points. The left plot shows the samples from Dalelva, and the right plot shows the samples from Leirungsåi, in 1997 (orange circles) and 2022 (green triangles). Points close to each other represents samples with more similar taxon composition than samples further apart. The polygons contain all the samples from 1997 (orange) and 2022 (green). Taxon names are distributed along the same NMDS axes, and the closer two names are to one another, the more likely it is that they are found in the same sample.

Modelling

Temperature (slope $\beta = 0.085$, $p < 0.001$), conductivity ($\beta = 0.194$, $p < 0.001$), and distance to glacier margin ($\beta = 0.039$, $p < 0.001$) was significantly positively correlated with Shannon diversity, while the correlation with turbidity ($\beta = -0.301$, $p < 0.001$) and Pfankuch index ($\beta = -0.024$, $p < 0.001$) were significantly negative (Fig. 14). Both organic material ($\beta = 0.359$, $p < 0.001$) and pH ($\beta = 0.234$, $p = 0.001$) correlated positively with Shannon diversity (Fig. 15). Total N and total P did not correlate with Shannon diversity (Fig. 14, table A10).
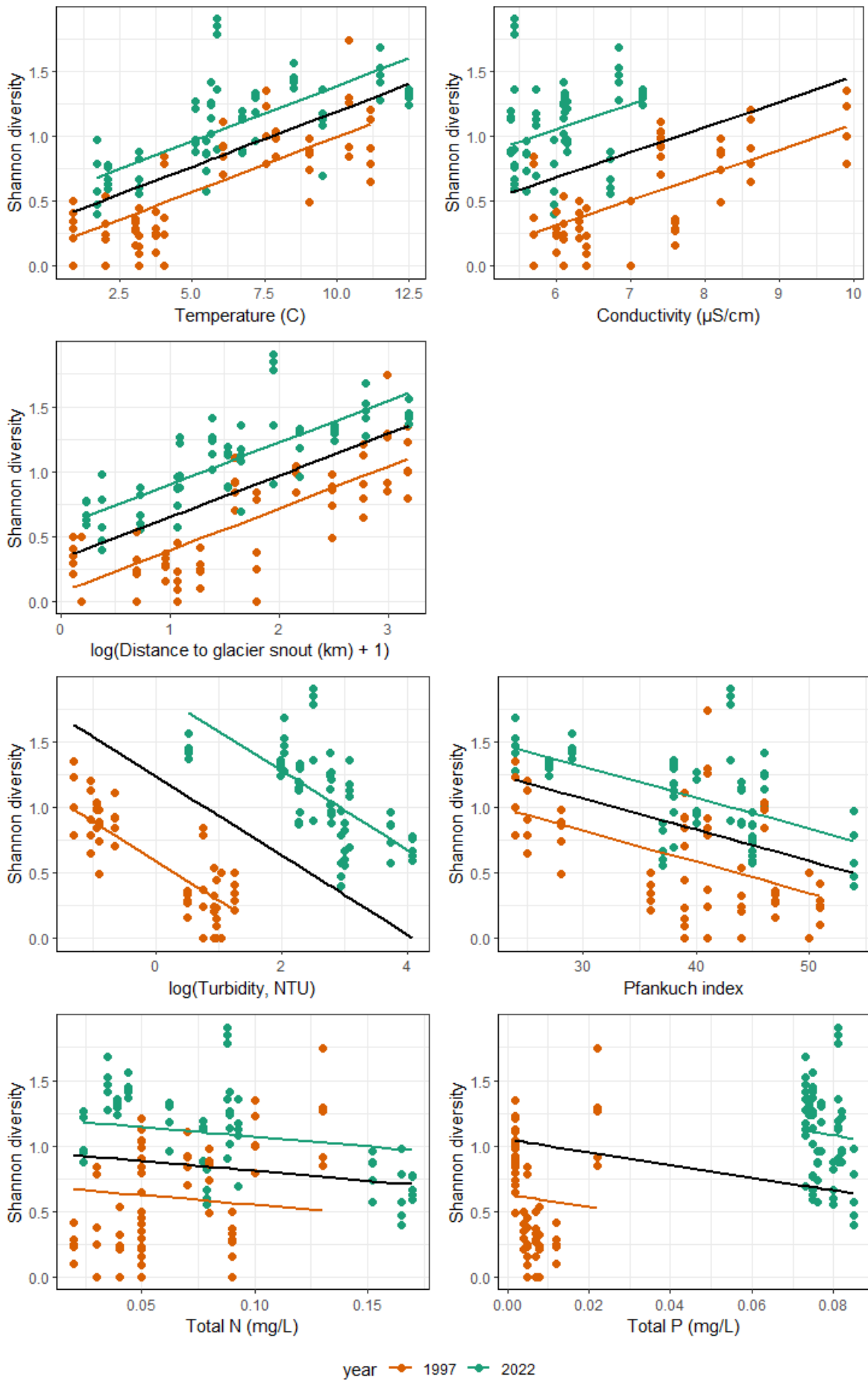
Fig. 14 Generalized linear mixed models (GLMMs) with Shannon diversity as response variable, the different environmental variables as fixed factors, and year as random factor. The points represent each measurement in 1997 (orange) and 2022 (green). The black lines represent the fitted values of the combined GLMM for both years, while the coloured lines represent the fitted values per year (1997: orange, 2022: green).
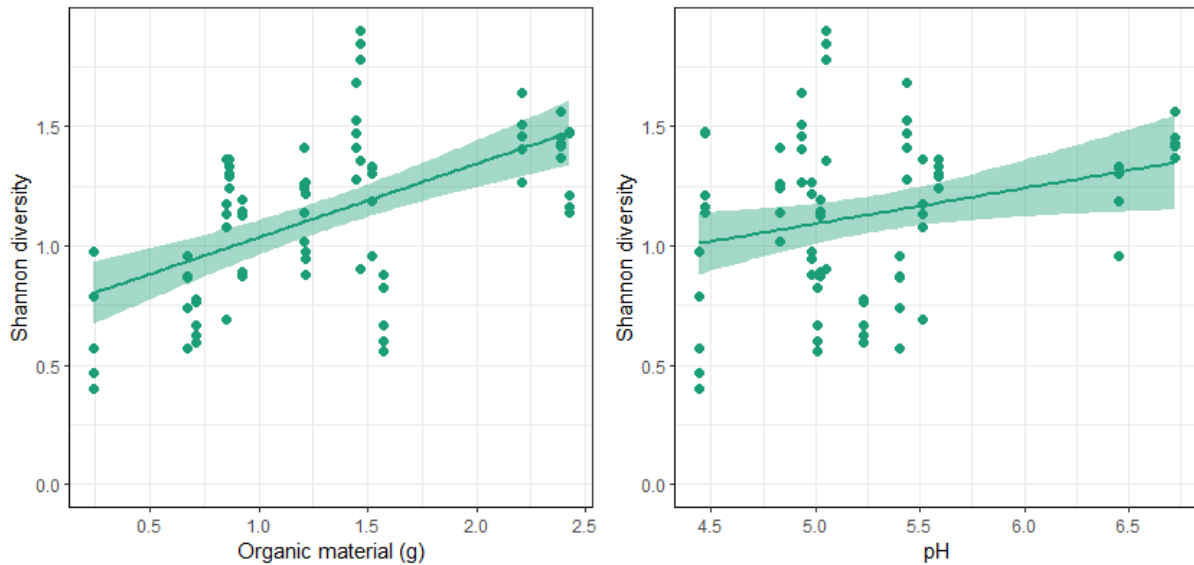
Fig. 15 Simple linear regression models of Shannon diversity as function of organic material (left) and pH (right) measured in 2022. The points represent the individual measurements, the solid lines represent the fitted values from the models, while the coloured areas around the lines represent the 95% confidence intervals.

