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Invertebrate community change in acidified rivers and lakes in Southern Norway

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FOREWORD

This research was conducted as part of the research master programme Sustainable Development at Utrecht University, focussing on the track Global Change and Ecosystems. The aim of the research is to gain better understanding of the temporal recovery trends of invertebrate communities in acidified lakes and rivers in Norway, and to disentangle the environmental causes of the observed trends. The research was performed in collaboration with ICP Waters, a programme for monitoring of the effects of acid deposition in rivers and lakes.

I want to thank all the researchers who collected, assembled, analysed, and quality controlled the ICP Waters data. Such a long-term monitoring programme is unique, and should be valued highly. I also want to thank Heleen de Wit for showing me around at NIVA in Oslo in November, and getting me started with the data. Further, I want to thank Arne Fjellheim for taking me along with his fieldwork in June as the second person on the lake team. It was informative and inspiring to see the sampling of invertebrates, and gave me a better understanding of the processes taking place at the study sites. I want to thank Gaute Velle for giving helpful advice on my statistical analysis, and giving me better insight in the ins and outs of invertebrates. Additionally, I want to thank my supervisor Karin Rebel for her enthusiasm on the research topic, and discussing my progress. Lastly, I want to thank both Karin Rebel, Heleen de Wit, and Gaute Velle for their useful comments on my writing.

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ABSTRACT

International policy action has led to significant reduction of sulphur emissions, and subsequent deposition, which resulted in widespread improvements in the water chemistry of acidified regions. However, biological recovery appears to be much slower than chemical recovery. The aim of this study was to analyze temporal changes of invertebrate communities in acidified rivers and lakes, and disentangle the environmental causes of the observed changes. The analysis was performed using long-term data from rivers (25-30 years) and lakes (~15 years) in three catchments along the west coast of Southern Norway, which represent a gradient of non-marine sulphur deposition. We performed statistical analysis using both biological indices and ordination methods. First, our results show that invertebrate communities in rivers shifted from a state with low or absence of acid-sensitive taxa to an alternate state with higher richness and abundance of acid-sensitive taxa. These biological shifts coincided with previously defined chemical thresholds. Second, there was no invertebrate community change recorded in the lakes, even though chemical recovery was comparable to the rivers. This finding may relate to limited variation in habitat and refuges, which may make them less susceptible to re-colonisation of acid-sensitive taxa, or it may relate to the taxonomic resolution. Third, our result indicate that the recovery of invertebrate communities in rivers is primarily related to reduced sulphur deposition, and associated water chemistry. Superimposed on the long-term trends, temperature fluctuations and sea-salt episodes have caused short-term variability in the invertebrate community. We did not identify impacts of temperature rise on the long-term invertebrate community trends. We conclude on the importance of a continuous research effort to disentangling the complex link between acidification, and climate on invertebrate community change.

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1 INTRODUCTION

1.1 BACKGROUND

In the early 1970s, acidification was first linked to observed extinction of fish populations (Schofield, 1976), forest diebacks (Tomlinson, 1983), and damage to buildings (Likens et al., 1972). Acidifying gases, primarily sulphur dioxides and nitrogen oxides, are emitted in the atmosphere as by-product of fossil fuel combustion. Prevailing winds can carry these polluted air masses over long distances across national boundaries, and create damage far beyond their country of origin (Likens et al., 1972; Cowling, 1982). The negative effects of acid deposition are most severe in rivers and lakes in regions where the soil has limited ability to neutralize acidic compounds (buffer capacity), e.g. north-eastern North-America, Sweden, Norway and the United Kingdom (Schindler, 1988). The water chemistry in acidified ecosystems is characterized by chronic low pH, and low acid neutralizing capacity, as well as increased concentrations of labile aluminium (Wright, 2008).

In 1983, the Convention on Long-Range Transboundary Air Pollution went into effect to control air pollution, and thereby protect the environment. Sulphur emissions, and to a lesser extent nitrogen emissions, and subsequent deposition have been reduced, which led to widespread improvements in the water chemistry in most regions since the 1990s (Garmo et al., 2014). Biological recovery appears to be much slower than chemical recovery (Battarbee et al., 2014; Hesthagen et al., 2011; Murphy et al., 2014; Raddum et al., 2001). It is suitable to assess the rate, and trajectory of biological recovery patterns by long-term data of invertebrates as different species have varying sensitivity to acidity (Hesthagen et al., 2011), and their response to changes in the environment is often rapid and dramatic, relative to longer-lived organisms (Jackson & Fureder, 2006).

Long-term monitoring studies of invertebrate communities demonstrated modest to more pronounced recovery trends from acidification in various regions, however no recovery in the entire community was evident. In the UK, about half of the 22 acidified lakes and rivers showed trends of recovery of the invertebrate community over a 20-year (1988-2007) record (Murphy et al., 2014). During the same period, acid-sensitive taxa in 11 Swedish lakes showed a weak response to decreasing acidification (Angeler & Johnson, 2012). In the rivers of six Norwegian catchments, the amount of acid-sensitive taxa increased between 1981 and 1998 (Raddum et al., 2001). An evaluation of 15-years (1988-2002) of invertebrate data in Canada showed an increase in the relative abundance of acid-sensitive taxonomic orders of Ephemeroptera, Plecoptera, and Trichoptera (EPT) in nine out of 17 lakes (Lento et al., 2012).

Invertebrate community changes have been related to water chemistry trends (Halvorsen et al., 2003; Murphy et al., 2014). Acid neutralizing capacity (ANC), a composite descriptor of acidification, most frequently explained the invertebrate community change in waters in the UK (Murphy et al., 2014). Several significant interactions with sulphate (SO_4) concentration, pH and groups of invertebrate taxa were identified in the Swedish lakes (Angeler & Johnson, 2012). Other chemistry compounds, related to acidification, can also influence invertebrate communities. Examples include high labile aluminium (LAL), which is toxic, low calcium (Ca), which can have negative physiological effects (Angeler & Johnson, 2012), high total organic carbon (TOC), which can have indirect effects on the light regime, energy- and nutrient supply, and metal toxicity (Evans et al., 2005).

Invertebrate recovery has not met the extent or pace of improvements in water chemistry, therefore it has been hypothesized that other factors limit the recovery, e.g. biological interactions (Ledger & Hildrew, 2005), slow dispersal (Snucins, 2003), climate variability, and climate change (Durance & Omerod, 2007). Climate variability may limit the recovery in terms of acid episodes related to storminess (Kolawik & Ormerod, 2006). Whereas climate change may impact the recovery by increased water temperatures related to global warming (Burgmer et al. 2009), and more extreme high and low flow events related to changing precipitation patterns (Suren & Jowett, 2006).

High deposition of sea-salts during storms with high wind and precipitation is the major driver of acid episodes in coastal areas (Wright, 2008). A fraction of the incoming sodium- and magnesium cations in sea-salts is exchanged for the acid cations hydrogen and aluminium in the soil. Chloride (Cl^-) is a mobile anion which passes through the soil. The runoff from the soil temporarily increases acidity, as well as aluminium and chloride concentrations in the surface waters, which can cause biological damage (Wright et al., 1988; Hesthagen et al., 2011). The biological impacts of episodic acid inputs may be more severe in rivers than in lakes, as the large water volume and long water residence time may reduce the severity of acid pulses in lakes (Wright et al., 2008). Toxic effects of sea-salt episodes on the biota are reduced with reduced acidification, however, sea-salt episodes may become more frequent and stronger in the future due to increased storminess (Hindar et al., 2004).

Climate change has lead to higher air temperatures, more heavy winter precipitation, and decreased summer precipitation in the acidified regions of Northern Europe (IPCC, 2014). Preliminary evidence suggests that increased temperatures have altered the invertebrate species composition in Swedish lakes (Burgmer et al. 2009; Johnson & Angeler, 2010). However, the change in species composition may also relate to increased dissolved organic carbon, and decreased acidification (Velle et al., 2013). Change in water temperature can affect the growth, metabolism, reproduction, and emergence of invertebrates (Vannote et al., 1980), and can cause a mismatch in predator-prey interactions (Senseth et al., 2002). Changing precipitation patterns can lead to flooding events during winter, and drought during summer, which can affect acidity of surface waters (Ormerod & Durance, 2009). Extreme high flow events might disturb the bottom substrate of river beds. The bottom substrate normally forms a safe refuge during high flow. These refuges are destroyed during extreme flow events (Holomuzki & Biggs, 2000).

1.1 PROBLEM DEFINITION

Firstly, long-term studies of invertebrate communities have mostly focussed on linear trends, i.e. gradual change over time that is consistent in direction (Raddum et al., 2001; Lento et al., 2012; Murphy et al., 2014). A conceptual model shows that continuously increasing pressures can result in abrupt change between alternate stable states when certain thresholds are reached, e.g. regime shifts (Andersen et al., 2009). Few studies have reported abrupt changes between alternate stable states from reduced pressures, such as acidification (Capon et al., 2015). To our knowledge no previous study has assessed whether invertebrates in acidified rivers and lakes changed gradually, or whether abrupt changes between alternate stable states took place.

The invertebrate community change has been assessed in both rivers and lakes, nevertheless, only one previous study compared their respective responses to acidification. Murphy et al. (2014) observed no systematic difference between the recovery of invertebrate communities in lake- and river stations in the UK. However, rivers and lakes differ in habitat and speed of water flow, which can affect dispersal of organisms, acquisition of essential resources, competition, and predation (Wetzel, 2001; Stockdale et al., 2014). Further, large volumes of water in lakes can dampen the affect of acid episodes (Wright. 2008). The results of Murphy et al. (2014) have not been validated for other acidified regions.

Lastly, climate-related factors may have constrained an invertebrate recovery from acidification, or acidification up to present may have overridden effects caused by climate-related factors (Durance & Ormerod, 2007). The climate is expected to change more rapidly in the future, highlighting the need to identify potential impacts of climate variability, and climate change (IPCC, 2014). No previous study has disentangled how sulphur deposition, climate-related factors, and associated hydro-chemistry have collectively impacted invertebrate community recovery from acidification.

1.2 AIM

The overall aim of our research is to analyze temporal changes of invertebrate communities in acidified rivers and lakes, and disentangle the environmental causes of the observed changes. First, it is aimed to identify whether the invertebrate communities recovered, and if the change was gradual, or if the community changed abruptly to an alternate stable state. Second, it is aimed to compare the invertebrate community changes in rivers and lakes. Third, it is aimed to assess if and how the invertebrate community changes were related sulphur deposition, climate, and associated hydro-chemistry. An overview of the potential relations between the environmental variables and invertebrate communities in acidified waters is conceptualized in Figure 1.

1.3 RESEARCH QUESTIONS

These aims resulted in the following research questions:

1. Have invertebrate communities recovered in acidified rivers and lakes in Norway, and were the changes gradual, or were the changes abruptly to an alternate stable state?
2. Is there a difference between the invertebrate community change in rivers and lakes?
3. Were the observed invertebrate community changes related to sulphur deposition, climate, and associated hydro-chemistry variables?

1.4 HYPOTHESES

The hypotheses about these research questions are:

1. Invertebrate communities recovered with abrupt shifts to an alternate stable state as particular chemical thresholds were reached (Monteith et al., 2005).
2. Recovery of invertebrate communities was more pronounced in rivers than in lakes, as rivers are more dynamic than lakes, which makes them more susceptible for re-colonization (Havas et al., 1995; Velle et al., 2013).
3. Recovery of invertebrate communities was related to reduced sulphur deposition, and associated changes in the water chemistry. Climate variability in terms of sea-salt-episodes has constrained the recovery from acidification (Hesthagen et al., 2011), whereas climate change was too small to impact the recovery (Durance & Ormerod, 2007).

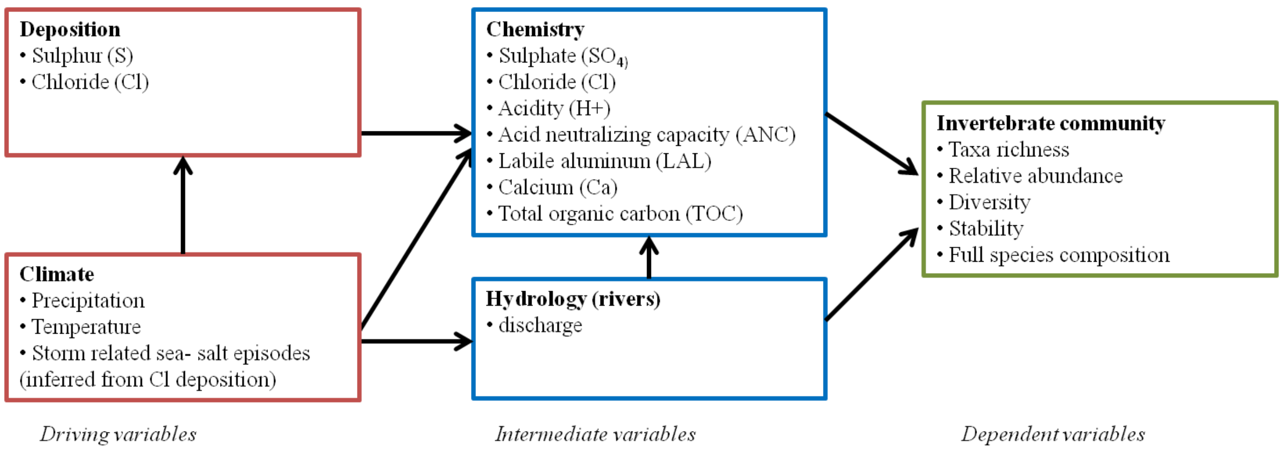

Figure 1: Overview of possible relations between sulphur deposition and climate (driving variables in red), hydro-chemistry (intermediate variables in blue), and invertebrates communities (dependent variables in green) in acidified rivers and lakes.

2 METHODOLOGY

2.1 STUDY SITES

Three catchments along the west coast of Southern Norway were studied, namely Gaular, the upstream part of Vikedal, and Farsund (Figure 3a). The catchments represent a gradient of non-marine sulphur deposition (NILU, 2012). The sulphur deposition is lowest in the catchment located in the northern part of the investigated area (Gaular catchment), and highest in the southernmost part (Farsund catchment). The gradient was chosen to assess if the biological recovery patterns are dependent on the amount of acid deposition. The studied catchments have a low-buffer capacity against acid deposition, as their bedrock consists mostly of granites and gneisses, which offers limited ability to neutralize acidic compounds (Fjellheim & Raddum, 1990). The catchments were selected based on three criteria: 1) the invertebrate data consisted of two sampling moments each year for a period of at least 15 years in both rivers and lakes, 2) environmental data was available, 3) the catchments were not significantly impacted by humans in terms of point source pollution, agriculture, or commercial forestry.

In each catchment, the invertebrates were monitored at one lake station (Nystølvatn, Røyravatn, and Saudlandsvatn), with water chemistry measured in the lake outlet stream (Figure 3b). The invertebrates were monitored at multiple locations in running water, referred to as river stations. Three river stations (Gaular st.5, Vikedal st.11, and Farsund st.4) were analyzed in detail, because they were located closest to a chemistry station (Figure 3b). For Gaular st.5 and Vikedal st.11, discharge was measured in the river, whereas discharge was modelled for Farsund st.4. The acid deposition monitoring stations were located in vicinity of the catchments. Temperature and precipitation were modelled for the grid cells in which the invertebrate stations were located. Details of the invertebrate and environmental data are provided in Table 1.