Discussion

Glacial catchment and river changes

Both glaciers had retreated substantially along the valleys since 1997, Briksdalsbreen by 1000m and Steindalsbreen by 305m. Dalelva generally had a larger catchment glacial cover than Leirungsåi in both 1997 and 2022, and the largest decrease in the catchment glacial cover in Dalelva was at the lower stations (Fig. 5). This may be due to changes in the glacier-fed tributaries joining Dalelva downstream, which contributed to continued high glacial influence in 1997. Like Briksdalsbreen, the source glaciers of the tributaries have likely also decreased since 1997, thereby reducing the overall input of meltwater further downstream Dalelva. The uppermost reaches still have high glacial influence, as they have few other water sources. Leirungsåi showed the opposite trend from Dalelva, with the largest decrease in catchment glacial cover at the uppermost stations. As Leirungsåi has few glacial tributaries, the main

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melt-off comes from Steindalsbreen, and a reduction in this glacier will have a direct effect on the closest river reaches.

When calculating the catchment glacial cover, it was found that the control station in Dalelva, BRI7, which previously was thought to have no glacial influence, had a glacial cover of 20.9 % from Flatebreen. However, the tributary river ran through one larger and two smaller lakes upstream of BRI7, so it likely had minimal glacial influence. This was supported by the environmental variables measured at the station: temperature was higher and turbidity lower than the glacially influenced stations in Dalelva (Fig. 8). BRI7 can therefore still be counted as a control.

The long-term environmental change in the two glacier-fed rivers was evaluated by investigating the discharge and water temperature during the past ~30 years. Discharge did not change in this period, but the temperature showed a marginally significant increase. While water temperature may be more directly connected to air temperature, discharge also depend on precipitation and the accumulation and ablation of the source glacier, and may therefore vary greatly between years. The low R^2's for all four models, ranging from 0.02 to 0.13 (table A1), show that there was large between-year variation which was not captured by the models (Fig. 6, 7). A larger timescale may be needed to catch the long-term pattern in discharge and water temperature.

It may be difficult to predict the effects of a warming climate on the water temperature and discharge of glacial rivers. On one hand, higher summer air temperatures would increase the water temperature through direct transmission of heat. On the other hand, warmer summers would also increase glacial melting, thereby increasing the discharge and keeping the temperature low. When a glacier is melting, the discharge will depend on the size and the previous melting of the glacier. Early in the melting process, the glacier volume is high, resulting in high summer discharge. As the glacier is shrinking, the runoff will decrease as there is less ice to be melted. Over time, the water discharge will therefore be reduced, and the temperature will increase. Eventually, the river will change from glacial-influenced to groundwater or snowmelt influenced (Braun et al., 2000; Milner et al., 2009).

Other environmental variables

Different environmental parameters were measured to investigate the state of the rivers at the time when macroinvertebrates were sampled. The same parameters were measured both in 2022 and 1997 in order to get comparable images of the rivers. However, these were point measurements of constantly changing variables which are heavily influenced by the weather, particularly the amount of precipitation. Therefore, the environmental parameters may vary greatly within and between days. When studying the ecosystem within a river, it is important to keep in mind the constant flow that affects the environment by continuously moving and transporting particles and objects in the water. Therefore, a reach affected by a varying input, like glacial melt-off, can have largely different properties of a parameter depending on the timing of the sampling and measured differences may be due to random variation (Brown et al., 2003; Smith et al., 2001). The spot measurements of environmental parameters in this study may therefore not be used to explain any long-term trend of environmental change, but to describe the rivers at the time of invertebrate sampling. This is also the reason why macroinvertebrates can be used as indicators of environmental change, as the species better reflect the long-term state of the river than spot measurements of environmental parameters do.

Temperature

Water temperature increased downstream both rivers, and the control stations (BRI7, LEI8) had higher temperatures than the glacier-influenced stations at similar altitude (BRI3, LEI3), indicating that glacial input reduced the water temperature in both 1997 and 2022 (Fig. 8). Almost all stations had higher temperatures in 2022 than in 1997, which may indicate warmer weather at the time of sampling in 2022. Despite the warm weather which likely enhanced glacial melting and thereby increasing meltwater input in 2022, the rivers were still warmer than in 1997, which might be an indication of the reduced catchment glacial cover. There was a decrease in temperature from LEI6 to LEI7 in both 1997 and 2022, which likely was due to the large lake Gjende upstream of LEI7. Gjende keeps a stable temperature due to its size and depth, and therefore has a cooling effect on the water in Leirungsåi, which had gradually been heated up by the air temperature on its way from the Steindalsbreen glacier front.

Pfankuch index

In Leirungsåi, the Pfankuch index showed a decreasing trend downstream in both 1997 and 2022, indicating that the substrate gets more stable with increasing distance to the glacier (Fig. 8). No such trend was visible in Dalelva, possibly due to continuously high glacial

influence across all stations (Fig. 5). There was no clear difference in the Pfankuch index between the years. As expected, the control stations (BRI7, LEI8) generally had lower Pfankuch index scores than the glacier influenced stations, indicating a more stable substrate in the controls.

The index score at the control station BRI7 increased from 1997 to 2022, indicating that this reach has become more unstable. This may be due to a large flooding event, possibly caused by spring snow melt, which changed the substrate composition there. As the glacial influenced stations experience floods and receive large amounts of suspended sediments each year during summer glacial melting period, large spring floods are less likely to make persistent changes to the riverbed. However, the station is located just by a camping site, so it is possible that some modifications have been made to make the reach more accessible for swimming and 'nicer to look at'.

Turbidity

There was a decreasing trend in turbidity downstream in Leirungsåi in both 1997 and 2022, indicating reduced glacial influence with increasing distance to the glacier front. This trend was less visible in Dalelva (Fig. 8), which was in line with the pattern of high glacial influence across all stations in this river (Fig. 5). As expected, the control stations (BRI7, LEI8) had lower turbidity than the glacial-influenced stations. The turbidity was generally higher in 2022 than in 1997 across all stations, which may be due to variations in glacial discharge and rainfall between the years. This difference could also be caused by the use of different methods, as the turbidity was measured in the laboratory in 1997, while it was estimated directly in the field in 2022.

Conductivity

The conductivity showed the same trend in both years, but opposite to each other in the two rivers – decreasing downstream in Dalelva, increasing downstream in Leirungsåi (Fig. 8). Even though glacial meltwater contains more dissolved ions than snowmelt and groundwater, conductivity is expected to be lowest at the period of peak runoff, as high water discharge quickly transports the dissolved ions downstream (Han et al., 2015). Higher temperatures would also increase the conductivity (EPA, 2022), suggesting higher conductivity as glacial influence is reduced. Due to this dynamic between input of ions from glacial meltwater and transportation downstream, in addition to the effect of temperature, it may be hard to predict the downstream pattern of conductivity.

The conductivity at BRI6 in 1997 and in LEI7 in 2022 were higher than at the other stations. Since LEI7 was situated downstream Gjende, it also received suspended sediment from many other melting glaciers and may therefore have a much higher conductivity than the other stations in Leirungsåi. LEI7 could possibly also have been polluted from two tourist cabins/camping sites upstream the station (Gjendesheim and Maurvangen). BRI6 was situated downstream the lakes Oldevatnet and Floen and may therefore have contained more run-off and pollutions from farms and households situated between BRI5 and BRI6. Since BRI6 was not sampled in 2022, it is difficult to say if this difference was still there.