Figure 2: Pictures of key study sites: a) Gaular st.5 (river; picture by G.A. Halvorsen); b) Nystølvatn (lake; picture by G.A. Halvorsen); c) Vikedal st.11 (river; picture by A. Fjellheim); d) Røyravatn (lake); e) Farsund st.4 (river); f) Saudlandsvatn (lake).

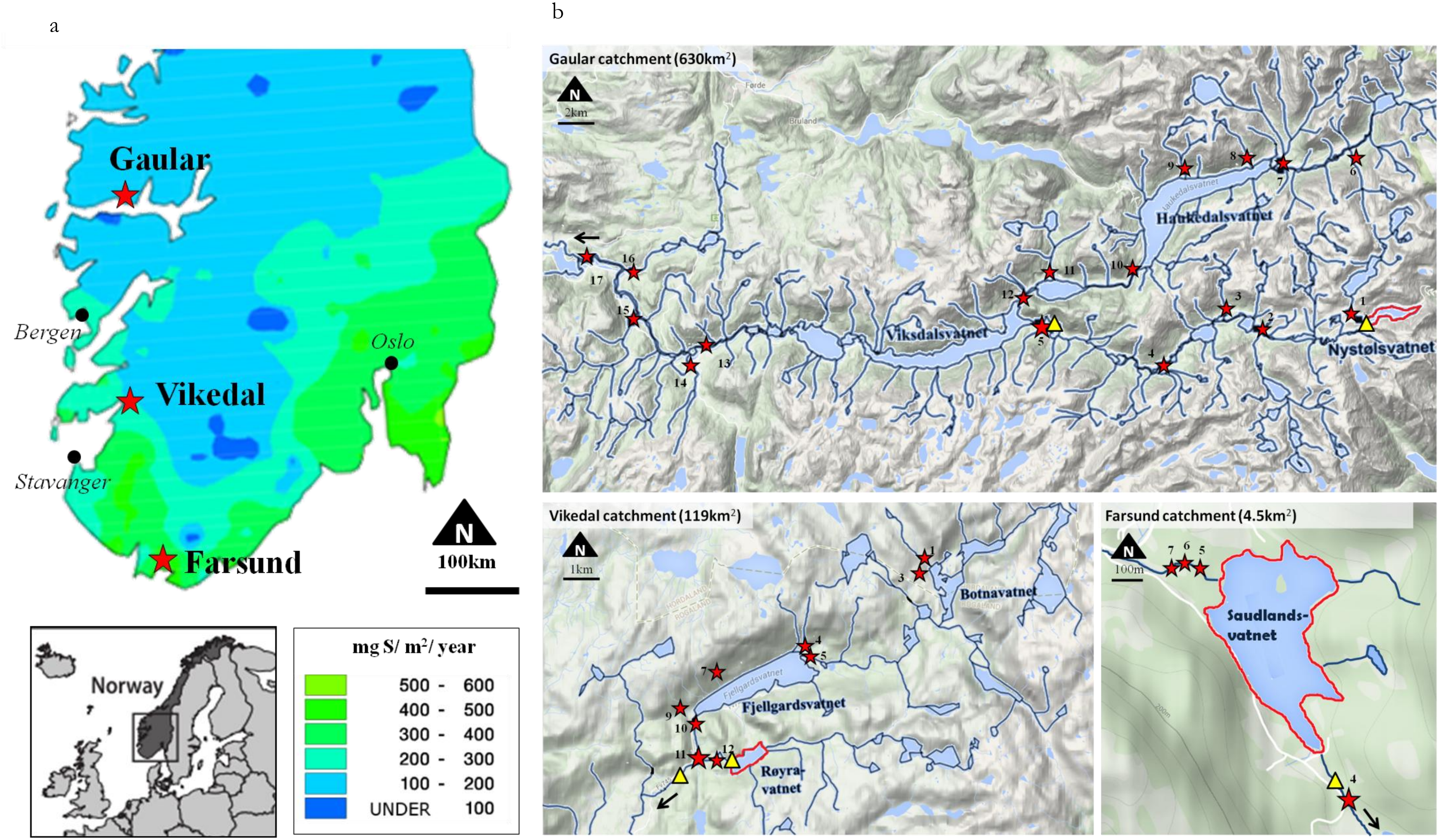

Figure 3: Location of study sites: a) catchments along the coast of Southern Norway with average non-marine sulphur deposition from 2007-2011 (NILU, 2012); b) monitoring stations within catchment, with invertebrate river stations as red star, invertebrate lake stations outlined in red, chemistry stations as yellow triangle, and direction of water flow in catchment as arrow. Note the difference in scales of the catchments.

Table 1: Details of invertebrate and environmental monitoring in the rivers and lakes in three catchments in Southern Norway.

	Gaular catchment	Vikedal catchment	Farsund catchment
River			
Characteristics			
Name	Gaular	Vikedal	Farsund
Catchment (km^2)	630	119	4.5
Elevation above sea level (m)	14-734	157-498	110
Invertebrates			
Number of stations	17	9	4
Key station with chemistry data	Gaular st. 5	Vikedal st. 11	Farsund st. 4
Years	1989-2014	1987-2014	1981-2013
Coordinates key station	61°34' 6°13'	59°54' 6°00'	58°20' 6°77'
Chemistry			
Name station	Eldal	Låkafossen	Outlet lake
Years	1989-2003	1987-2014	1997-2013
Coordinates	61°34' 6°13'	58°54' 5°98'	58°20' 6°77'
Discharge			
Name station	Byttevatn	Holmen	Modelled
Years	1980-2014	1982-2014	2000-2013
Coordinates	61°34' 6°34'	59°50' 5°91'	58°20' 6°77'
Lake			
Characteristics			
Name	Nystølvatn	Røyravatn[1]	Saudlandsvatn
Lake area (km^2)	1.25	0.42	0.14
Elevation above sea level (m)	715	230	110
Invertebrates			
Years	1998-2011	1998-2012	1997-2012
Coordinates	61°34' 6°49'	59°54' 6°02'	58°20' 6°77'
Chemistry (in outlet of lake)			
Years	1997-2012	1998-2012	1997-2012
Coordinates	61°34' 6°49'	59°54' 6°02'	58°20' 6°77'
Climate (modelled)			
Years[2]	1980-2012	1980-2012	1980-2012
Coordinates	61°34' 6°13'	59°54' 6°00'	58°20' 6°77'
Acid deposition			
Name station	Nausta	Vikedal	Birkenes
Years	1985-2012	1983-2012	1972-2012
Coordinates	61°34' 5°53'	5°32' 5°58'	58°23' 8°15'
Distance to catchment (km)	20	0	50

1) Additionally, lake Botnavatn (59°59', 6°12') in the Vikedal catchment was sampled from 1987-2014 (lake area 0.67km^2 and elevation above sea level 457m). No chemistry data was available for this station, and is therefore only mentioned in the appendices.
2) The starting date of the climate data was set to 1980 to match the time span covered by the biological data

2.2 DATA

2.2.1 DATA PROVIDERS

Invertebrate, chemistry and deposition data were taken from the Norwegian Monitoring Programme for Long Range Transported Air Pollutants. Discharge data was obtained from the Norwegian Water Resources and Energy Directorate, with modelled data produced for the Monitoring Programme Riverine Inputs and Direct Discharges. The Climate Research Unit (CRU) provided TS3.21 modelled temperature and precipitation data. Details of the data providers, methods of sampling or modelling, and frequency of measurements for all study sites is provided in Table 2.

Table 2: Overview of data acquisition for all study sites indicating data provider, sampling or modelling method, frequency of measurement, and variables used from the data.

Data	Data provider	Method	Frequency	Variables
Invertebrate	Norwegian Monitoring Programme for Long Range Transported Air Pollutants-Uni[1]	Qualitative kick-sweep method (Frost et al., 1971). Details in ICP Waters Programme Centre (2010)[2]	Spring (Apr.-Jun.); autumn (Sept.-Nov.)	Relative abundance (%)
Chemistry	The Norwegian Monitoring Programme for Long Range Transported Air Pollutants-NIVA[1]	Standardized sampling according to ICP Waters Programme Centre (2010)	Irregular	H^+ (moles/l), Labile Aluminium (LAL- µg/l), Acid Neutralizing Capacity (ANC)[3], Chloride (Cl), Sulphate (SO_4), Calcium (Ca), Total Organic Carbon (TOC) (all mg/l)
Discharge	Norwegian Water Resources and Energy Directorate (NVE); Monitoring Programme Riverine Inputs and Direct Discharges (RID)	Measured at gauging station; modelled 1km² grid cells using land surface and climate data (Beldring et al., 2003)	Daily	Discharge (m^3/s)
Climate	Climate Research Unit (CRU) TS3.21	High-resolution (0.5x0.5 degree) grid model based on data provided by weather stations (Harris et al., 2014)	Monthly	Temperature (monthly mean C°), Precipitation (mm/month)
Acid deposition	Norwegian Monitoring Programme for Long Range Transported Air Pollutants-NILU[1]	Bulk sampling of precipitation and analysis of chemical composition (NILU, 2012)	Daily/Weekly	Cl ($mg/m^2/day$), Non-marine S ($mg/m^2/day$)

1) Responsible Norwegian research institutes: Uni = University Research; NIVA= Norwegian Institute for Water Research; NILU=Norwegian Institute for Air Research (Johannessen, 1995)
2) Ephemeroptera, Plecoptera and Trichoptera (EPT) were identified to the lowest possible taxonomic level, i.e. species or genus. Most other taxa were identified to family or genus (appendix 1). Taxonomic resolution was standardized over time by dr. G. Velle (appendix 2)
3) Acid neutralising capacity: equivalent sum of base cations (Ca, Mg, K, Na) minus equivalent sum of strong acid anions (Cl, SO_4, NO_3)

2.2.2 DEPENDENT AND EXPLANATORY VARIABLES

The dependent data includes the relative abundance of the invertebrates measured in spring (April-June) and autumn (September-November). Eligible explanatory environmental variables were (Table 2): chemistry (H^+, acid neutralizing capacity, labile aluminium, chloride, sulphate, calcium and total organic carbon), hydrology (minimum, mean, and maximum discharge), deposition (non-marine sulphur and chloride deposition), and climate (temperature and precipitation). Chemistry data was included if sampled no more than two weeks after, or six weeks before the time of invertebrate sampling. When more than one chemistry sample was taken during this period it was preferred to use the sample taken preceding the moment of invertebrate sampling, as it was assumed that invertebrates were influenced by past chemistry (Velle et al., 2013). The hydrology, acid deposition, and climate data was summarized over intervals of six weeks, three months, six months, and one year prior to the invertebrate sampling as it is unknown at what time interval they influence the invertebrate community. Additionally, a dummy variable called Time was included based on the Julian date of the invertebrate sampling. A dummy variable called Season was coded 0 for the spring samples, and 1 for the autumn samples.

2.3 STATISTICAL ANALYSIS

The statistical analysis consisted of three main steps (Figure 4). First, the linear changes and correlations in the environmental variables were analyzed to understand the environmental changes (Section 2.3.1). Second, the temporal changes in the invertebrate community were analyzed to answer research question one and two (Section 2.3.2). This step consisted of three sub-steps, namely a) analyze the gradual linear changes, b) identify if there were abrupt changes, and c) describe the results for rivers and lakes. Third, the changes in the invertebrate community were related to the environmental variables to answer research question three (Section 2.3.3). Steps two (except 2c) and three were conducted using two different methods, i.e. biological indices and ordination methods. Indices describe the community in an aggregate number (Moe et al., 2010), whereas ordination techniques arrange samples along gradients on basis of their full species composition resulting in a low (usually two)-dimensional plot (Ter Braak, 1987).

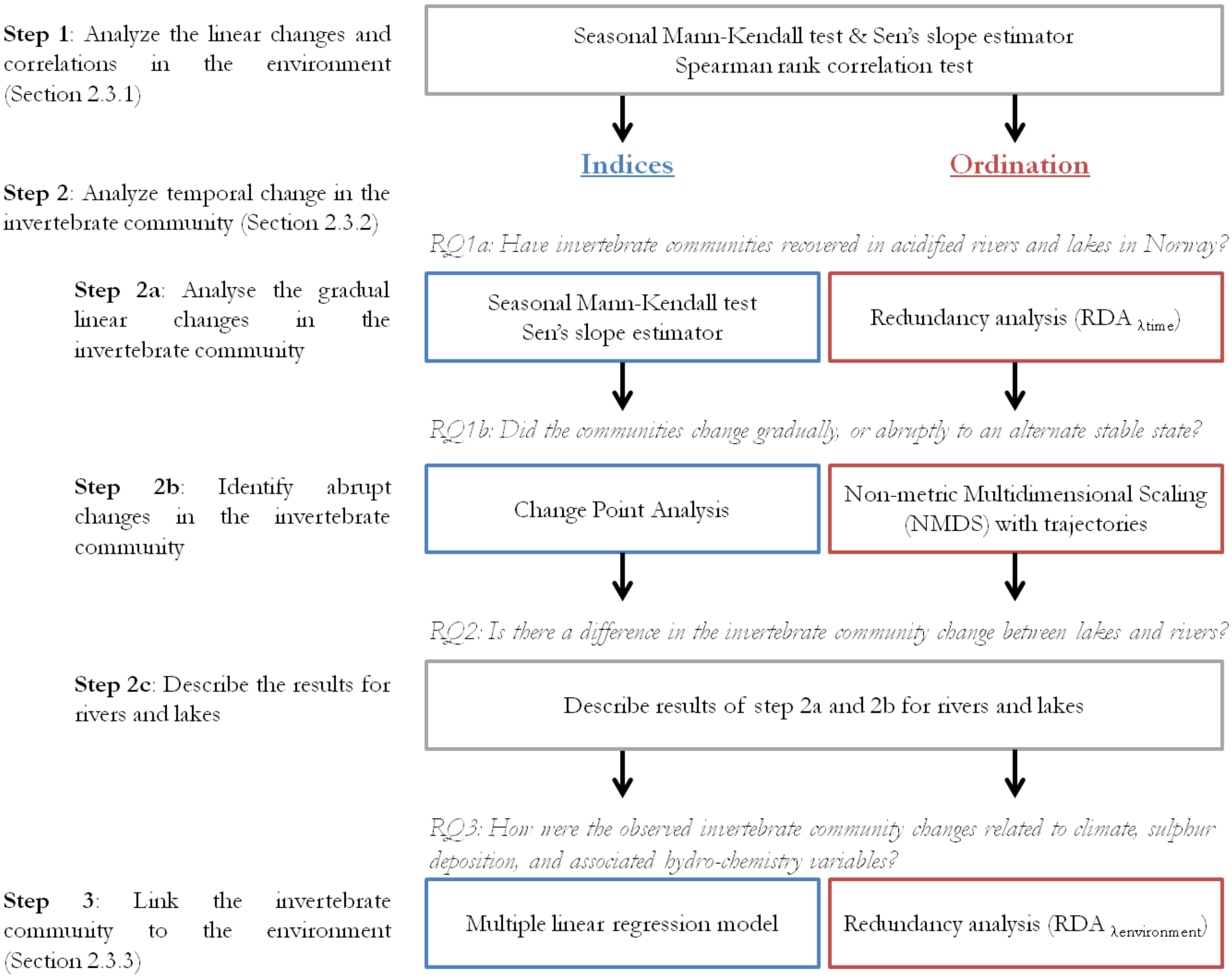

Figure 4: Schematic overview of steps taken in statistical analysis using biological indices (blue box), and ordination methods (red box).

All statistical tests were considered significant at $p<0.05$. In this explorative study, significance levels were not corrected for multiple testing, as this would inhibit detecting potentially interesting relationships. We are aware that multiple testing increases the probability of rejecting a null hypothesis (Moran, 2003). All numerical analyses, except the Change Point Analysis, were performed using the statistical package R (R core team, 2014) using several statistical libraries (rkt, vegan, leaps, relaimpo, ggplot2, stringr, Hmisc, cars). The Change Point Analysis is a statistical tool for determining whether a change has taken place (Taylor Enterprises, 2000).

2.3.1 STEP 1: TRENDS AND CORRELATIONS IN THE ENVIRONMENT

Assumptions of parametric methods were not met by the environmental data. Therefore, the gradual linear trends of the environmental variables were analyzed using the non-parametric Seasonal Mann-Kendall test (Hirsch & Slack, 1984), which is robust towards non-normally distributed data, and missing values (Van Belle & Hughes, 1984). Seasons for the hydro-chemistry data were spring and autumn, whereas deposition and climate data were computed for each month. The slope of the trend was estimated using the Sen's slope estimator, which calculates the median of the slopes from all pairs of values in the data series (Sen, 1968). To compare the slope amongst sites and amongst variables, the relative change (%) was calculated as the Sen's slope divided by the mean. Additionally, sea-salt episodes were identified by plotting the relative deviation from the mean chloride deposition. Large deviations from the mean chloride deposition indicate sea-salt episodes (Hindar et al., 2004). The correlations between the environmental variables were tested using the Spearman rank correlation test, which is robust to non-normal distributed data (Spearman, 1904).

2.3.2 STEP 2: TEMPORAL CHANGE IN THE INVERTEBRATE COMMUNITY

The analysis of temporal change in the invertebrate community included: data preparation, quantifying gradual linear change, and detection of abrupt changes. The methodology is first described for analysis using indices (Section 2.3.2.1), and then for analysis using ordination techniques (Section 2.3.2.2).

2.3.2.1 Indices

Data preparation

Four types of biological indices were calculated to characterize the invertebrate community change (Table 3): 1) richness, 2) relative abundance, 3) diversity, and 4) stability.

The invertebrate community can fundamentally be described by richness (i.e. number of taxa), and relative abundance (i.e. percent of composition) (Gotelli & Colwell, 2001). Richness was calculated for all taxa, however this index is not specific to acidification. Additionally, richness and relative abundance were calculated for EPT taxa (i.e. species in the order of Ephemeroptera, Plecoptera and Trichoptera), and acid-sensitive taxa. The EPT indices were included, because they have often been used in acidification studies (see for example Mackay & Kerseay, 1985; Lento et al., 2012; Stockdale et al., 2014). EPT taxa are generally acid-sensitive, however some species are acid tolerant, notably *Leptophlebiidae sp.* (Moe et al., 2010). Therefore, richness and relative abundance of previously defined acid-sensitive taxa in Norway were included. These acid-sensitive taxa become locally extinct at $pH<5.0$ (Fjellheim & Raddum, 1990). In total 131 taxa were identified to EPT, of which 23 were acid-sensitive, and three acid-sensitive taxa belonged to other orders (see for details Appendix 1).

Diversity combines richness and relative abundance of the invertebrate community. A common diversity measure is the Shannon-Wiener index (Jost, 2006). The Shannon-Wiener index was calculated as: $H = -\Sigma Pi(\ln Pi)$, where Pi is the relative abundance, and ln the natural logarithm (Shannon & Weaver, 1949). Thereafter, the exponential of H was calculated to convert the Shannon-Wiener index to effective number of taxa to obtain a unified and intuitive interpretation of diversity (Jost, 2006).

Stability was calculated as the Bray-Curtis index of similarity (Bray & Curtis, 1957). The Bray-Curtis index of similarity was calculated as $1-(\Sigma|x_i-x_j|/\Sigma|x_i-x_j|)$, where x represents the relative abundance of each taxa at the current (i) sampling moment, and the preceding (j) sampling moment. The values range from 0 (low stability, high rate of change) to 1 (high stability, low rate of change).

Table 3: Summary of the biological indices, including richness, relative abundance, diversity, and stability.

Richness	Number of taxa present in sample: - All taxa - EPT taxa[1] - Acid-sensitive taxa[2]
Relative abundance	Relative abundance of taxa present in sample: - EPT taxa[1] - Acid-sensitive taxa[2]
Diversity	Diversity index accounts for both richness and relative abundance of the taxa present: - Exponential of the Shannon-Wiener Index (H) = $\exp(-\Sigma\ Pi(\ln Pi))$[3]
Stability	Measure of stability in the invertebrate community: - Bray-Curtis index of similarity (B)= $1- (\Sigma|x_i-x_j|/ \Sigma|x_i-x_j|)$[4]

1) EPT taxa are species within the order of Ephemeroptera, Plecoptera and Trichoptera (Appendix 1).
2) Acid-sensitive taxa are listed by Fjellheim & Raddum (1990) to become locally extinct at pH < 5.0 (Appendix 1)
3) Pi is the relative abundance of each taxa in a sample, and ln is the natural logarithm
4) x represents the relative abundance of each taxa at the current sampling moment i and preceding sampling moment j.

Quantifying gradual linear change

Assumptions of parametric methods were not met by the indices describing the invertebrate community. Therefore, the Seasonal Mann-Kendall test (Hirsch & Slack, 1984) was used to evaluate linear trends the in invertebrate community indices (for details see Section 2.3.1). This test has often been used to describe environmental trends, however Lento et al. (2012) showed it is also a useful statistical tool to describe invertebrate community changes. Seasons in this study were spring and autumn. The Sen's slope estimator (Sen, 1968) was used to calculate the slope of the trend (for details see Section 2.3.1).

Detection abrupt changes to an alternate stable state

Abrupt changes in the indices were detected using the Change Point Analyser (Taylor Enterprises, 2000), a statistical tool developed to detect multiple shifts in time in non-normal distributed data. For each temporal change, it indicates the likelihood that a change occurred (confidence level in %), and the moment of change (confidence-interval). The moment of change was plotted for each key site, and the confidence-interval and confidence level were reported. The change points were included in the table if the confidence level was over 90%, and the confidence-interval was over 95% (default settings).

2.3.2.2 Ordination

Data preparation

The relative abundance of the invertebrates was square-root transformed prior to all ordination analyses, to reduce heteroscedasticity in the data, and to reduce the influence of dominant taxa on the analysis. To provide indication whether to use linear or unimodal ordination methods, a Detrended Correspondence Analysis (DCA) was used to estimate the compositional turnover, or gradient lengths, in units of standard deviation (Hill & Gauch, 1980). The relation between taxa abundance and environmental variables is assumed to follow an unimodal curve. A full compositional turnover covers about 4.0 standard deviation units. Species abundance may change linearly through a short section of the environmental gradient, which covers less than 3.0

standard deviation units (Ter Braak & Prentice, 1988). The gradient length of the invertebrate community in our stations was between 1.5 and 2.5 standard deviation units, and therefore linear methods were chosen for subsequent ordination analysis.

Quantifying gradual linear change

A principal components analysis (PCA) was performed to quantify the unconstrained variation in the biological data, representing the underlying gradient in the data (Jongman et al., 1995). A Redundancy Analysis ($RDA_{\lambda time}$), with Time as sole explanatory variable and Season as covariate, was used to assess the gradual linear change in the invertebrate community. A restricted permutation (999 Monte Carlo permutations) was used to test for significance of the changes (Jongman et al., 1995).

Detection abrupt changes to an alternate stable state

Unconstrained ordination analysis, with trajectories added between subsequent samples in time, was used to analyse the year-to-year change in the invertebrate community (Philippi, 1998). The autumn (year X) and spring (year X+1) samples were amalgamated to reduce noise in the trajectories. The invertebrates in these samples were of the same group of species. The Non-metric Multidimensional Scaling (NMDS) method was considered highly suitable for analysing biological data containing numerous zero-values (Minchin, 1987). The Bray-Curtis dissimilarity index was used as distance metric. In a NMDS diagram, sampling moments are placed in proximity when the invertebrate community is similar, and further distant when the invertebrate community is more dissimilar. The scale of the axis of the NMDS plot is arbitrary. To aid visual inspection of the plots, the trajectories of the invertebrate communities were analysed according to the framework provided by Matthews et al. (2013). In sum, communities can change gradual or abrupt (i.e. saltatory), and directional to an alternate state, directional with return towards a previous state, or non-directional (Figure 5).

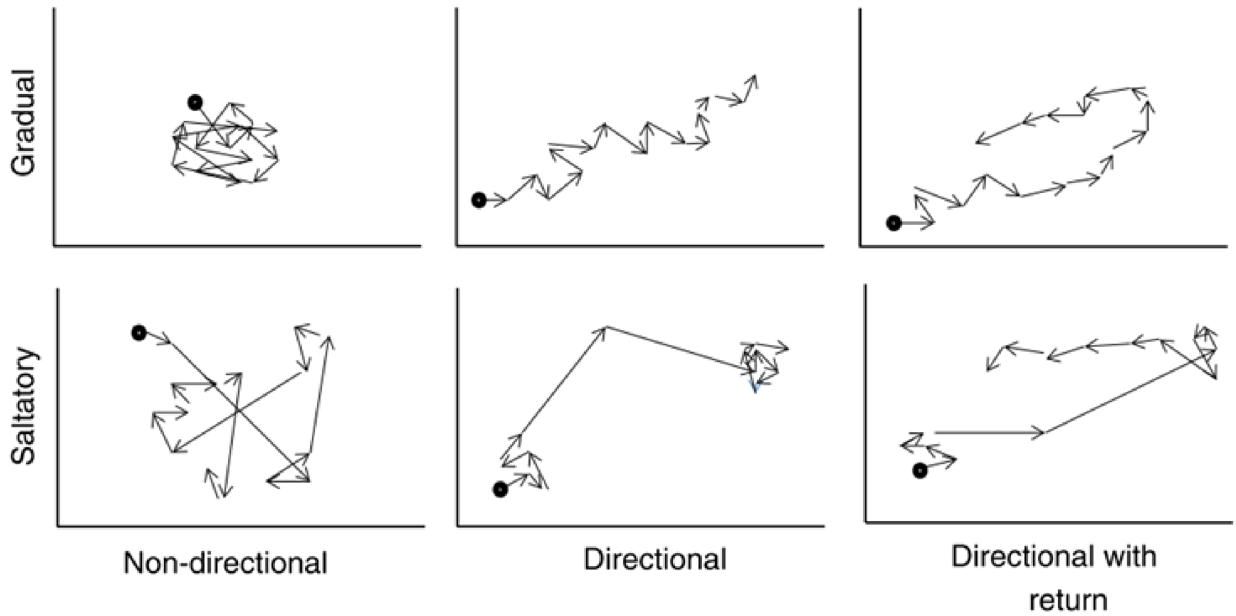

Figure 5: Hypothetical trajectories of temporal change in communities, depicting gradual versus abrupt (saltatory) change crossed with non-directional, directional, or directional with return. The black dot represents the start of the time series (Matthews et al., 2013).

2.3.3 STEP 3: LINKING INVERTEBRATE COMMUNITY AND ENVIRONMENT

First, it is described how a multiple regression model was build to assess which environmental variables best explained the variance of the indices (Section 2.3.3.1). Second, it is described how partial constrained ordination was used to assess how much of the trends and variation in the invertebrate community could be explained by the environmental variables (Section 2.3.3.2). Eligible explanatory environmental variables were previously described in Section 2.2.2.

2.3.3.1 Indices

Building the multiple regression model

Multiple regression models were build in which the biological indices were explained by one or more environmental variables. Chemistry, acid deposition, and precipitation variables were log-transformed to attain normality of the error distribution. A given environmental variable was not allowed in the model for different time intervals before invertebrate sampling, i.e. either six weeks, three months, six months, or one year. Additionally, discharge was not allowed in the model for different summary statistics, i.e. either minimum, mean, or maximum. These constraints reduced the correlation between the model variables.

All possible combinations of explanatory variables were included in an all-subsets regression, and ranked according to the adjusted R-squared. The adjusted R-squared only increases if an additional environmental variable improves the model more than by chance, which allowed the minimum number of variables to be included in the model. The model with the highest adjusted R-squared was reported as the best model. For the best model, the relative importance of each predictor variable was quantified, i.e. the adjusted R-squared was partitioned by averaging over orders, and normalized to sum to 100% (Lindemann et al., 1980).

No models were computed for the indices that contained many zero values as these cannot be adequately predicted by regression models, specifically indices related to acid-sensitive taxa in lakes and rivers, and indices related to EPT taxa in lakes.

Testing for assumptions of multiple regression

Three principal assumptions of the linear regression methods were tested, specifically no or little multi-collinearity, homoscedasticity, and no auto-correlation. Violation of the assumptions may lead to misleading coefficient estimates (Berry & Feldman, 1985). Multi-collinearity occurs when two or more explanatory variables are highly correlated with each other. The model was tested for multi-collinearity using the Variance Inflation Factor (VIF), and highly correlated variables (VIF>10) were excluded from the model (Marquaridt, 1970). Homoscedasticity means the variance of the errors is constant, which was tested by the Breusch-Pagan test (Breusch & Pagan, 1979). Auto-correlation occurs when consecutive residuals are not independent from each other, and auto-correlation at lag-1 was tested by the Durbin-Watson test (Durbin & Watson, 1950).

Evaluating the ability of the model to explain the observations

A 'dummy' or 'non-causal' regression model was build, including the dummy variables Time (long-term trend) and Season (seasonal variation). The output of the 'dummy' model was compared to the output of the 'best' or 'causal' model, to evaluate if the causal model is better at explaining the invertebrate indices than a non-causal model (De Wit et al., 2007).

2.3.3.2 Ordination

A partial redundancy analysis (partial RDA) was used to quantify how much the variance in the invertebrate community could be explained by trends and variability in the environmental variables. Environmental variables were not transformed as the statistical significance is assessed by randomisation tests, and statistical assumptions do not need to be fulfilled (Ter Braak & Prentice, 1988). A restricted Monte Carlo permutation test (999 permutations) was performed to calculate the significance of the partial RDA analysis.

Trends in the invertebrate community

First, it was assessed how much of the trends in the invertebrate community were explained by the environmental variables separately. Season was used as covariate to detrend the residuals of each environmental variable for seasonality to focus on inter-annual trends. Each environmental variable was applied as single explanatory variable at different time intervals, i.e. six weeks, 3 months, six months, and one year. The measurement interval which significantly explained the largest variance in the invertebrate community was reported. All significant explanatory variables were applied together in the partial RDA (Season as covariate) to obtain the total percent of variance explained by trends in the environment.

Variation in the invertebrate community

Second, it was assessed how much of the invertebrate community was explained by variability in the environmental variables. Season and Time were applied as covariates to represent the non-linear inter-annual variation (Monteith et al., 2005). Each environmental variable was applied as single explanatory variable in the partial RDA.

3 RESULTS

3.1 TRENDS AND CORRELATIONS IN THE ENVIRONMENT

Non-marine sulphur and chloride deposition

Mean non-marine sulphur deposition during the monitoring period was highest near the southernmost Farsund catchment (6.3mg/m^2/day), intermediate near the Vikedal catchment (3.5mg/m^2/day), and lowest near the northernmost Gaular catchment (1.3mg/m^2/day) (Table 4). In all catchments, non-marine sulphur deposition decreased significantly with a relative slope between -3.6% and -5.4%. The Vikedal catchment received the highest loads of chloride deposition, which decreased significantly during the monitoring period with a relative slope of -0.8%. Graphs displaying the temporal change in non-marine sulphur deposition and chloride deposition are presented in Appendix 3, Figure 1.