Total nitrogen

The total nitrogen (N) concentration had a decreasing trend downstream in Leirungsåi in 2022, but this trend was not seen in Dalelva 2022, nor in neither of the rivers in 1997 (Fig. 8). Total N was particularly high at BRI6 in 1997, which may be due to runoff from roads and agricultural land along the lower reaches of Dalelva. Glacier-fed rivers are expected to contain more N than snowmelt-fed rivers due to accumulation of atmospheric N from anthropogenic emissions (Gao et al., 2020) and leaching from bedrock and tundra (Baron et al., 1994; Saros et al., 2010; Williams & Tonnessen, 2000). However, the distribution of N along a river may be difficult to predict. Because of the nutrient spiralling in river ecosystems, nutrients are fluctuating between being in and out of the food web, and nutrients currently taken up by an organism will not be detectable in the water. The length of the spirals depends on both the river discharge, with higher discharge giving longer spirals, and the amount of biological uptake (Newbold, 1992). Therefore, while higher glacier runoff will increase the nutrient input to the river, higher discharge will also remove the nutrients more quickly. A predictable pattern downstream glacial rivers during peak glacier runoff may therefore not be expected.

Total phosphorus

The total phosphorus (P) concentration showed no downstream trend in neither of the rivers, but there was a large difference in total P concentrations between 1997 and 2022 (Fig. 8). Even though this may be due to differences in methods in 1997 and 2022, it may also be due to more glacial runoff at the sampling time in 2022 than in 1997, as glacial meltwater is expected to contain high levels of P bound to suspended particles (Hodson et al., 2004). During a surveillance of Norwegian lakes in 2019 (Lyche Solheim et al., 2020), it was found especially high values of total P in lake Gjende due to the glacial influence. However, as most of this P was likely bound to suspended particles and therefore not bioavailable (Hodson et

al., 2004), a high total P concentration may not have a large influence on the biology of the glacial rivers.

Organic material

The organic material showed an increasing trend downstream in both rivers in 2022 (Fig. 9), which is in line with previous findings of increased periphyton biomass with increasing distance to the glacial margin during periods of high summer runoff (Uehlinger et al., 1998). Glacier-fed reaches located above the treeline have low input of terrestrial biomass (allochthonous) and receive high amounts of solar radiation. Organic material produced within the river (autochthonous) will therefore be most important to the macroinvertebrates in these reaches (Hauer et al., 1997; Zah et al., 2001). Autochthonous production is usually highest in spring after snow melt and is reduced in summer during peak glacial runoff due to the high current velocity, low nutrient availability and high turbidity (Hieber et al., 2001; Uehlinger et al., 1998).

In Dalelva, the downstream samples had higher organic material content than BRI0. This may be due to the presence of dense birch forest from BRI1 and downstream, providing allochthonous material to the river. Another reason may be the lake between BRI0 and BRI1, which stabilizes the river downstream the outlet and thereby enhancing periphyton production (Hieber et al., 2001). These are likely also the reasons why LEI7 in Leirungsåi had more organic material than the other stations, as it is situated below lake Gjende and with dense riparian vegetation. The control stations (BRI7, LEI8) had higher organic material content than the glacial influenced stations at similar altitude (BRI3, LEI3), indicating more stable substrate and less turbid water, which increases the periphyton production (Hieber et al., 2001; Uehlinger et al., 1998).

pH

In 2022, pH was generally similar across all stations (~5.0-5.5). Exceptions from this was BRI0 and BRI7 in Dalelva, which were lower than the rest, and LEI 4 and LEI 7 in Leirungsåi, which were higher (Fig. 9). High pH has previously been connected to reaches with low glacial meltwater contributions (Brown et al., 2007), which would suggest an expectation of increased pH downstream the study rivers and higher pH at the control stations (BRI7, LEI8) than the glacier influenced stations. However, pH depend on the water discharge and may therefore vary greatly depending on the timing of the sampling (Hill & Neal, 1997). This might be the reason why LEI4 had a higher pH than the other stations, as this was sampled on a separate day. BRI0 and BRI7 ran over bedrock, while the beds at the

other stations were dominated by moraine material. Bedrock may have less buffer capacity, which could have caused lower pH at BRI0 and BRI7 than the other stations. The high pH measured at LEI7, which was located downstream Gjende and the camping site Maurvangen, may be connected to the high conductivity measured at the site.

Macroinvertebrate community

There was a general increase in both taxon richness and Shannon diversity from 1997 to 2022 in both rivers (Fig. 10, 11). This can be connected to the glacial retreat observed over the same period, as it is an expected reaction to reduced glacial influence (Brown et al., 2007; Brown et al., 2018; Castella et al., 2001; Lencioni, 2018). Furthermore, the Shannon diversity showed a positive correlation with distance to the glacier snout (Fig. 12), which is in line with Milner and Petts' (1994) theoretical model, later confirmed by Milner et al. (2001).

While the uppermost stations of Dalelva (BRI1-BRI4) had no change in neither taxon richness nor Shannon diversity in 1997, they showed a downstream increase in both richness and diversity in 2022 (Fig. 10, 11). This change was likely due to the reduced glacial influence in Dalelva, partly as a result of the lake that has emerged between BRI0 and BRI1. The lake, which in 1997 was almost totally covered by the glacier Briksdalsbreen, was completely glacier free in 2022. This likely had a large influence on the river by reducing the sediment transport and increasing the water temperature, thereby reducing the glacial influence of the river downstream the lake outlet (Milner & Petts, 1994). Furthermore, because the stream ran over bare rock before reaching the lake in 2022, the sun exposed bedrock would warm the water up further. Decreased catchment glacier cover in 2022 compared to 1997 also reduced the glacial influence in Dalelva (Fig. 5).

In Leirungsåi, there was a gradual increase in both richness and Shannon diversity downstream in both years (Fig. 10, 11). The increase in richness between 1997 and 2022 was largest at the downstream stations, with a gradual declining difference between the years at the stations closer to the glacier (Fig. 10). While there was a significant increase in richness at the control station LEI8, there was no change at the glacial station at similar altitude (LEI3; fig. A2). This indicates a gradual succession in Leirungsåi, with new species entering the river system from downstream reaches, also in the non-glacial reaches. In contrast to taxon richness, Shannon diversity in Leirungsåi had a similar increase from 1997 to 2022 across all stations (Fig. 12), and neither LEI3 nor the control (LEI8) showed a significant change (Fig. A3). This suggests that even though there has been an increase in the number of taxa in

Leirungsåi between 1997 and 2022, the abundances of the new species are low. Due to the low evenness, the new species have only had a minor effect on the Shannon diversity index. Considering the low richness and Shannon diversity at the top stations (LEI1-LEI3) in 2022, and the fact that both indexes were significantly higher at the control station (LEI8) than at the glacial station at similar altitude (LEI3), the succession of the macroinvertebrate community in Leirungsåi is still repressed by the glacial influence.

The increased richness at the control station in Leirungsåi (LEI8; Fig. A2) indicates some general succession in the area, which may be due to the changing climate. A growing species pool in tributary rivers increases the potential for new taxa to enter the glacier-fed rivers once the environment is favourable for the specific species. The control station in Dalelva (BRI7) did however not show an increase in neither richness nor Shannon diversity, while this was seen in the glacier-influenced station at similar altitude (BRI3; Fig. A2, A3). This indicates that even though there has been no further succession at the control station BRI7, the community in the glacial reach has developed. The succession in Dalelva is therefore likely caused by the dispersal of species already present in the non-glacial tributaries and in reaches further downstream (Lencioni, 2018). South-eastern Norway generally has higher species richness than western Norway, mostly due to north-south mountain ranges which is restraining western dispersal and because of the oceanic climate and the more constant annual temperature in the west, which provides fewer niches (Brittain et al., 2022; Aagaard & Dolmen, 1996). Leirungsåi therefore has a larger potential than Dalelva for increased richness due to species dispersing from other areas (Alther et al., 2019; Cauvy-Fraunié et al., 2015).

Shannon diversity was higher in Leirungsåi than in Dalelva in 1997, while they were of similar value in 2022 (Fig. A3). This means that Dalelva have had the largest increase in diversity of the two rivers. In 1997, Dalelva had the highest catchment glacial cover of the rivers, likely restricting the invertebrate community more than in Leirungsåi. Leirungsåi, with a lower glacial influence, had a more developed benthic community due to the. After the reduction in catchment glacial cover since 1997, the rivers have reached similar successional stages in 2022.

Impact of environmental parameters on the macroinvertebrate community

Even though the environmental parameters of a glacier-fed river can show high variability between years, the macroinvertebrate community is more persistent and may therefore reflect the long-term condition of the river (Brown et al., 2007). Due to the harsh conditions in

glacier-fed rivers, it is mainly the environment which constrains the development of the benthic community (Milner & Petts, 1994; Ward, 1994). This makes it possible to create a direct link between the invertebrate fauna and the environmental state of the river. Hence, even though discharge and water temperature did not show a significant change (Fig. 6, 7), the increased macroinvertebrate biodiversity indicates environmental changes within the rivers. The relative abundance of the chironomid subfamily Diamesinae has been found to be a good indicator to separate streams with different glacial input (Lencioni, 2018), and it can therefore be used to indicate the glacial influence in a river.

Shannon diversity was positively correlated with spot measurements of temperature, conductivity, organic material and pH, as well as distance to glacier snout, and negatively correlated with turbidity and Pfankuch index (Fig. 14, 15). As the diversity has increased during the past 25 years, the correlations may suggest that there have also been some changes in the environment of the rivers. For example, the increased diversity may be coupled with an increase in water temperature and a more stable substrate, indicated by a decrease in Pfankuch index. This is supported by the marginally significant long-term increase in water temperature (Fig. 7) and the increase in spot measurements of water temperature between 1997 and 2022 (Fig. 8). However, this was not the case for the Pfankuch index, which did not show any change between the years. As this index is the sum of scores of different components, it will to some extent depend on the person giving the scores. It may therefore be difficult to compare Pfankuch indices assessed by different people or at different times (Naas et al., 2023), such as after a major flood.

The increased diversity during the past 25 years may further suggest an increase in conductivity and a reduction in turbidity during the same period. However, the opposite was found, with lower conductivity and higher turbidity in 2022 than in 1997. This may be due to high discharge at the time of sampling in 2022. As these parameters are highly variable and rely heavily on the amount of discharge at the time of sampling (Brown et al., 2003; Smith et al., 2001), spot measurements are not enough to identify the long-term changes.

Furthermore, increased organic material and pH is expected in connection to the increased biodiversity. These parameters could not be compared between the years, as they were not measured in 1997. However, the downstream trend of increasing organic material is in line with what is expected with increasing diversity. Climate warming may cause increased organic material in mountain rivers, both due to reduced glacial influence which likely

increases autochthonous material, and a possible increase in riparian vegetation, which will increase the input of allochthonous material. pH was generally stable downstream both rivers, meaning that the positive correlation found between the parameter and Shannon diversity may be due to the high pH measured at LEI4 and LEI7, stations which also had high diversities. More continuous measurements of pH are needed to get a better indication of how this parameter is connected to the macroinvertebrate diversity.

Neither total P nor N were correlated with Shannon diversity. Periphyton, the main food source of macroinvertebrates in glacier-fed rivers (Woodward et al., 2010), is often P or N limited in glacial rivers and lakes (Morris & Lewis, 1988; Saros et al., 2005; Saros et al., 2010). Increased availability of P and N may therefore be expected to enhance periphyton production, which in turn would increase abundance of macroinvertebrates. However, such a link was not found, which may in part be due to other environmental variables that can be limiting to periphyton and/or macroinvertebrate growth. In an experiment on periphyton growth limitations in glacial rivers by Rinke et al. (2001), it was found that current velocity, rather than nutrient limitation, was the main constrain to algal growth during the peak runoff period in summer. Furthermore, as P and N may show large temporal variation in a river, the few spot measurements that was sampled in this study may not be enough to identify a correlation with macroinvertebrate diversity. Also, as most of the P in glacier-fed rivers are not bioavailable (Hodson et al., 2004), this nutrient may be of minor importance for the benthic community.

The greater similarity between the samples in 2022 compared to 1997 (Fig. 13) indicates that despite an increase in alpha diversity, the beta diversity (between reaches) in the rivers may have decreased. This means that the new species may have similar abundance in several of the reaches, resulting in similar community compositions. The subfamily dominating in the uppermost reaches was Diamesinae (Chironomidae), and as the glacial influence is reduced, they are replaced by species from the genera Ephemeroptera, Plecoptera and Trichoptera, in addition to other Chironomids (e.g., Orthocladiinae) and Simuliidae, which are dominating further downstream the glacier (Castella et al., 2001; Lencioni, 2018). There were two species of Ephemeroptera, five species of Plecoptera and six species of Trichoptera found only in 2022 (Appendix 6). These were all generalist species with large distributions in Norway (GBIF.org, 2023) and were therefore likely to disperse in alpine rivers once the glacial influence was reduced (Brown et al., 2006). The decrease in beta diversity may be caused by the rivers becoming more homogeneous as the variation in water sources is reduced and the

benthic community composition in the glacier-fed rivers becomes more similar to those in snowmelt-fed or groundwater-fed rivers (Brown et al., 2003; Brown et al., 2007; Malard et al., 2006).

The future macroinvertebrate community composition of currently glacier-fed rivers may be difficult to predict, as biotic interactions will have an increasing impact on the species composition as glacial meltwater input is reduced and the environmental constrains are relaxed (Hannah et al., 2007). Species specialized to glacial river systems are vulnerable to a warming climate and may become extinct once the source glaciers disappear completely, thereby resulting in reduced gamma (regional) diversity. Furthermore, the changes in alpha diversity in upstream reaches may shift from increasing to decreasing when the source glacier is small enough to remove environmental filtering of competitively strong species, resulting in decreased alpha diversity through competition exclusion (Cauvy-Fraunié et al., 2014; Cauvy-Fraunié et al., 2015; Jacobsen et al., 2012). The effects of climate change and subsequent glacier retreat on alpine river ecosystems are complex and the extent of the consequences may be difficult to predict (Milner et al., 2017). Continued monitoring of glaciers and glacier-fed rivers, as well as research on the connection between environmental parameters and the macroinvertebrate taxa in alpine streams, are needed to get a better understanding of the future of these ecosystems in light of climate change.