Sea-salt episodes were illustrated by positive deviations from the mean chloride deposition (Figure 6). The timing of the sea-salt episodes was roughly comparable among the catchments, however the relative strength of each episode was varying for each catchment. Relatively high deviations from the mean chloride deposition were evident in all catchments from 1989 to 1993, 1997, 2000, and 2008. Additionally, in the Vikedal and Farsund catchment a large deviation from the mean chloride was recorded in 2011.

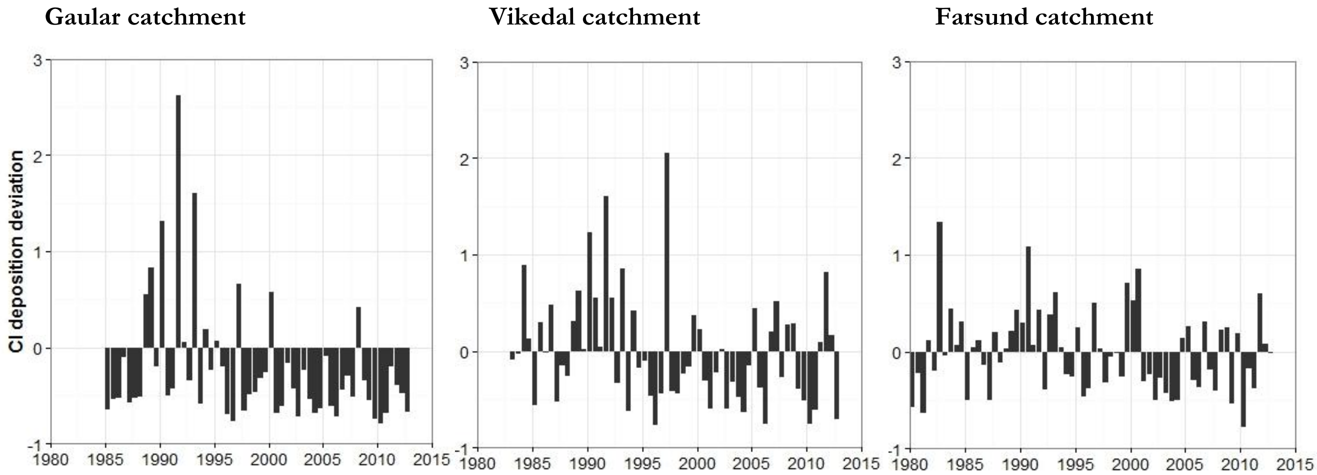

Figure 6: Relative deviation from the mean chloride deposition for the Gaular, Vikedal and Farsund catchment indicate sea-salt episodes using semi-annual data (January to June and July to December).

Temperature and precipitation

The mean monthly temperature was highest in the two southernmost catchments Farsund and Vikedal, and lowest in the northernmost Gaular catchment (Table 4). In all catchments, the mean monthly temperature increased significantly between 1980 and 2012 with ~1.0C° in the Gaular and Vikedal catchment, and ~1.6C° in the Farsund catchment (calculation based on the slope presented in Table 4). Mean precipitation in the catchments ranged from 160 mm/month to 202mm/month. Precipitation only increased significantly in the Vikedal catchment (Table 4). The changes in temperature and precipitation are illustrated by graphs in Appendix 3, Figure 1.

Hydro-chemistry

The gradient of declining non-marine sulphur deposition from South to North is reflected in the water chemistry (Table 5). The mean sulphate concentration in the water was highest in the river- and lake water of the Farsund catchment, and lowest in the Gaular catchment. Whereas, the acid neutralizing capacity (ANC) was highest in the river- and lake water of the Gaular catchment, and lowest in the Farsund catchment.

In all catchments, the sulphate (SO_4) and acidity (H^+) concentrations in the rivers and lakes decreased significantly over the monitored period (Table 5). The relative slope for the different chemistry stations was between -2.3% and -3.5% for SO_4, and between -3.2% and -8.1% for H^+ concentration. ANC increased significantly in the rivers, but the increase was not significant in the lakes. The labile aluminium (LAL) concentration decreased significantly in the river- and lake water of the two northern catchments Gaular and Vikedal, while the decrease in LAL was not significant for the southern Farsund catchment.

The annual discharge did not change significantly in the rivers (Table 6). Addressing the discharge data for autumn (September to November) and spring (April to June) sampling separate, showed that the discharge in the Vikedal river increased significantly during autumn with a relative slope of 1.4%. The discharge in the Gaular and Farsund rivers also increased during autumn, but not significantly. Appendix 3 shows graphs of the temporal change of the hydro-chemistry of the rivers in Figure 2, and of the lakes in Figure 3.

Correlations between the environmental variables

Appendix 3 provides a separate correlation matrix of the environmental variables in the Gaular catchment (Table 1), Vikedal catchment (Table 2), and the Farsund catchment (Table 3). Table 7 summarizes the results from the tables in Appendix 3 by indicating the significant correlations. Mean precipitation showed significant positive correlations to both temperature, discharge, and chloride deposition. For all localities except lake Nystølvatn, higher sulphate deposition in the catchment correlated with higher sulphate concentration in the rivers and lakes. Higher acidity, higher labile aluminium concentration, and lower acid neutralizing capacity in the rivers and lakes, coincided with a significantly higher chloride deposition (exception for H^+ and LAL in lake Røyravatn). These water chemistry variables were also significantly inter-correlated.

Table 4: Results of the Seasonal Mann-Kendall test of trends for non-marine sulphur deposition, chloride deposition, temperature, and precipitation in the catchments computed per month. The absolute change (Abs. change) was calculated with the Sen slope estimator per year. The relative change (Rel. change) is the Sen slope divided by the mean. The significance level is reported as p<0.5=*, p<0.01=**, p<0.001=, and the p value is reported if non-significant. Significant positive trends are reported in green, significant negative trends in red, and non-significant trends in black.***

		Gaular catchment	Vikedal catchment	Farsund catchment
		1980-2012[1]	1980-2012[1]	1980-2012
Non-marine S deposition ($mg/m^2/day$)	Rel. change (%)	-3.66	-5.10	-3.55
	p value	***	***	***
	Mean	1.30	3.50	6.29
Cl deposition ($mg/m^2/day$)	Rel. change (%)	0.17	-0.82	-0.36
	p value	0.42	***	0.05
	Mean	22.14	38.15	20.12
Temperature (monthly mean C°)	Abs. change (C°/yr)	0.03	0.03	0.05
	p value	***	***	***
	Mean	3.7	7.1	7.1
Precipitation (mm/month)	Abs. change (mm/yr)	0.79	0.76	0.27
	p value	0.06	*	0.42
	Mean	194	202	160

1) Deposition measured from 1985 for the Vikedal catchment and from 1983 for the Gaular catchment.

Table 5: Results of the Seasonal Mann-Kendall test of trends for chemistry variables in the river- and lake stations with seasons (spring and autumn) computed separately. The relative change (Rel. change) is the Sen slope divided by the mean. The significance level is reported as p<0.5=, p<0.01=**, p<0.001=***, and the p value is reported if non-significant. Significant positive trends are reported in green, significant negative trends in red, and non-significant trends in black.*

		Gaular st.5	Vikedal st.11	Farsund st.4	Nystøl-vatn	Røyra-vatn	Saud-landsvatn
		River	River	River	Lake	Lake	Lake
		1989-2003	1987-2013	1997-2013	1998-2011	1998-2012	1997-2012
H^+ (*10^{-6} moles/l)	Rel. change (%)	-5.82	-5.10	-6.49[1]	-3.15	-8.12	-3.68
	p value	***	***	***	**	***	*
	Mean	2.7	2.0	4.4	1.5	3.0	2.1
ANC (mg/l)	Rel. change (%)	5.98	2.83	1.28	2.42	1.60	1.47
	p value	***	***	*	0.10	0.15	0.29
	Mean	-1.1	-2.1	-5.7	-0.6	-1.58	-5.8
Sulphate (mg/l)	Rel. change (%)	-3.45	-2.57	-2.57[1]	-2.31	-2.82	-2.58
	p value	***	***	***	***	***	***
	Mean	1.0	1.7	3.3	0.6	1.2	3.3
Chloride (mg/l)	Rel. change (%)	-2.80	-0.40	-0.35[1]	0.25	0.76	-0.01
	p value	*	0.27	0.47	0.66	0.33	0.97
	Mean	2.0	3.5	10.0	1.2	2.7	10.3
LAL (µg/l)	Rel. change (%)	-11.19	-7.68[1]	-4.59	-7.49	-8.29	-4.57
	p value	***	***	0.08	*	***	0.11
	Mean	19.1	10.6	21.8	6.0	16.7	21.9
Calcium (mg/l)	Rel. change (%)	1.76	-0.13	-1.09[1]	0.90	-0.64	-0.18
	p value	0.14	0.42	***	0.14	0.27	0.69
	Mean	0.4	0.7	1.1	0.3	0.1	1.1
TOC (mg/l)	Rel. change (%)	0.61	0.88	2.59	0.76	0.00	2.49
	p value	0.53	*	**	0.53	0.67	0.06
	Mean	1.2	1.1	2.1	0.3	1.5	2.0

** ANC=Acid Neutralizing Capacity calculated as (Ca+Mg+K+Na) - (Cl+SO_4+NO_3); LAL=Labile Aluminium; TOC=Total Organic Carbon.*

1) These variables were measured at a different time interval: Vikedal st.11 LAL missing 5 years between 1988-1991; Farsund st. 4 H^+ and Ca also available for 1983-1990, sulphate and chloride also available for 1987-1990.

Table 6: Results of the Seasonal Mann-Kendall test of trends for discharge in the river stations for the whole year, spring (April-June), and autumn (September-November) computed per month. The relative change (Rel. change) is the Sen slope divided by the mean. The significance level is reported as p<0.5=, p<0.01=**, p<0.001=***, and the p value is reported if non-significant. Significant positive trends are reported in green, significant negative trends in red, and non-significant trends in black.*

		Gaular st.5	Vikedal st.11	Farsund st.4
		1989-2014	1987-2014	2000-2013
Annual discharge (m^3/s)	Rel. change (%)	-0.33	0.02	-0.05
	p value	0.13	0.93	0.89
	Mean	9.90	12.30	0.29
Spring discharge (m^3/s)	Rel. change (%)	0.10	-0.04	0.08
	p value	0.78	0.90	0.85
	Mean	15.39	11.59	0.29
Autumn discharge (m^3/s)	Rel. change (%)	1.23	1.38	0.49
	p value	0.07	0.01	0.49
	Mean	9.56	15.53	0.32

Table 7: Spearman Rank Correlation matrix of all environmental variables in rivers (upper panel) and lakes (lower panel). Starting letter of site reported when the two-tailed test was significant at p<0.05 (G= Gaular river; V=Vikedal river; F=Farsund river; N= Nystølvatn lake; R= Røyravatn lake; S=Saudlandsvatn lake). The letter is printed with a capital letter when the correlation is strong (r<-0.6/r>0.6). Positive correlations are reported in green and negative correlation in red.

River / Lake	H+	ANC	SO_4	Cl	LAL	Ca	TOC	Disch	Dep S	Dep Cl	Temp	Prec
H+		G/V/F	g/V	G/v/F	G/V/F		v	f	V	g/v/F	f	g/f
ANC	n/r/S		G/V	G/V/F	G/V/f		v/F	F	V	g/v/F	F	g/F
SO_4	N/r	N/r		G/v	G/V		v		G/V/F		v	
Cl	n/S	N/R/S			G/v/f	v	v/f	f		g/v/F	F	v/F
LAL	N/R/S	N/r/S	N/R	n/s					g/V	g/v/F	v	g/f
Ca		s		s			G/v/f					
TOC	n/s	n/r/S		n/r/S	n/s	s		v		v		v
Disch									f	g/V/F	g/V/F	G/V/f
Dep S			R/S	r	r	r					v	f
Dep Cl	n/s	n/r/S		N/r/S	n/s	r			r		f	G/V/f
Temp		r/s		n/r/S	n				s	r/s		g/V/F
Prec	n/s	r/S		r/S	n/s		s			n/R/s	n/r/f	

** ANC=Acid Neutralizing Capacity calculated as (Ca+Mg+K+Na) - (Cl+SO_4+NO_3); LAL= Labile Aluminum; TOC=Total Organic Carbon; Disch=Discharge; Dep S=Non-marine sulphur deposition; Dep Cl=Chloride deposition; Temp=Temperature; Prec=Precipitation.*
** Two chemistry samples each year correlated with mean discharge 6 weeks before invertebrate sampling, and mean temperature, precipitation, sulphate and chloride deposition 6 months before invertebrate sampling to include the effect of sea-salt episodes.*

3.2 TEMPORAL CHANGE IN THE INVERTEBRATE COMMUNITY

The temporal change in the invertebrate community is presented by two main approaches, specifically indices (Section 3.2.1), and ordination methods (Section 3.2.2). For each section, first the results of the gradual linear change are presented, and second the abrupt changes.

3.2.1 INDICES

3.2.1.1 Gradual linear change

The gradual linear change of the invertebrate indices is presented for the key river- and lake stations as relative change in Table 8 (see Appendix 4 for all stations). In some cases, a significant trend with a relative change of 0% was reported, e.g. richness of acid-sensitive taxa for Farsund st.4 (Table 8). The relative change is calculated as the median of all estimated slopes for all pairs of years. If more than 50% of the slopes for all pairs of years are zero, the median will also be zero despite the presence of a significant trend.

Rivers

The three richness indices (all taxa, EPT taxa, and acid-sensitive taxa) increased significantly in 25 of 30 river stations located in the Gaular, Vikedal, and Farsund catchment (Appendix 4). The relative change in richness, averaged for all river stations, was lowest for all taxa (1.3%), intermediate for EPT taxa (1.8%), and highest for acid-sensitive taxa (4.7%). The relative abundance of EPT taxa increased significantly in 13 of 30 river stations, and all significant increases were observed in the Gaular and Vikedal catchment. The relative abundance of acid-sensitive taxa increased significantly in 25 of 30 river stations, and the average relative change for all stations combined was 4.2%. For the diversity and stability indices, no significant trends were recorded in 25 of 30 river stations.

Separating the relative abundance of the EPT orders showed that the trends varied among the catchments for Ephemeroptera and Plecoptera (Appendix 4). The relative abundance of Ephemeroptera increased significantly in 13 of 26 river stations in the Vikedal and Gaular catchment, but decreased significantly in three of four river stations in the Farsund catchment. The decrease in Ephemeroptera in the river stations of the Farsund catchment was mainly related to the decrease in the relative abundance of the non acid-sensitive *Leptophlebia sp.* The relative abundance of Plecoptera increased significantly in three of four river stations in the Farsund catchment, whereas no significant trend was recorded in 18 of 26 river stations in the Vikedal and Gaular catchment. Trichoptera showed no significant trend in relative abundance in 22 of 30 river stations in all catchments.

Overall, the changes in invertebrate indices in the key sites Gaular st.5, Vikedal st.11, and Farsund st.4 were representative for the observations in the other river stations in the respective catchments (Table 8). Exceptions were the lack of relative change in richness and relative abundance of acid-sensitive taxa in Farsund st.4, and the significant decrease in relative abundance of Plecoptera in Gaular st.5, and Vikedal st.11.