Conclusion

This study has investigated the impact of 25 years with glacial retreat on macroinvertebrate community composition in two Norwegian glacier-fed rivers. It was found that both glaciers had retreated, and the catchment glacier cover had decreased for Dalelva and Leirungsåi. There was no change in discharge during the 25 years, while water temperature showed a marginally significant increase. This supports the hypothesis of increased water temperature connected to reduced glacier cover. Spot measurements of water temperature, turbidity and total P were higher, and conductivity lower, in 2022 than in 1997. However, as these were spot measurements of highly variable parameters, these results need to be interpreted with caution. Richness and Shannon diversity had increased since 1997, indicating succession in both rivers. Even though this shows an increase in alpha diversity, the taxa compositions of the samples were more similar to each other in 2022 than in 1997, suggesting a decrease in beta diversity. Due to the correlation between Shannon diversity and spot measurements of temperature, conductivity, organic material, pH, turbidity and Pfankuch index, the increased

alpha diversity since 1997 also suggests environmental changes. These findings support the hypothesis that reduced glacial cover has resulted in increased water temperature and channel stability, causing an upstream shift in the macroinvertebrate community. The results from this study suggest that while the alpha diversity of upstream reaches will increase as the glaciers continues to retreat, a reduction in beta and gamma diversity may be expected as the environment of alpine rivers become more homogeneous and specialised species go extinct.

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Appendixes

Appendix 1 - Output from analyses of environmental variables
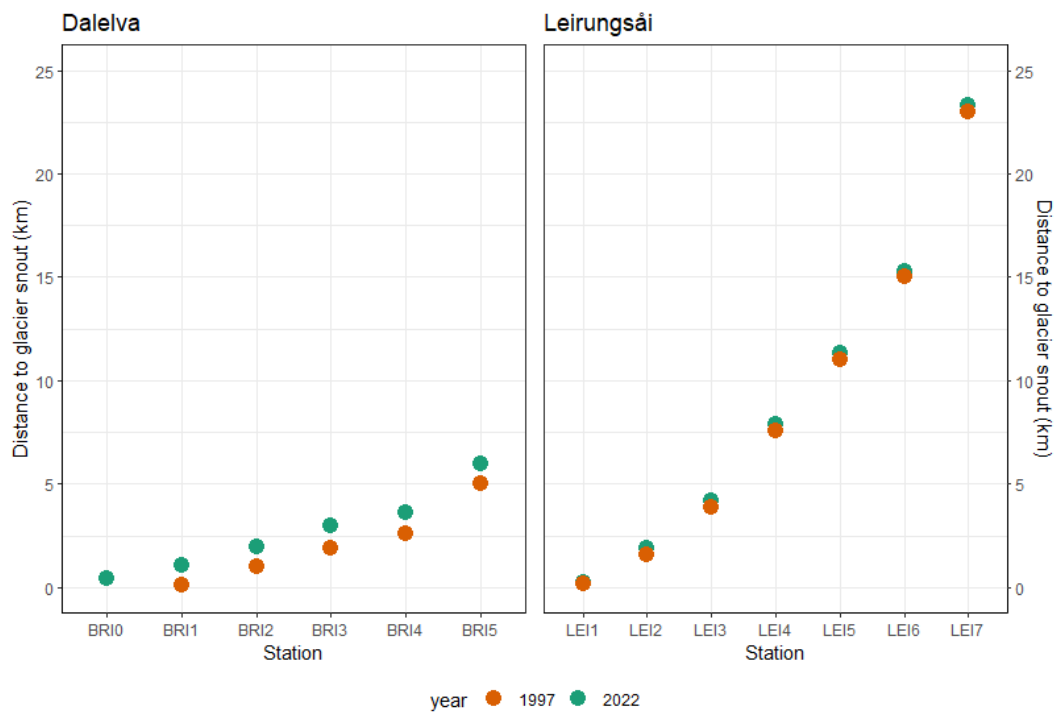
Fig. A1 Distance (km) from glacier snout to the stations in Dalelva (left) and Leirungsåi (right) in 1997 (orange) and 2022 (green).

Table A1 Output from linear models with summer discharge and temperature as a function of time since the beginning of data monitoring.

Variable	River	Slope	Std. error	t-value	R^2	p-value
Discharge	Dalelva	0.0790	0.1035	0.764	0.017	0.4503
	Leirungsåi	0.0916	0.1052	0.871	0.019	0.3889
Temperature	Dalelva	0.0266	0.0151	1.757	0.123	0.0928
	Leirungsåi	0.0387	0.0209	1.857	0.126	0.0756

Table A2 Output from paired samples t-test of difference in spot measurements of environmental variables between 1997 and 2022.

Variable	Mean difference	p-value
Temperature	1.98	< 0.001
Pfankuch index	1.17	0.389
Turbidity	2.57	< 0.001
Conductivity	-1.18	0.005
Total N	-0.0193	0.151
Total P	0.072	< 0.001

Appendix 2 – Output from analyses of macroinvertebrates

Table A3 Output of linear models with mean Shannon diversity as function of log-transformed distance (ln(distance+1)). There were made separate models for each year (1997 and 2022).

Year	Slope	Std. error	t value	R^2	p-value
1997	0.3333	0.0530	6.286	0.782	< 0.001
2022	0.3049	0.0468	6.518	0.794	< 0.001

Table A4 Mean richness per sample in 1997 and 2022, and the differences between them.

Station	Richness 1997	Richness 2022	Difference
BRI0	-	3.4	-
BRI1	2.6	6.0	3.4
BRI2	2.0	8.2	6.2
BRI3	2.2	7.4	5.2
BRI4	2.0	10.0	8.0
BRI5	2.4	10.6	8.2
BRI6	12.2	-	-
BRI7	10.6	13.2	2.6
LEI1	1.2	3.2	2.0
LEI2	3.2	4.8	1.6
LEI3	3.6	6.2	2.6
LEI4	3.2	11.6	8.4
LEI5	5.6	13.8	8.2
LEI6	7.8	14.2	6.4
LEI7	7.0	16.4	9.4
LEI8	9.8	15.2	5.4

Fig. A2 Taxon richness per year, compared between Dalelva and Leirungsåi, with median values (horizontal lines), 50% interquartile range (IQR, coloured boxes), 1.5 * IQR (whiskers) and data outside the 1.5 * IQR (black points). **Left panel**: richness per year in Dalelva (orange) and Leirungsåi (green). **Mid panel**: richness per year in the control station (BRI7, green) and the glacial station in similar altitude (BRI3, orange) in Dalelva. **Right panel**: richness per year in the control station (LEI8, green) and the glacial station in similar altitude (LEI3, orange) in Leirungsåi.

Table A5 Output from Tukey's Honest Significant Difference (HSD) test of the ANOVA model with taxon richness in Dalelva's control station (BRI7) and the glacial station at similar altitude (BRI3) as response variable, and year and station as predictor variables. An interaction term was included between year and station. 'diff' is the difference between the group means, 'lwr' and 'upr' are the lower and upper end points of the intervals, respectively, and 'p adj' is the p-value adjusted for multiple comparisons.

Comparison	diff	lwr	upr	p adj
2022:BRI3-1997:BRI3	5.2	2.5	7.9	0.001
1997:BRI7-1997:BRI3	8.4	5.7	11.1	<0.001
2022:BRI7-1997:BRI3	11.0	8.3	13.7	<0.001
1997:BRI7-2022:BRI3	3.2	0.5	5.9	0.018
2022:BRI7-2022:BRI3	5.8	3.1	8.5	<0.001
2022:BRI7-1997:BRI7	2.6	-0.1	5.3	0.063

Table A6 Output from Tukey's Honest Significant Difference (HSD) test of the ANOVA model with taxon richness in Leirungsåi's control station (LEI8) and the glacial station at similar altitude (LEI3) as response variable, and year and station as predictor variables. An interaction term was included between year and station. 'diff' is the difference between the group means, 'lwr' and 'upr' are the lower and upper end points of the intervals, respectively, and 'p adj' is the p-value adjusted for multiple comparisons.

Comparison	diff	lwr	upr	p adj
2022:LEI3-1997:LEI3	2.6	-0.8	6.0	0.164
1997:LEI8-1997:LEI3	6.2	2.8	9.6	<0.001
2022:LEI8-1997:LEI3	11.6	8.2	15.0	<0.001
1997:LEI8-2022:LEI3	3.6	0.2	7.0	0.034
2022:LEI8-2022:LEI3	9.0	5.6	12.4	<0.001
2022:LEI8-1997:LEI8	5.4	2.0	8.8	0.002

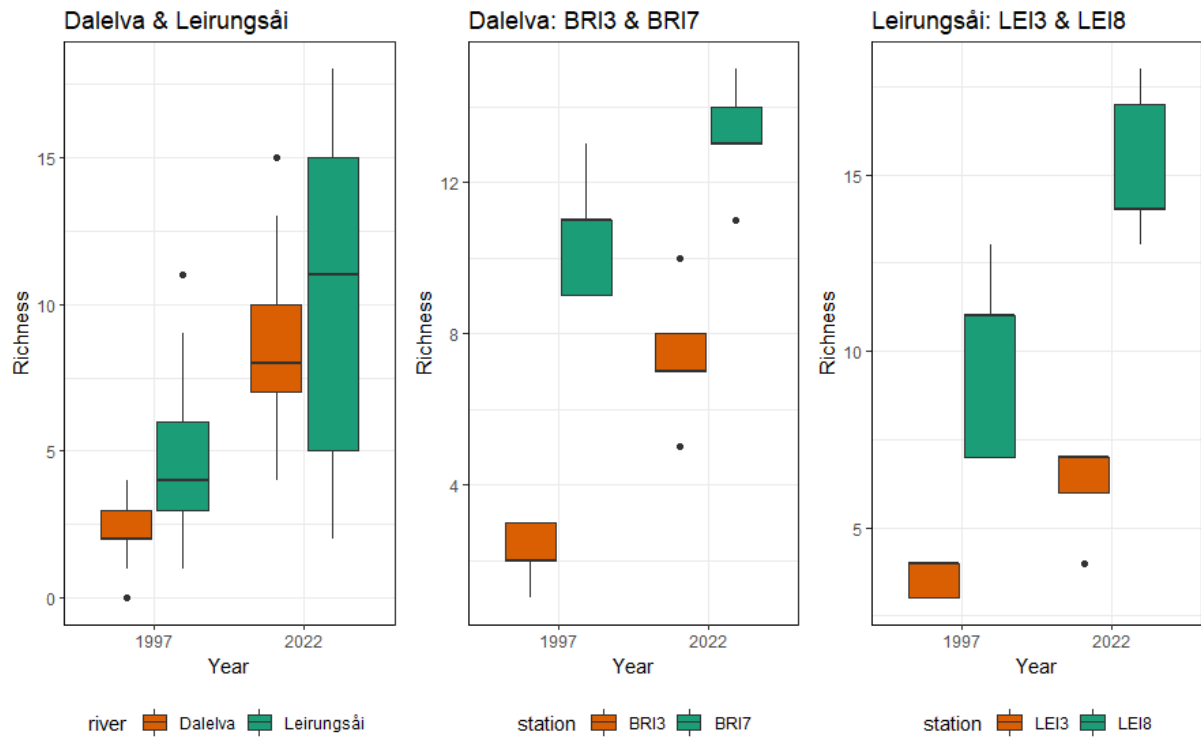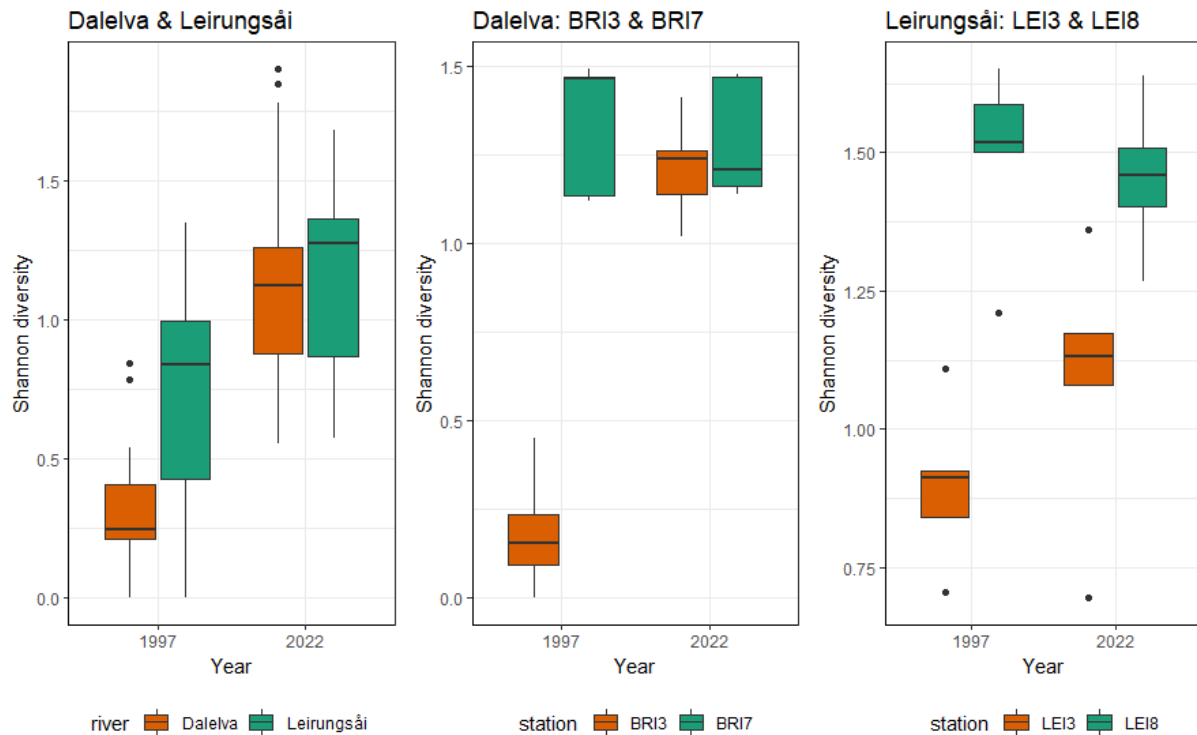**Fig. A3** Shannon diversity index per year compared between Dalelva and Leirungsåi, with median values (horizontal lines), 50% interquartile range (IQR, coloured boxes), 1.5 * IQR (whiskers) and data outside the 1.5 * IQR (black points). **Left panel**: Shannon diversity per year in Dalelva (orange) and Leirungsåi (green). **Mid panel**: Shannon diversity per year in the control station (BRI7, green) and the glacial station in similar altitude (BRI3, orange) in Dalelva. **Right panel**: Shannon diversity per year in the control station (LEI8, green) and the glacial station at similar altitude (LEI3, orange) in Leirungsåi.

Table A7 Output from Tukey's Honest Significant Difference (HSD) test of the ANOVA model with Shannon diversity as response variable, and year and river as predictor variables. An interaction term was included between year and river. 'diff' is the difference between the group means, 'lwr' and 'upr' are the lower and upper end points of the intervals, respectively, and 'p adj' is the p-value adjusted for multiple comparisons.