Table 8:* *Results of the Seasonal Mann-Kendall test of trends for the invertebrate indices in the river- and lake stations with seasons (spring and autumn) computed separately. The relative change (Rel. change) is the Sen slope divided by the mean. The significance level is reported as p<0.5=*, p<0.01=**, p<0.001=, and the p value is reported if non-significant. Significant positive trends are reported in green, significant negative trends in red, and non-significant trends in black.***

	Gaular st.5	**Vikedal st.11**	**Farsund st.4**	**Nystølvatn**	**Røyravatn**	**Saudlandsvatn**
	River	**River**	**River**	**Lake**	**Lake**	**Lake**
	1989-2014	**1987-2014**	**1981-2013**	**1997-2012**	**1998-2012**	**1997-2012**
Richness all taxa						
Rel. change (%)	1.93	1.31	1.28	0.00	0.00	0.00
p value	***	***	***	0.22	0.45	0.67
Richness EPT taxa						
Rel. change (%)	2.52	1.78	2.16	0.00	4.46	0.00
p value	**	***	***	0.30	*	0.38
Richness acid-sensitive taxa						
Rel. change (%)	8.33	9.26	0.00[1]	0.00	0.00	0.00
p value	***	***	***	1.00	0.61	0.34
% Ephemeroptera						
Rel. change (%)	4.86	8.81	-0.70	0.00	4.43	-4.13
p value	***	***	***	1.00	*	0.17
% Plecoptera						
Rel. change (%)	-3.56	-1.75	4.59	0.00[1]	1.76	0.00
p value	**	*	***	**	0.30	0.20
% Trichoptera						
Rel. change (%)	0.75	2.73	-0.18	5.92	0.00	0.00
p value	0.32	**	0.85	0.12	0.54	0.89
% EPT taxa						
Rel. change (%)	-0.01	1.98	-0.20	-0.11	4.31	-2.53
p value	1.00	***	0.76	0.92	0.07	0.16
% Acid-sensitive taxa						
Rel. change (%)	5.28	10.40	0.00[1]	0.00	0.00	0.00
p value	***	***	***	1.00	0.47	0.42
Diversity (Shannon-Wiener $_{exp}$)						
Rel. change (%)	-0.33	0.95	0.49	-2.95	0.58	-3.85
p value	0.59	0.09	0.26	*	0.51	**
Stability (Bray-Curtis $_{similarity}$)						
Rel. change (%)	0.67	-0.19	0.14	1.84	-0.86	0.66
p value	0.17	0.47	0.78	**	0.26	0.40

1) A significant trend with a relative change of 0% has been reported. The Sen slope estimator ranks all estimated slopes for all pairs of years, and takes the median. If more than 50% of the slopes for all pairs of years are zero, the median will also be zero despite the presence of a significant trend in the Seasonal Mann-Kendall test.

Lakes

None of the lake stations changed significantly in the richness or relative abundance indices, except for the increase in EPT taxa richness and relative abundance of Ephemeroptera in lake Røyravatn (Table 8). Almost no acid-sensitive taxa were recorded in the lakes, e.g. a maximum of two taxa (Figure 7), and a relative abundance of less than 5% (Figure 9) at any sample moment. A significant decrease in invertebrate diversity was recorded between 1997 and 2012 in both lake Nystølvatn and lake Saudlandsvatn (Table 8). The taxa richness did not change, suggesting a lower evenness, i.e., an assemblage with a few dominating taxa and several rare taxa. A significant increase in stability was observed in lake Nystølvatn only.

3.2.1.2 Abrupt change

Significant change points in the invertebrate indices are illustrated for the key river- and lake stations in Figure 7 until Figure 11. Statistical details about the change points are presented in Appendix 5. The confidence-interval of the change point provides detail about how abrupt the change was, e.g. the shorter the confidence-interval the more abrupt the change. Several change points, with varying confidence-interval, were identified for the invertebrate indices in the key river stations. No change points were identified for lake Røyravatn and lake Saudlandsvatn, and the three change points identified for lake Nystølvatn had longer confidence-intervals of six to ten years (see richness of all taxa in Figure 7, diversity in Figure 10, and stability in Figure 11). The change points in the river stations are described in more detail.

Rivers

Figure 11The three richness indices (all taxa, EPT taxa, and acid-sensitive taxa) in the river stations showed several significant moments of increase (Figure 7). The change points of richness of acid-sensitive taxa were indentified with shortest confidence-interval. The most abrupt change in richness of acid-sensitive was recorded in 2003 for Gaular st.5, in 2002 for Vikedal st.11, and in 2004 for Farsund st.4 (confidence-interval between one and four years).

Even though moments of change were identified for the relative abundance of EPT, the timing, and direction of change were varying among the river stations (Figure 8). The moment of change in Gaular st.5 was identified with a long confidence-interval of 15 years. In Vikedal st.11, high relative abundance of EPT was recorded between 2007 and 2010. Four change points were identified in Farsund st.4, but the overall direction of change was ambiguous.

The moments of increase in relative abundance of acid-sensitive taxa were detected with relative short confidence-interval of one to six years (Figure 9). In Gaular st.5, the relative abundance of acid-sensitive taxa increased from 2.3% to 17.8% in 2008. The relative abundance of acid-sensitive taxa in Vikedal st.11 showed three change points, specifically from 0.5% to 4.1% in 1996, from 4.1% to 13.8% in 2001, and from 13.8% to 25.8% in 2008. In Farsund st.4, the relative abundance in acid-sensitive taxa increased from 0.2 to 5.6% in 2004.

The change points identified for diversity (Figure 10), and stability (Figure 11) resulted from fluctuations in the indices. A period of high diversity was observed in Vikedal st.11 between 2007 and 2010, and a period of low diversity was observed in Farsund st.4 between 1998 and 2002 (Figure 10). Gaular st.5 showed no significant moments of change in diversity. Change points in diversity were identified with a confidence-interval between one and six years.

Instability in the invertebrate community was observed in all key river stations, specifically for Gaular st.5 between 1997 and 1998, for Vikedal st.11 between 1991 and 1995, and for Farsund st.4 before 1988 and after 2009 (Figure 11). The decrease in stability was determined with a low confidence-interval, i.e. less than one year in Gaular st.4 and Vikedal st.11, and four years in Farsund st.4. The increase in stability was generally determined with a longer confidence-interval, indicating the invertebrate community changed abruptly to an instable state, but returned more gradually to a stable state.

Figure 7: Temporal change in richness of all taxa indicated in red, richness of EPT taxa indicated in green, and richness of acid-sensitive taxa indicated in blue. The moment of change is illustrated by a dashed line with the confidence-interval shaded.

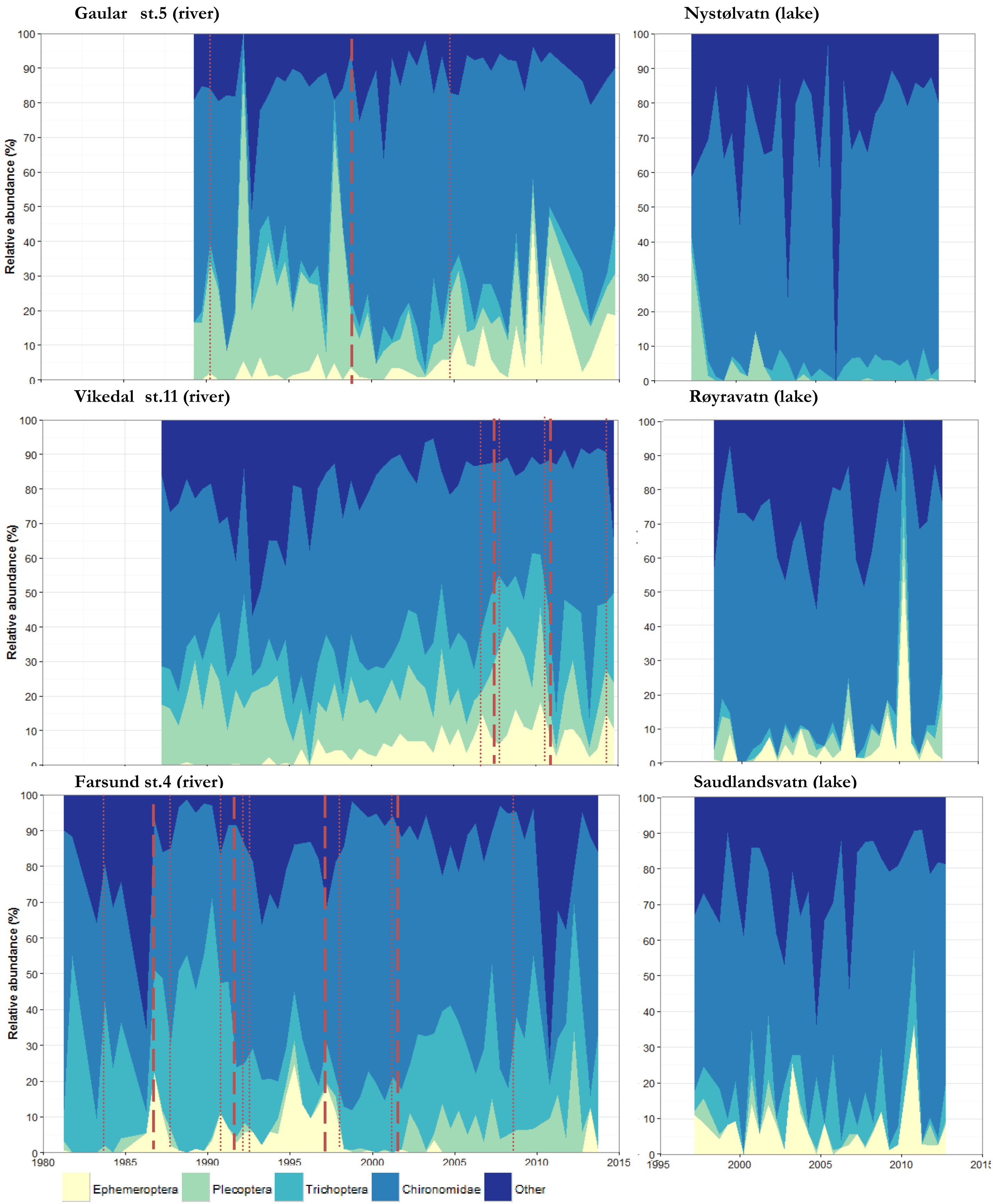

Figure 8: Temporal change of relative abundance (%) of different EPT orders (Ephemeroptera in yellow, Plecoptera in green, Trichoptera in turquoise), Chironomidae family (most common taxon) in light blue, and other taxa in dark blue. The moment of change is illustrated by a dashed line and the confidence-interval is indicated by a dotted line.

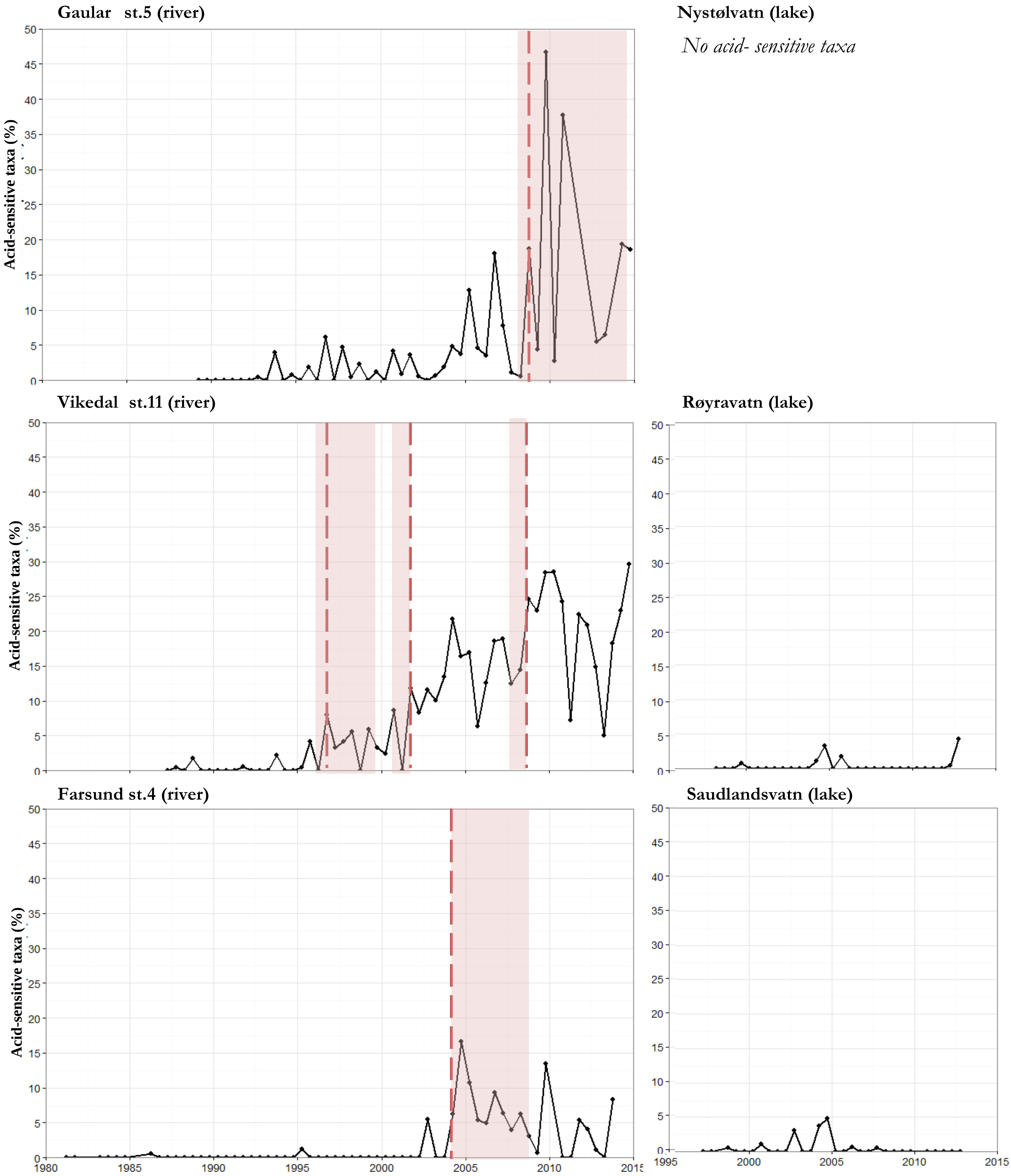

Figure 9: Temporal change in the relative abundance of acid-sensitive taxa. The moment of change is illustrated by a dashed line with the confidence-interval shaded.