Comparison	diff	lwr	upr	p adj
2022:Dalelva-1997:Dalelva	0.813	0.569	1.056	<0.001
1997:Leirungsåi-1997:Dalelva	0.420	0.195	0.645	<0.001
2022:Leirungsåi-1997:Dalelva	0.843	0.618	1.068	<0.001
1997:Leirungsåi-2022:Dalelva	-0.392	-0.617	-0.167	<0.001
2022:Leirungsåi-2022:Dalelva	0.030	-0.195	0.255	0.985
2022:Leirungsåi-1997:Leirungsåi	0.423	0.217	0.628	<0.001

Table A8 Output from Tukey's Honest Significant Difference (HSD) test of the ANOVA model with Shannon diversity in Dalelva's control station (BRI7) and the glacial station at similar altitude (BRI3) as response variable, and year and station as predictor variables. An interaction term was included between year and station. 'diff' is the difference between the group means, 'lwr' and 'upr' are the lower and upper end points of the intervals, respectively, and 'p adj' is the p-value adjusted for multiple comparisons.

Comparison	diff	lwr	upr	p adj
2022:BRI3-1997:BRI3	1.027	0.720	1.334	<0.001
1997:BRI7-1997:BRI3	1.151	0.844	1.458	<0.001
2022:BRI7-1997:BRI3	1.105	0.796	1.412	<0.001
1997:BRI7-2022:BRI3	0.123	-0.184	0.431	0.665
2022:BRI7-2022:BRI3	0.077	-0.230	0.384	0.888
2022:BRI7-1997:BRI7	-0.046	-0.353	0.261	0.973

Table A9 Output from Tukey's Honest Significant Difference (HSD) test of the ANOVA model with Shannon diversity in Leirungsåi's control station (LEI8) and the glacial station at similar altitude (LEI3) as response variable, and year and station as predictor variables. An interaction term was included between year and station. 'diff' is the difference between the group means, 'lwr' and 'upr' are the lower and upper end points of the intervals, respectively, and 'p adj' is the p-value adjusted for multiple comparisons.

Comparison	diff	lwr	upr	p adj
LEI8:1997-LEI3:1997	0.596	0.271	0.921	<0.001
LEI3:2022-LEI3:1997	0.190	-0.135	0.515	0.369
LEI8:2022-LEI3:1997	0.557	0.232	0.882	0.001
LEI3:2022-LEI8:1997	-0.406	-0.731	-0.081	0.012
LEI8:2022-LEI8:1997	-0.039	-0.364	0.286	0.986
LEI8:2022-LEI3:2022	0.367	0.042	0.692	0.024

Appendix 3 – Output from GLMMs

Table A10 Output from models with Shannon diversity as response variable. In the Generalised linear mixed models (GLMMs), using data from both 1997 and 2022 were used, the environmental variables were used as fixed factors and year were used as random factor. In the simple linear models, with data from 2022 only, the environmental variables (weight of organic material and pH) were used as explanatory variables.

Model	Explanatory variable	Slope	Std. error	DF	p-value
GLMM	Temperature	0.0849	0.0071	127	<0.0001
	ln(Turbidity)	-0.3007	0.0251	117	<0.0001
	Conductivity	0.1944	0.0313	117	<0.0001
	Pfankuch index	-0.0236	0.0035	127	<0.0001
	ln(Distance to glacier snout + 1)	0.3208	0.0226	127	<0.0001
	Total N	-1.4771	0.8499	127	0.0847
	Total P	-4.8571	6.3846	127	0.4482
Simple linear model	Organic material	0.3595	0.0703	63	3.18e-06
	pH	0.2343	0.0657	63	0.0007

Appendix 4 – Pfankuch stability score table

Table A11 Pfankuch stability score assessment criteria (Pfankuch, 1975).

Component		Score		Score		Score		Score
1. Rock angularity	Sharp edges and corners, plane surfaces roughened.	1	Rounded edges and corners. Surfaces smooth and flat.	2	Corners and edges well rounded in 2 dimensions.	3	Well rounded in all dimensions, surfaces smooth.	4
2. Brightness	Surface dull, darkened, stained by algae or minerals. Bright surface <5% of area.	1	Mostly dull but may have up to 35% bright surfaces, some dull on larger rocks.	2	Mixture 50-50% dull and bright (± 15%).	3	Predominantly bright >65% exposed or scoured surfaces.	4
3. Consollidation and particle size of substrate	Assorted sizes tightly packed or overlapping.	2	Moderately packed with some overlapping.	4	Mostly a loose assortment with no apparent overlap.	6	No packing evident, loose assortment easily moved.	8
4. Percent of riverbed stable	80-100%	4	50-80%	8	20-50%	12	0-20%	16
5. Scouring and deposition	<5% channel length affected by scouring and deposition.	6	5-30% affected. Scour at constrictions and where gradient steepens. Some deposition in backwaters and pools.	12	30-50% affected. Deposits and scour at obstructions, constructions at bends. Some filling in pools.	18	>50% of the bottom in a state of flux or change nearly year long.	24
6. Clinging aquatic vegetation (mosses and algae)	Abundant. Growth largely moss like, dark green year round. In swift water.	1	Common. Algae forms in low velocity and pol areas. Moss in swift waters.	2	Present but spotty. Mostly in backwater areas. Seasonal blooms make rocks slick.	3	Perennial types scarce or absent. Yellow-green short-term bloom may be present.	4

Total stability score = sum of the six components

Lower scores = higher stability

Appendix 5 – Environmental variables

Table A12 Environmental parameters measured in July 2022.

station	altitude	slope	dist_snout	mainChanWidth	pfan	date	time	northing	easting	temp	turbidity
BRI0	350	NA	451	10	54	19.07.2022	10:05	61°39.764'	006°52.068'	1.7	18.85
BRI1	340	0.03353	1060	18.5	37	19.07.2022	11:50	61°39.861'	006°51.410'	3.15	20.25
BRI2	300	0.0148	1960	9.3	40	19.07.2022	13:50	61°39.909'	006°50.510'	5.1	16.13
BRI3	180	0.0701	2999	14.8	46	18.07.2022	14:30	61°663.412'	6°825.217'	5.65	16.005
BRI4	70	0.02103	3600	25.5	44	18.07.2022	11:30	61°674.304'	6°814.754'	6.75	9.59
BRI5	40	0.00601	6000	20	43	18.07.2022	09:30	61°701.801'	6°813.143'	5.85	12.12
BRI7	150	0.0682	NA	8.8	32	18.07.2022	16:00	61°39.881'	006°49.012'	8.85	1.84
LEI1	1550	0.08033	264	4	45	21.07.2022	13:00	61°24.182'	008°41.626'	2.1	59.4
LEI2	1380	0.03387	1901	21	45	21.07.2022	15:40	61°25.017'	008°41.992'	5.5	42
LEI3	1270	0.00753	4208	15	38	21.07.2022	17:00	61°25.542'	008°43.789'	9.5	21.665
LEI4	1150	0.106	7905	20	38	23.07.2022	09:15	61°26.478'	008°46.829'	7.2	9.915
LEI5	1100	0.00733	11305	35	27	22.07.2022	14:30	61°27.975'	008°45.797'	12.5	7.24
LEI6	986	0.0514	15305	20	24	22.07.2022	11:30	61°29.274'	008°42.784'	11.5	7.655
LEI7	970	0.00092	23305	50	29	23.07.2022	11:00	61°29.515'	008°50.648'	8.5	1.69
LEI8	1250	0.04433	NA	13	19	20.07.2022	16:30	61°25.333'	008°47.802'	15.3	0.81