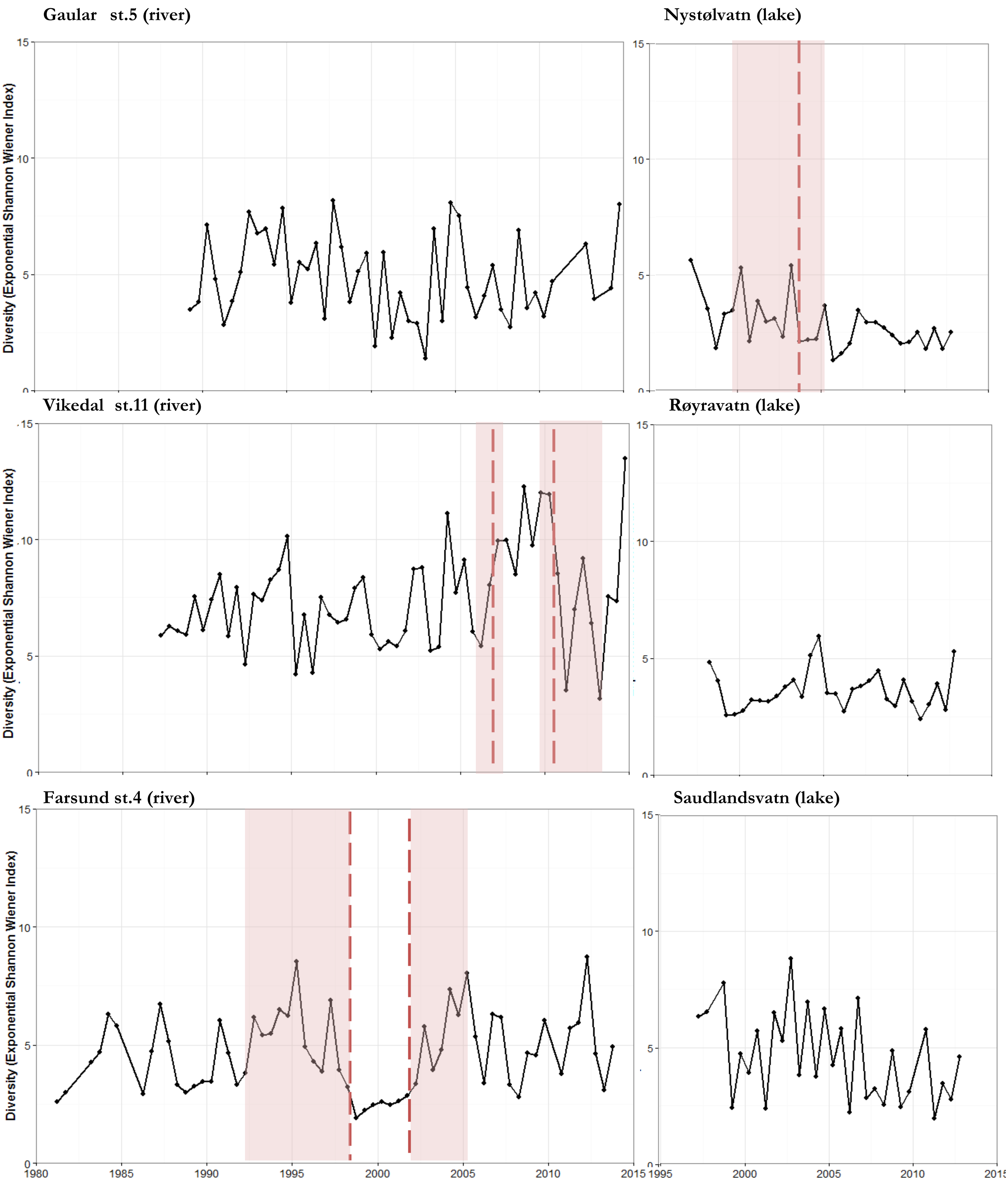

Figure 10: Temporal change in the diversity calculated as the Shannon-Wiener$_{exp}$. The moment of change is illustrated by a dashed line with the confidence-interval shaded.

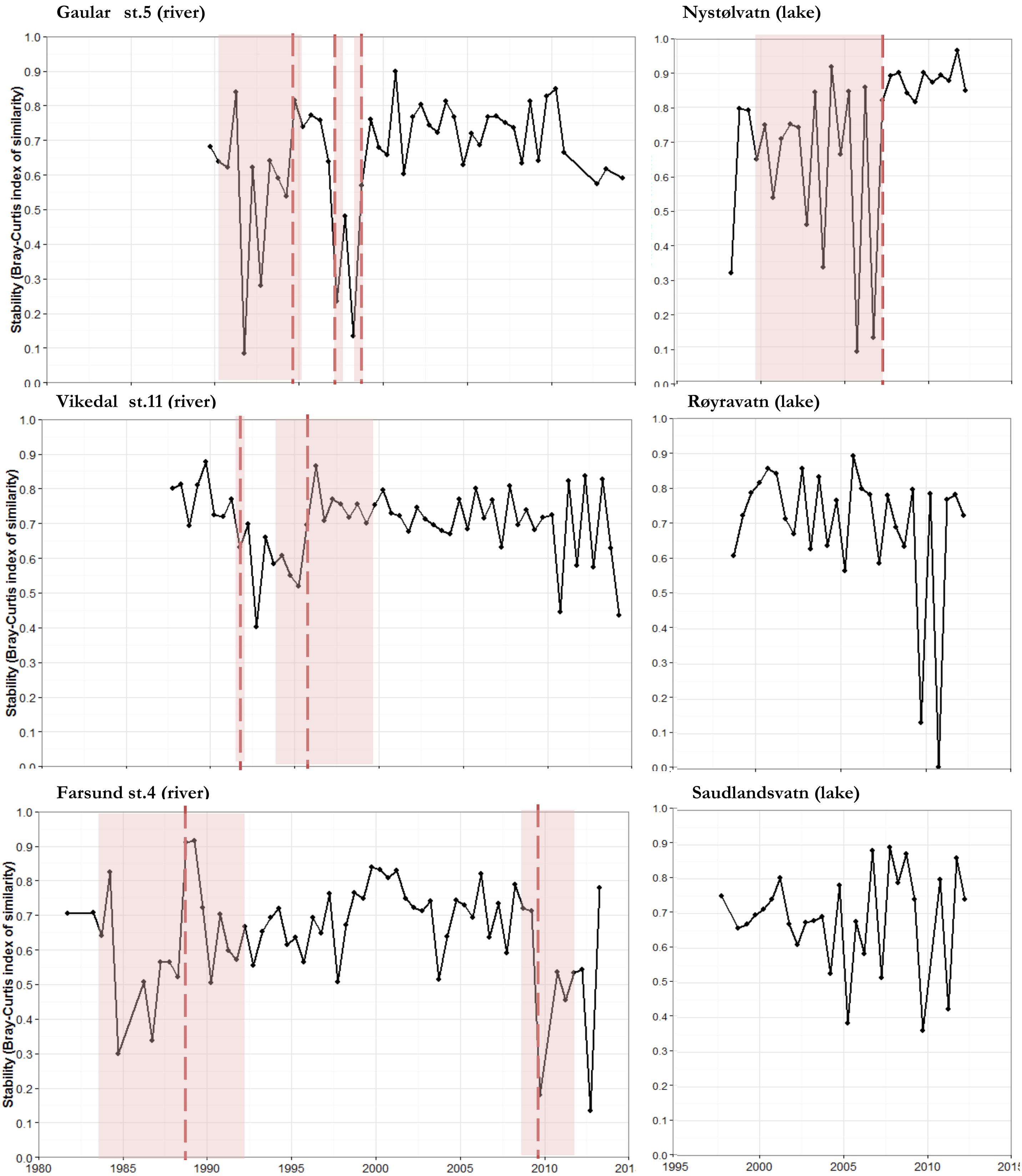

Figure 11: Temporal change in the stability calculated as the Bray-Curtis index of similarity. The moment of change is illustrated by a dashed line with the confidence-interval shaded.

3.2.2 ORDINATION

3.2.2.1 Gradual linear change

The small eigenvalues identified by the Principle Component Analysis (PCA) indicate a large part of the community changes can be attributed to stochasticity, and there is no underlying, or hidden gradient in the data (Table 9, see other river stations in Appendix 6, Table 1). The redundancy analysis ($RDA_{\lambda\ time}$) indicated that the invertebrate communities in all river- and lake stations changed significantly over time. No more than 24.1% of the variation in the invertebrate communities could be significantly explained by time in the rivers, and no more than 13.2% in the lakes. Taxa that were primarily responsible for driving the invertebrate community change are listed in Appendix 6, Table 2.

Table 9: Unconstrained gradient in the invertebrate community analyzed by Principle Component Analysis (PCA), and Time constrained gradient with Season as covariate analyzed by the Redundancy analysis ($RDA_{\lambda time}$). The eigenvalues and percentage between-sample variance explained are reported for both analysis. The significance level of the $RDA_{\lambda time}$ was reported as p<0.5=*, p<0.01=**, p<0.001=, and the p value is reported if non-significant.***

		Gaular st.5	**Vikedal st.11**	**Farsund st.4**	**Nystølvatn**	**Røyravatn**	**Saudlands-vatn**
		River	**River**	**River**	**Lake**	**Lake**	**Lake**
		1989-2014	**1987-2014**	**1981-2013**	**1997-2012**	**1998-2012**	**1997-2012**
PCA	*Eigenvalue*	6.8	6.5	5.5	6.3	2.7	7.0
	% explained	25.7	28.9	19.5	34.3	22.2	32.1
$RDA_{\lambda\ time}$	*Eigenvalue*	3.6	5.2	2.1	2.3	0.9	1.5
	% explained	14.2	24.1	7.8	13.2	7.7	9.4
	p-value	***	***	***	***	*	***

3.2.2.2 Abrupt change

The Non-metric multi-dimensional (NMDS) plots illustrate the time trajectories of the invertebrate communities for the key river- and lake stations in Figure 12 (see Appendix 7 for other river stations). Despite the noise in the trajectories, resulting from stochastic changes in the invertebrate community, abrupt directional changes to an alternate stable state were identified in many river stations. The temporal trajectories in the lake stations were largely chaotic, and non-directional. The general trajectory observed in the river stations is outlined in detail

Rivers

An outline of the general trajectory of the river stations was obtained by comparing the NMDS plots in Appendix 7.The first part of the trajectory up to 1987 was only recorded in the Farsund catchment, and invertebrate community changed between 1981 and 1986. A stable state of the invertebrate community was observed between 1989 and 1995, after which the invertebrate communities changed abruptly on the first axis of the plot. In many river stations, this abrupt change was accompanied by an upwards, and subsequent downwards movement on the second axis of the plot between 2000 and 2002. An alternate stable state was reached by the invertebrate communities in the river stations from 2005 to the end of monitoring in 2013/2014. In some river stations, the invertebrate community changed abruptly again after 2010 on the first axis of the plot, e.g. Vikedal st.9. In some river stations the trajectory deviated from the general observed trajectory, as directional change took place with more gradual increments, e.g. Vikedal st.11. Exceptions to the general trajectory were observed in Gaular st.7, Gaular st.8, and Vikedal st.4, as these river stations showed non-directional chaotic behaviour.

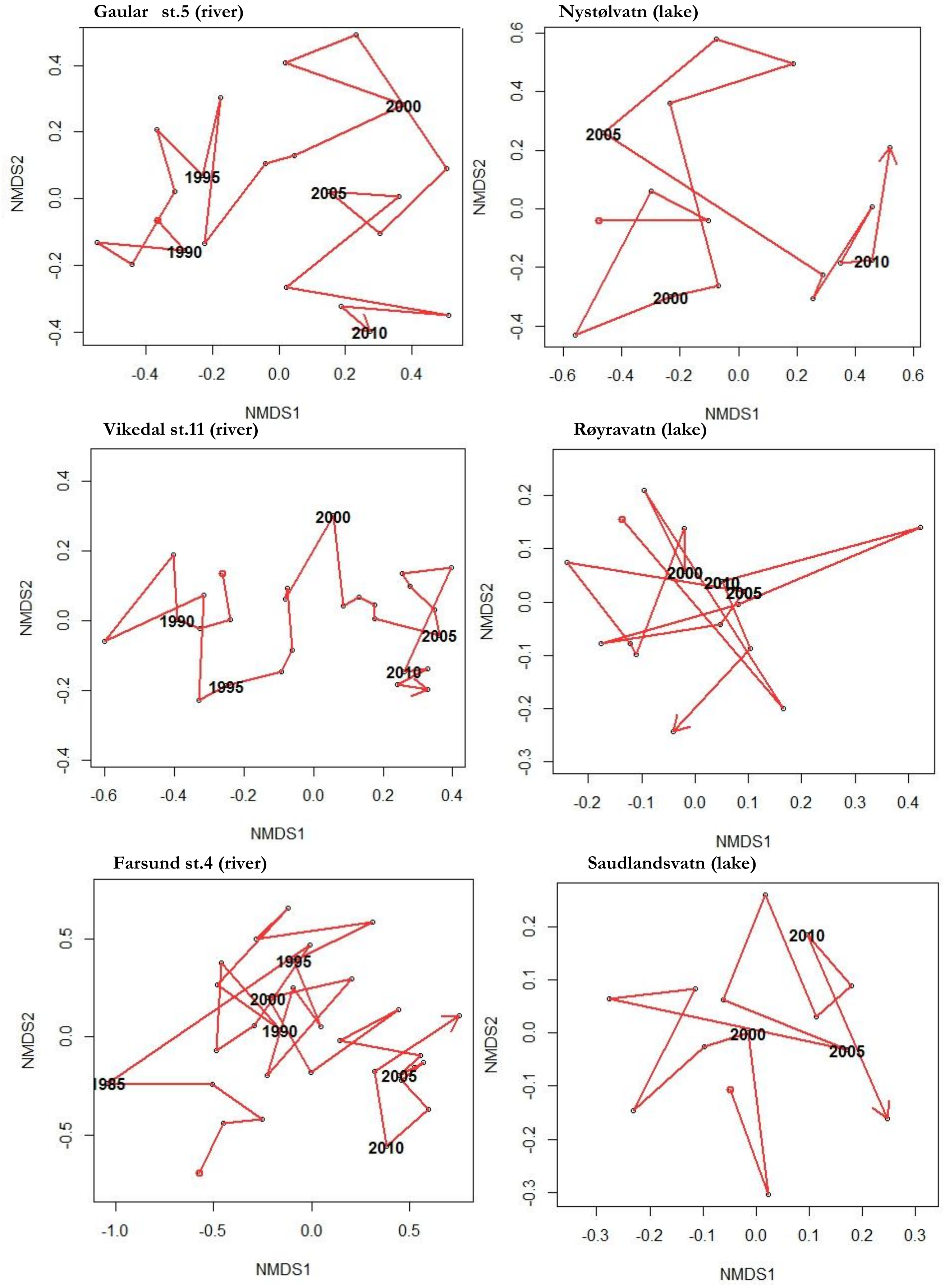

Figure 12: Non-metric multidimensional scaling (NMDS) plots of acid-sensitive invertebrates with time trajectories. The start of the monitoring period is indicated by a dot and the end is indicated by an arrow. Closely placed samples have similar species composition.

3.3 LINKING INVERTEBRATE COMMUNITY AND ENVIRONMENT

The results linking the invertebrate community and the environmental variables is presented by two main approaches, specifically multiple linear regression models describing biological indices (Section 3.3.1), and constrained gradient analysis (Section 3.3.2).

3.3.1 INDICES

Table 10 presents the 'best' linear regression models, which explain the highest amount of variance in the invertebrate indices (adjusted R^2). All models were tested for statistical assumptions of linear regression. The Variance Inflation Factor (VIF) detected severe multi-collinearity for acid neutralizing capacity (ANC) in all models, as it was comprised of other chemistry variables (VIF>10). ANC was therefore removed from the models to prevent unstable, and difficult to interpret coefficient estimates. Other cases of multi-collinearity were reported in Table 10. In some models the assumption of homoscedasticity was violated, which was resolved by the suggested power transformation of the Breusch-Pagan test (see details in Table 10). The Durbin-Watson test detected no autocorrelation at lag-1 in the models.

The adjusted R^2 of the 'best' causal model was compared to the 'dummy' model, including the dummy variables Time and Season, to assess if the models including environmental variables explained the variance in the invertebrate indices better than a non-causal model. All causal models explained the indices better than the dummy models (Table 10).

Rivers

In Gaular st.5, the causal models significantly explained between 35% and 59% of the variance in the biological indices, except for the causal model describing stability which was insignificant (Table 10). The richness of all taxa was best explained by the causal model. The most important components of the models were chloride deposition, precipitation, and non-marine sulphur deposition, and their combined relative importance ranged between 48% and 61%.

In Vikedal st.11, the causal models significantly explained between 48% and 68% of the variance in the biological indices. The richness indices were best explained by the causal models, however these models were most similar to the dummy models. Non-marine sulphur deposition over one year interval formed the most important component of the richness models with a relative importance between 41% and 53%. The causal models for %EPT and stability were comprised of various equally important environmental variables. Calcium concentration was the most important environmental variable in describing diversity.

In Farsund st.4, the causal models significantly explained the variance in biological indices between 61% and 80%. Richness of all taxa and stability were best explained by the causal models. Non-marine sulphur deposition over an interval of three or six months, and sulphate concentration formed the most important component in the models with a combined relative importance between 42% and 55%. The causal model describing richness formed an exception as chloride deposition was the most important component.

Additionally, to the regression model we observed that the periods of instability in the invertebrate community (Figure 11) followed the pattern of major sea-salt episodes (Figure 6). This pattern is not adequately described by the linear regression models as the impact of sea-salt episodes were often longer lasting than the one year time interval at which we included the environmental variables.

Lakes

In the lakes, the causal models significantly explained between 36% and 68% of the variance in the biological indices, except for the causal model describing stability in Saudlandsvatn which was insignificant (Table 10). The best causal model, describing diversity in Saudlandsvatn, was performing only slightly better than the dummy model. The most important component in this model is temperature, which will follow seasonal fluctuations computed by the dummy variable Season. Selection and relative importance of the environmental variables was unequivocal among the lake stations.

3.3.2 ORDINATION

The results of the constrained gradient analysis are presented in Table 11. Detrending for season shows the percent between-sample variance of the invertebrate community that is explained by trends in environmental variables. Detrending for both season and time gives the percent variance explained by variability in the environmental variables. Only a few environmental variables remained significant after detrending for season and time (Table 11)

Rivers

The invertebrate community trends in the river stations was best explained by non-marine sulphur deposition measured over one year interval, and associated sulphate and H^+ concentrations in the water (Table 11). The between-sample variance explained by these acidification-related variables ranged from 7% to 22%. In Gaular st.5 and Vikedal st.11, the invertebrate community trends were to a similar extend explained by acid neutralizing capacity in the water. The combination of all single significant environmental variables explained between 17% and 26% of the invertebrate communities trends.

After detrending for time and season, temperature was the only environmental variable that significantly explained between 4% and 6% of the variability in the invertebrate communities in all river stations (Table 11). The impact of sea-salt episodes may be reflected in the 4% and 7% of the variability significantly explained by chloride concentration in Vikedal st.11 and Gaular st.5, and chloride deposition in Gaular st.5 and Farsund st.4. Maximum discharge measured over six weeks time interval significantly explained 5% variability in the invertebrate community in Vikedal st.11. Minimum discharge measured over one year interval significantly explained 11% of the invertebrate community variability in Farsund st.4.

Lakes

The only environmental variable that significantly the invertebrate community trends in all lake stations was sulphate concentration in the water with a between-sample variance explained between 8% and 10% (Table 11). All significant single explanatory variables combined explained between 10% and 16% of the trends in the invertebrate communities in the lakes. None of the environmental variables explained the variability in the invertebrate community consistently among the lake stations.

Table 10: Multiple regression model for invertebrate indices with highest adjusted R^2 (best model). Dummy model including variables Time and Season to compare ability of best model to explain invertebrate indices. The relative importance of each environmental variable is provided over 100%. In brackets it shows the optimal time interval of environmental variables (6w=6 weeks, 3m=3 months, 6m=6 months, and 1yr=1 year), and the optimal summary statistic of discharge (mean, min=minimum, max=maximum). The significance level of the model is reported as $p<0.5$=, $p<0.01$=**, $p<0.001$=***, and for non-significant trends the p value is reported.*

		Chemistry						Discharge	Deposition		Climate		best model		dummy model	
Site	**Metric**	**SO_4**	**H+**	**LAL**	**TOC**	**Cl**	**Ca**		**Dep S**	**Dep Cl**	**Temp**	**Prec**	**Adj. R^2**	**p-value**	**Adj. R^2**	**p-value**
Gaular st.05 (river, N=29, 1989-2003)	**Richness all**						7.3	2.4 *(3m mean)*		49.8 *(6m)*	28.9 *(1yr)*	11.6 *(6m)*	**0.59**	***	**0.24**	*
	Richness EPT[3a]	3.9		5.7			7.0	*18.3 (1yr mean)*		21.3 *(6m)*	16.2 *(1yr)*	27.6 *(3m)*	**0.55**	**	**0.19**	*
	% EPT	4.8		8.4	19.2			18.3 *(1yr min)*	14.1 *(6w)*	22.1 *(1yr)*		13.1 *(3m)*	**0.35**	*	**0.04**	**0.36**
	Diversity	3.8		4.5	3.9			15.1 *(1yr max)*	17.9 *(3m)*	7.1 *(1yr)*	25.2 *(1yr)*	22.5 *(3m)*	**0.47**	**	**0.14**	**0.05**
	Stability					9.3		14.2 *(6m min)*		32.7 *(3m)*	17.5 *(6w)*	26.3 *(6w)*	**0.20**	**0.07**	**0.00**	**0.38**
Vikedal st.11 (river, N=38, 1987-2010)	**Richness all[1]**		17.4			3.1	5.2	2.0 *(6w min)*	41.1*(1yr)*	6.7 *(6w)*	17.7 *(6w)*	6.8 *(3m)*	**0.68**	***	**0.45**	***
	Richness EPT[1]			12.5			1.8	1.7 *(6w min)*	53.1*(1yr)*	4.6 *(6w)*	5.8 *(6w)*	20.5 *(3m)*	**0.58**	***	**0.42**	***
	% EPT[2]	15.0	19.1	12.0			5.2	14.1 *(6m max)*	8.9 *(6m)*	7.8 *(6m)*	17.9 *(6m)*		**0.57**	***	**0.26**	**
	Diversity[2]	10.7		4.5	2.8		27.5	10.1 *(6m max)*	16.1 *(1yr)*	17.5 *(6w)*	10.8 *(6m)*		**0.48**	***	**0.14**	*
	Stability			20.1		11.4		11.2 *(1yr min)*	17.9 *(3m)*	12.6 *(6m)*	8.1 *(1yr)*	18.7 *(6m)*	**0.46**	***	**0.00**	**0.73**
Farsund st.04 (river, N=22, 2000-2013)	**Richness all[3b]**		4.8		13.1		13.4	17.5 *(1yr min)*	12.8 *(3m)*	*23.3 (6w)*		15.1 *(3m)*	**0.61**	**	**0.12**	**0.10**
	Richness EPT[2]	18.5			13.7	11.0	5.3	1.5 *(6m min)*	23.6 *(3m)*	*11.3 (6w)*		15.1 *(3m)*	**0.80**	***	**0.39**	**
	% EPT		4.3	3.8				7.0 *(6m mean)*	57.2 *(6m)*	10.2 *(6m)*	*5.7 (3m)*	11.8 *(1yr)*	**0.65**	**	**0.21**	**0.08**
	Diversity		17.7		1.1	5.5		7.9 *(3m min)*	48.7 *(6m)*	*5.3 (6m)*	11.8 *(1yr)*	2.0 *(1yr)*	**0.79**	***	**0.11**	**0.12**
	Stability[1]	28.5			17.5		4.5	4.9 *(6w mean)*	26.5 *(6m)*		7.1 *(3m)*	11.0 *(3m)*	**0.80**	***	**0.49**	***
Nystølvatn (lake, N=29, 1997-2012)	**Richness all**		5.5	33.9	18.0		23.7		3.5 *(6w)*	7.3 *(6m)*	3.6 *(6m)*	4.5 *(1yr)*	**0.46**	**	**0.00**	**0.50**
	Diversity	12.5		22.0			10.1		5.1 *(6m)*	35.9 *(3m)*		14.4 *(1yr)*	**0.36**	*	**0.22**	*
	Stability		3.2	11.1					52.9 *(3m)*	18.9 *(6m)*	6.1 *(6m)*	7.8 *(6w)*	**0.57**	***	**0.20**	*
Røyravatn (lake, N=30, 1998-2012)	**Richness all**	32.8		13.2						6.0 *(1yr)*	23.5 *(6m)*	24.5 *(3m)*	**0.43**	**	**0.04**	**0.24**
	Diversity		14.8		18.7	10.5			23.0 *(6m)*	16.9 *(6m)*		16.1 *(3m)*	**0.47**	**	**0.00**	**0.52**
	Stability								12.8 *(6m)*	48.1 *(3m)*	16.7 *(6w)*	22.4 *(6w)*	**0.47**	**	**0.03**	**0.28**
Saudlandsvatn (lake, N=29, 1997-2012)	**Richness all**			18.6						12.9 *(1yr)*	63.0 *(6w)*	5.5 *(6w)*	**0.42**	**	**0.18**	*
	Diversity			2.1			5.7		10.2	7.1 *(1yr)*	70.0 *(6m)*	4.9 *(1yr)*	**0.68**	***	**0.60**	***
	Stability	16.1	16.4							20.9 *(1yr)*		46.6 *(6w)*	**0.16**	**0.09**	**0.07**	**0.15**

** LAL= Labile Aluminum; TOC=Total Organic Carbon; Disch=Discharge; Dep S=Non-marine sulphur deposition; Dep Cl=Chloride deposition; Temp=Temperature; Prec=Precipitation.*
1) Homoscedasticity violated, resolved by suggested power transformation of two; 2) minor case of multi-collinearity (VIF>5); 3) severe case of multi-collinearity (VIF>10): a) Cl deleted; b) LAL deleted

Table 11: Partial redundancy analysis (partial RDA) presents percentage between-sample variance of invertebrate community explained by single environmental variables with season as covariate, and season and time as covariate. "All" represents the net effect of all individually significant environmental variables. The presented values are all significant at p<0.05. The optimal time interval of environmental variables given in brackets (6w=6 weeks, 3m=3 months, 6m=6 months, and 1yr=1 year).

		Chemistry							**Discharge**			**Deposition**		**Climate**		**All**
Site	**Covariates**	**SO_4**	**H+**	**ANC**	**LAL**	**TOC**	**Cl**	**Ca**	**min**	**mean**	**max**	**Dep S**	**Dep Cl**	**Temp**	**Prec**	
Gaular st.5	Season	8.5	8.2	9.1			10.0				4.4 *(6w)*	7.8 *(1yr)*	7.9 *(1yr)*	5.5 *(6w)*		**17.6**
(river)	Season and time						7.3						5.9 *(6m)*	5.5 *(6w)*		
Vikedal st.11	Season	22.5	17.1	16.6	13.4	7.2	5.4				4.7 *(1yr)*	22.2 *(1yr)*	7.6 *(1yr)*	4.8 *(6w)*		**26.4**
(river)	Season and time			3.5	4.1		4.1			4.1 *(6w)*	4.8 *(6w)*	*4.8 (1yr)*		4.5 *(3m)*		
Farsund st.4	Season	6.7	6.8			9.6			11.1 *(1yr)*		7.4 *(3m)*	7.6 *(1yr)*		7.5 *(1yr)*	5.0 *(6w)*	**24.8**
(river)	Season and time	3.5							11.0 *(1yr)*				3.4 *(6w)*	6.2 *(1yr)*	5.5 *(6w)*	
Nystølvatn	Season	10.6										11.4 *(1yr)*		8.6 *(6w)*		**15.8**
(lake)	Season and time											11.5 *(1yr)*		9.9 *(6w)*		
Røyravatn	Season	8.9			9.1			6.7								**10.3**
(lake)	Season and time				6.7											
Saudlandsvatn	Season	8.0	6.5	6.1		6.1						5.9 *(1yr)*				**10.4**
(lake)	Season and time			6.9		6.9							7.8 *(1yr)*			

** ANC=Acid Neutralizing Capacity calculated as (Ca+Mg+K+Na) - ($Cl+SO_4+NO_3$); LAL= Labile Aluminum; TOC=Total Organic Carbon; Disch=Discharge; Dep S=Non-marine sulphur deposition; Dep Cl=Chloride deposition; Temp=Temperature; Prec=Precipitation.*

4 DISCUSSION

The of our study was to analyze temporal changes of invertebrate communities in acidified rivers and lakes, and disentangle the environmental causes of the observed changes. The analysis was performed using long-term data from three catchments along the west coast of Southern Norway. First, the temporal pattern of invertebrate community recovery in the rivers will be discussed in terms of gradual, or abrupt change to an alternate stable state (Section 4.1), followed by a discussion on the difference in recovery between lakes and rivers (Section 4.2). Thereafter, it will be discussed how changes in the invertebrate community were related to variability and change in the environmental variables (Section 4.3). Then, the two methods used in this study will be compared, and limitations of the methodology will be addressed (Section 4.4). Last, the implications of the findings will be synergized, and highlighted (Section 4.5).

4.1 GRADUAL VERSUS ABRUPT CHANGE

The first research question was: *"Have invertebrate communities recovered in acidified rivers and lakes in Norway, and were the changes gradual, or were the changes abruptly to an alternate stable state?"*. The results from the river sampling stations indicate a recovery of the invertebrate community, and abrupt changes to an alternate stable state. No apparent difference in recovery patterns along the gradient of decreasing sulphur deposition was observed. The results indicate lack of recovery in the lakes.

The biological recovery in the rivers was foremost substantiated by a significant increase in richness and relative abundance of acid-sensitive invertebrate taxa from a low base-line at nearly all river sampling stations. The initial re-establishment of acid-sensitive invertebrate taxa was comparable to the observations in rivers in the United Kingdom (Monteith et al., 2005). Complementary signs of biological recovery in Southern Norway were also found for acid-sensitive fish species, such as brown trout (Hesthagen et al., 2001; Hesthagen et al., 2011). Despite the re-establishment of acid-sensitive invertebrate taxa, diversity based on the richness and abundance of all taxa did not increase (Shannon-Wiener $_{exp}$). The observations were similar to national trends in the diversity observed in other lakes and rivers in Norway, as well as the in the UK, but contrasted with significant increases in diversity in Swedish rivers and lake littoral zones (Velle et al., 2013). Diversity indices comprise only for a part of acid-sensitive taxa. Unknown interactions of competition and predation, between acid-sensitive taxa and tolerant taxa, may have impacted the invertebrate diversity (Menge & Sutherland, 1976; Layer et al., 2013).

A new aspect in the study of biological effects of acidification was the use of the Change Point Analyser (Taylor, 2000), and temporal trajectories (Philippi et al., 1998), to detect whether invertebrate communities changed gradually, or abruptly to an alternate stable state. Previous studies focussed primarily on gradual linear trends in the invertebrate community (Halvorsen et al., 2003; Lento et al., 2012; Murphy et al., 2014). Angeler & Johnson (2012) recognized different temporal patterns in invertebrate communities, including linear change and fluctuations, but did not analyse this further. It has been conceptualized that ecological systems do not respond smoothly to changing external drivers, but rather jump abruptly to an alternate stable state when drivers exceed specific thresholds (Andersen et al., 2009). The presence of alternate stable states is classically illustrated by a ball rolling down a rugged landscape (Noy-Meir, 1975; Figure 13 a).