station	conductivity	pH	weightOrganic	percBoulder	percCgrav	percFgrav	percSandSilt	tot_N	tot_P	glac_cov	glac_cov_diff
BRI0	5.97	4.44	0.2398	12	58	30	0	0.165	0.085	78.82	NA
BRI1	6.73	5.01	1.5732	10	71	19	0	0.079	0.08	71.41	0.13
BRI2	6.14	4.98	1.2138	1	80	19	0	0.024	0.082	66.82	2.62
BRI3	6.1	4.83	1.2079	7	9	9	75	0.089	0.075	63.70	3.64
BRI4	5.39	5.02	0.9252	6	75	19	0	0.077	0.081	54.79	5.58
BRI5	5.43	5.05	1.4657	6	84	10	0	0.088	0.081	57.42	4.89
BRI7	3.9	4.47	2.4234	11	57	32	0	0.004	0.075	20.92	10.28
LEI1	5.44	5.23	0.7108	3	54	43	0	0.17	0.075	29.24	5.98
LEI2	5.6	5.4	0.6691	2	68	30	0	0.152	0.076	16.53	5.71
LEI3	5.72	5.51	0.8525	0	75	25	0	0.093	0.073	14.18	3.86
LEI4	6.11	6.45	1.5209	0	40	60	0	0.062	0.077	13.79	3.57
LEI5	7.16	5.59	0.8614	0	41	59	0	0.039	0.074	7.87	2.15
LEI6	6.83	5.44	1.4482	11	74	15	0	0.035	0.073	7.04	1.75
LEI7	17.02	6.72	2.3870	10	82	8	0	0.044	0.075	8.20	2.03
LEI8	10.54	4.93	2.2040	7	62	31	0	0.144	0.077	0.00	0.00

Table A13 Environmental parameters measured in 1997.

station	altitude	slope	dist_snout	mainChanWidth	pfan	motemp97	evtemp97	temp97	minturb97	maxturb97	turb97
BRI1	340	0.03353	120	18.5	36	0.7	1.1	0.9	3.5	5.30	3.50
BRI2	300	0.01480	1000	9.3	44	1.5	2.5	2	2.5	7.40	2.50
BRI3	180	0.07010	1900	14.8	39	2.6	3.7	3.15	2.6	NA	2.60
BRI4	70	0.02103	2600	25.5	51	3.4	4.1	3.75	NA	NA	NA
BRI5	40	0.00601	5000	20	41	3.7	4.4	4.05	2.1	NA	2.10
BRI6	10	0.00220	19000	30	41	9.7	11.1	10.4	NA	NA	NA
BRI7	150	0.06820	NA	8.8	24	9.1	NA	9.1	NA	NA	NA
LEI1	1550	0.08033	200	4	50	0.6	1.2	0.9	NA	2.80	2.80
LEI2	1380	0.03387	1600	21	47	2.1	4.0	3.05	NA	1.65	1.65
LEI3	1270	0.00753	3900	15	39	3.2	8.9	6.05	NA	0.52	0.52
LEI4	1150	0.10600	7600	20	46	4.8	11.0	7.9	NA	0.39	0.39
LEI5	1100	0.00733	11000	35	28	5.8	12.3	9.05	NA	0.40	0.40
LEI6	986	0.05140	15000	20	25	10.8	11.5	11.15	NA	0.35	0.35
LEI7	970	0.00092	23000	50	24	6.8	8.3	7.55	NA	0.27	0.27
LEI8	1250	0.04433	NA	13	28	12.2	15.0	13.6	NA	0.11	0.11

station	conductivity97	percOrganic97	percBoulder	percCgrav	percFgrav	percSandSilt	chla96	chla97	tot_P_97	tot_N_97
BRI1	6.3	0.09	NA	NA	NA	NA	NA	63.2	0.004	0.050
BRI2	6.1	1.38	28.0	22.0	39.0	1.0	NA	25.2	0.008	0.040
BRI3	6.4	0.34	53.5	16.0	29.5	1.0	NA	25.3	0.005	0.050
BRI4	6.0	1.26	24.5	36.0	37.0	2.5	NA	14.4	0.012	0.020
BRI5	5.7	0.67	NA	NA	NA	NA	5.4	43.9	0.005	0.030
BRI6	12.8	10.12	NA	NA	NA	NA	NA	8.6	0.022	0.130
BRI7	4.8	10.42	31.0	22.5	35.0	1.5	25.3	30.5	0.002	0.000
LEI1	7.0	0.33	53.3	18.8	6.3	20.0	1.3	21.1	0.007	0.090
LEI2	7.6	0.35	41.0	26.0	16.0	17.0	4.0	19.3	0.007	0.090
LEI3	7.4	0.31	22.0	26.0	29.0	23.0	3.1	15.3	0.002	0.070
LEI4	7.4	0.30	32.0	18.0	30.0	20.0	0.6	14.3	0.002	0.050
LEI5	8.2	1.31	44.0	22.0	13.5	20.5	0.7	3.2	0.002	0.080
LEI6	8.6	2.40	57.0	25.0	15.5	2.5	1.8	24.7	0.002	0.050
LEI7	9.9	4.96	63.0	21.0	8.5	7.5	4.5	5.5	0.002	0.100
LEI8	11.7	10.70	47.5	22.5	24.0	6.0	1.1	12.9	0.002	0.060

Appendix 6 – Macroinvertebrates

Table A14 Macroinvertebrate taxa list. Marked with an x if the taxon was found in samples from Dalelva or Leirungsåi in 1997 or 2022.

Taxa	1997		2022	
	Dalelva	*Leirungsåi*	*Dalelva*	*Leirungsåi*
OLIGOCHAETA	x	x	x	x
CHIRONOMIDAE				
Diamesinae	x	x	x	x
Tanypodinae	x	x	x	x
Orthocladiinae	x	x	x	x
Chironomini				x
Tanytarsini	x	x	x	x
EPHEMEROPTERA				
Acentrella lapponica				x
Ameletus inopinatus		x		x
Baetis sp.				x
Baetis rhodani	x	x	x	x
Ephemerella aurivillii		x		x
Ephemerella mucronata				x
PLECOPTERA				
Amphinemura standfussi	x	x	x	x
Amphinemura sulcicollis				x
Amphinemura sp.			x	x
Brachyptera risi	x		x	
Capnia sp.			x	x
Capnia bifrons			x	x
Diura nanseni	x		x	x
Isoperla sp.		x		
Isoperla grammatica		x		x
Isoperla obscura		x		x
Leuctra digitata				x
Leuctra fusca	x	x		
Leuctra hippopus	x			
Nemouridae indet.			x	
Nemoura sp.			x	
Nemoura cinerea			x	
Perlodidae sp.			x	x
Protonemura meyeri	x			x
TRICHOPTERA				
Trichoptera pupae				x
Annitella obscurata			x	
Apatania sp.		x		
Apataniidae sp.			x	x
Halesus_tessellatus				x
Limnephilidae sp.		x		x
Philopotamus montanus			x	
Plectrocnemia conspersa			x	
Potamophylax cingulatus			x	
Potamophylax latipennis			x	
Rhyacophila sp.			x	x

Rhyacophila nubila	x	x	x	x
Amphipoda				x
Collembola	x	x	x	x
Copepoda				x
Corixidae	x			
Gastropoda			x	
Hydracarina	x	x	x	x
Hymenoptera	x			
Lamellibranchia	x			x
Nematoda			x	x
Simuliidae	x	x	x	x
Tabanidae	x			
Limnoniidae	x	x	x	x
Turbellaria			x	x
Other Diptera			x	x