Our study indicated that the invertebrate communities in the majority of the river stations followed a trajectory in which there was an abrupt shift from one stable state to an alternate stable state between 1995 and 2005. During the latter half of this period (2000-2005), abrupt increases in richness of acid-sensitive taxa were recorded. The abrupt shifts may relate to the chemical thresholds reached between 2000 and 2005. The pH ranged from 5.7 to 6.0 for all river sites during the shift to alternate stable state (Appendix 3). The labile aluminium was <20µg/l in the Gaular and Vikedal catchment, but showed peaks up to 50µg/l in the Farsund catchment. The observed pH is comparable to typical pH thresholds for presence and absence of many acid-sensitive taxa in the UK (Kowalik & Ormerod, 2006), and elsewhere (Snucins, 2003). Most studies indicated labile aluminium thresholds for invertebrate communities between 10-30µg/l, and in some cases up to 50µg/l (Herrmann, 2001).

Despite a re-establishment of acid-sensitive taxa in the rivers, it is not straightforward to conclude on the state of recovery. First, baseline conditions from the pre-acidification period are lacking as monitoring programmes were started after the delayed recognition of the impacts of acid emissions and deposition (Johnson & Angeler, 2010). Second, studies covering the Holocene have indicated that after environmental change, the invertebrate communities may not return to the pre-disturbance state, but rather move to an alternate state (Velle et al., 2005; Brodersen & Quinlan, 2006). Water chemistry has certainly not returned to pre-acidification levels, in part because of depletion of base cations stores in the soil (Futter et al., 2014).

Our current study suggests that invertebrate communities changed from a state with low or absence of acid-sensitive taxa to an alternate state with higher richness and abundance of acid-sensitive taxa, and that the biological shifts coincided with chemical thresholds. The state with diverse presence of acid-sensitive taxa may be more resilient to environmental changes (Elmqvist et al., 2003). The invertebrate community change in acidified rivers in Norway can be compared to the classical ball rolling down a rugged landscape, however the valleys may be wider, the changes more gradual, and the ball may roll further to the right, towards more recovery (Figure 13 b). Lack of historical data on the baseline pre-acidification make it difficult to assess the extent to which invertebrate communities have recovered to the pre-acidification state, or perhaps more likely to an alternate stable state.

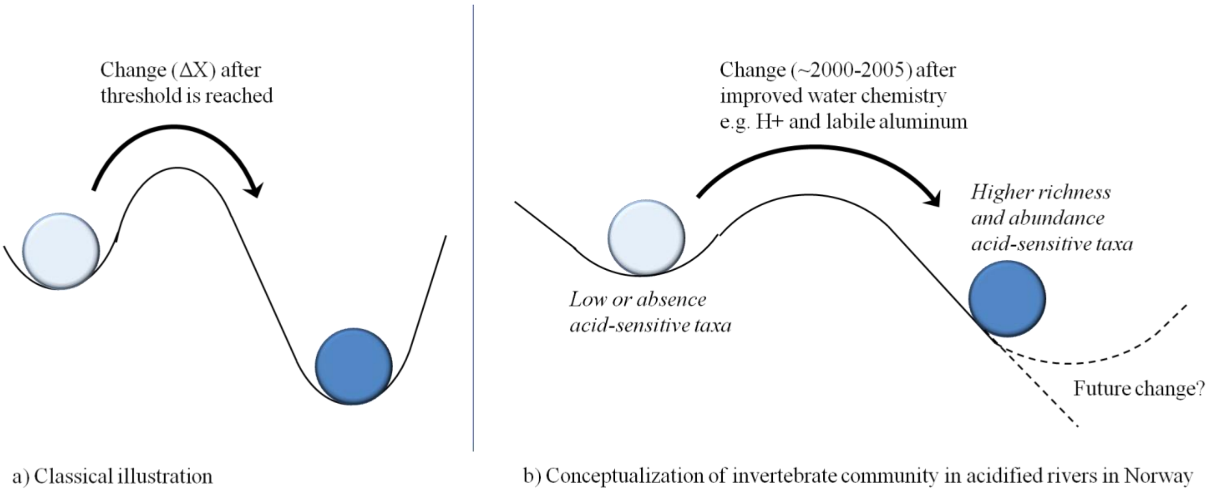

Figure 13: Alternate stable states theorem with a) classical illustration (after Noy-Meir, 1975), and b) conceptualization of invertebrate community in acidified rivers in Norway

4.2 RIVERS VERSUS LAKES

The second research question was: *"Is there a difference between the invertebrate community change in rivers and lakes?"*. The results showed that the recovery of the invertebrate community was pronounced in the rivers, whereas no change was observed in the lakes, even though the chemical recovery was comparable.

In Sweden, invertebrate communities were generally more diverse in rivers than in lakes (Johnson et al., 2004). Biological response to reduced acidification in Swedish lakes was weak for invertebrate species (Angeler & Johnson, 2012), as well as for fish species (Holmgren, 2014). Contrary, recovery of the invertebrate community was recorded for about half of the lake sites in

Canada (Lento et al., 2012). Murphy et al. (2014) did not find systematic differences in the invertebrate recovery of the rivers and lakes in the UK. Stockdale et al. (2014) assessed the actual and modelled taxa richness of the orders Ephemeroptera, Plecoptera and Trichoptera (EPT) for the same sites in the UK, and found significantly lower actual recovery rates in lakes than in rivers, despite predicted recovery rates being equivalent.

One possible reason for the lack of observed invertebrate community change in the lakes relates to the shorter monitoring period in lakes compared to rivers (approximately 15 vs. 25 years). The water chemistry was already recovering when the lake monitoring started around 1997 (Appendix 3). The invertebrate communities may have responded already to improved water chemistry before the start of the lake monitoring. However, the longer time series of lake Botnavatn in the Vikedal catchment refute this assumption, as the invertebrate community at this locality did not show signs of invertebrate community change despite the start of the monitoring in 1987 (Appendix 4 and Appendix 7).

Alternatively, the lack of recovery in lakes may relate to their homogeneous environment compared to more spatially heterogeneous and temporal dynamic rivers, e.g. the fluctuation in chemistry and temperatures is more pronounced in rivers than in lakes (Havas & Rosseland, 1995; Velle et al., 2013). Rivers potentially have a large variation in habitats and refuges along the streambed and its tributaries (Brown & Brussock, 1991). More persistent acid-tolerant taxa may have occupied the niche of acid-sensitive taxa during the acidified period (Ledger & Hildrew, 2005). The acid-tolerant species can be dislodged during extreme events, which may allow for re-colonization of acid-sensitive species (Velle et al., 2013). Recovery in lakes may be limited compared to rivers as lakes are less susceptible to extreme events, and consequently less open for re-colonization (Velle et al., 2013). Further, the variation in habitat and refuges in rivers may increase possibilities of invertebrate taxa to re-colonize (Wetzel, 2001).

Another explanation for the limited recovery recorded in lakes is related to the taxonomic resolution of the data. The majority of the invertebrates in the order of Ephemerptera, Plecoptera and Trichoptera were identified to species level, and the acid-sensitive taxa addressed in this study are primarily from these orders. EPT taxa thrive in rivers, whereas Chironomids are most abundant in lakes (Velle et al., 2013). Some Chironomid species are also acid-sensitive, however in monitoring studies they are rarely determined to species level (Orendt, 1999). We recommend to increase the data resolution of monitoring studies to identify if acid-sensitive Chironomids occur in acidified lakes (Fjellheim & Raddum, 1990).

4.3 LINKING INVERTEBRATE COMMUNITY AND ENVIRONMENT

The third research question was: *"Were the observed invertebrate community changes related to sulphur deposition, climate, and associated hydro-chemistry variables?"*. The changes in the invertebrate community in the river stations related best to sulphur deposition, and sulphate concentrations, however it was not straight forward to separate the impact of multiple-collinear stressors. The results were therefore inconclusive with regard to the ultimate environmental drivers of invertebrate community change.

The studied catchments showed significant trends of reduced non-marine sulphur deposition, and associated improvements in acidity (H^+), labile aluminium concentration, and acid neutralizing capacity (ANC) in the water. The trends of improved surface water quality were consistent with observations in other acid-sensitive regions of Europe and North-America (Garmo et al., 2014). The invertebrate community trends in the rivers of our study were most frequently explained by sulphur deposition and sulphate concentrations, which indicates that biological recovery from reduced acidification is occurring. Angeler & Johnson (2012) also found most significant correlations between the invertebrate community patterns and sulphate concentration, whereas Murphy et al. (2014) observed most influence of ANC. Sulphur deposition is most likely a proxy for other processes, and it is not straightforward to separate the influence from sulphate on collinear variables such as H^+, ANC, and labile aluminium.

The results of our study indicate that the variability in the invertebrate community was related to fluctuations in temperature. This is in line with the study of Johnson & Angeler (2010) who observed significant correlations between the inter-annual variability of invertebrate communities and temperature. Temperature may influence the invertebrate community by impacting the growth, and phenology of each invertebrate species differently (Briers et al., 2004). Additionally, we found that the variability in the invertebrate community was related to fluctuation in chloride deposition and concentration in the water. Our study further showed that periods of instability in the invertebrate community coincided with high deviations from the mean chloride deposition. High deviations in chloride deposition are related to sea-salt episodes in coastal regions, which mobilize toxic aluminium (Wright et al., 1988; Hindar et al., 2004). Transplantation experiments have indicated that exposure to short-term episodic conditions leads to increased mortality of the invertebrate species (Kolawik & Ormerod, 2006). Biological recovery from acidification may be set-back by sea-salt episodes (Hesthagen et al., 2011).

Mean temperatures did increase significantly over the monitoring period, but our findings only documented relations between short-term temperature variability and the invertebrate community. Reduced acidification has presumably dominated the changes in the invertebrate communities, and the long-term influence of temperature has so far been limited. This finding is in line with Durance & Ormerod (2007) who observed an impact of temperature rise in circum-neutral streams in the UK, but no impact in acidified streams. The temperature increase in circum-neutral streams moderately influenced the invertebrate community, causing a reduced abundance of less common taxa. The impacts of temperature rise may have been less evident in acidified streams than in circum-neutral streams, due to previous reduction of the taxa richness (Durance & Ormerod, 2007).

Overall, the findings were inconclusive on the impacts of long-term temperature change on the invertebrate community. Indirect effects of temperature rise were not included in our study, e.g. higher temperatures may reduce aluminum mobilization from the soil (Veselý et al., 2003). Lastly, accelerated temperature rise is predicted for the 21st century (IPCC, 2014), which may influence the invertebrate communities in unexpected way in the future. We therefore recommend a continuation of the research efforts on the effect of climate on the long-term change in invertebrate communities in acidified waters.

4.4 METHODOLOGICAL LIMITATIONS

Previous studies have analysed the influence acidification on invertebrate communities using either biological indices (Raddum et al., 2001; Moe et al., 2010; Lento et al., 2011), or indirect and direct gradient analysis of the community (Monteith et al., 2005; Angeler & Johnson et al., 2012). In this study, the methods were used complementary, as suggested by Halvorsen et al. (2003). Rice (2000) evaluated the use of multiple methods to describe the impacts of fishery on ecosystems, and concluded that the use of complementary methods is necessary to obtain a better understanding of how and why communities are changing over time. However, the application of multiple methods can increase the influence of preconceptions on the interpretation of the results (Rice, 2000).

The indices applied in this study showed varying response to reduced acidification, e.g. the richness of acid-sensitive taxa increased, whereas the diversity showed no significant trend. Similar, Sandin & Johnson (2000) found that the richness indices had a high statistical power to detect recovery from acidification, whereas diversity indices had a low statistical power. Richness indices are however more prone to bias caused by sampling effort, and inconsistencies in the taxonomic resolution (Velle et al., 2013). A weakness of using indices is that it entails comparison to a reference value to give conclusive results on the state of recovery, while pre-disturbance data of the invertebrate community is not available (Johnson & Angeler, 2010). The constrained gradient analysis in our study indicated low percent between-sample variance explained by time, which was comparable to other studies (Halvorsen et al., 2003; Murphy et al., 2014). A large part of the community changes in our study were attributed to stochasticity.

To our knowledge, no study has previously aimed to disentangle how sulphur deposition, climate-related factors, and associated hydro-chemistry have collectively impacted invertebrate community change. This study made a first attempt, however challenges related to classical (or frequentist) statistics were encountered: 1) auto-correlation in the data (e.g. it was not possible to separate the influence from sulphate on collinear variables such as H^+, ANC, and labile aluminium), 2) difference in time-scales in the invertebrate and environmental data (e.g. discharge was measured daily whereas invertebrates were sampled twice a year), 3) unknown delayed response of the invertebrate communities to environmental change (e.g. our study gave indication that invertebrate communities sampled at time X were influenced by sea-salt episodes at time X-y, but y was unknown).

It is recommended to overcome the challenges related to limitations of classical statistics in future studies by exhaustive statistical modelling, e.g. using Bayesian methods. Additionally, intensive year-round sampling of the invertebrates, as well as hydro-chemistry, and weather is needed to better understand the invertebrate community responses to climate-related factors. The results from this study can help to carefully design statistical models, and thereby aid to unravel the (collective) effect of environmental variables on the invertebrate community.

4.5 IMPLICATIONS OF THE FINDINGS

Our study verified that acid-sensitive invertebrate taxa are re-establishing in rivers due to reduced acidification, indicating that a biological recovery is taking place. Failure to identify the re-establishment of acid-sensitive taxa in lakes may denote that the biological recovery is lagging behind the improvements in water quality due to the homogeneous environment of lakes, or the limited variation in habitat and refuges. Another explanation relates to the taxonomic resolution of the data. An interesting finding is that the invertebrate communities in rivers appear to have changed abruptly to an alternate state, which coincided with previously defined chemical thresholds. The identification of alternate stable states may have implications on future impacts of temperature rise on invertebrate communities, although we do not know if biotic responses to reduced acidification are directly transferable to the biotic responses to warming. The long-term influence of temperature on invertebrate communities has so far been limited, as reduced acidification has presumably dominated the changes in the invertebrate communities. However, accelerated climate change predicted for the 21st century may result in unpredictable, and possibly abrupt changes to an alternate state. We therefore stress the importance of a continuous research effort to disentangling the complex link between acidification, and climate on invertebrate community change.

5 CONCLUSION

International policy action has led to significantly reduced sulphur deposition, and associated recovery of water chemistry in both rivers and lakes in Southern Norway. This study added encouraging evidence that the invertebrate communities in acidified rivers show signs of recovery in terms of increased richness and abundance of acid-sensitive taxa. Our first hypothesis that invertebrate communities shifted abruptly to an alternate stable state when certain chemical thresholds were reached, was accepted for the rivers. Our second hypothesis that the recovery was more pronounced in rivers than in lakes was confirmed by the lack of invertebrate community change in the lakes. This finding may relate to the homogenous environment of lakes, and limited variation in habitat and refuges, which may make them less susceptible to re-colonisation of acid-sensitive taxa. However, another possible explanation is the lower taxonomic resolution in lakes. The results from the rivers indicate that long-term trends in the invertebrate community were related to the reduced sulphur deposition. Superimposed on the long-term trends, temperature fluctuations and sea-salt episodes may have caused short-term variability in the invertebrate community. We did not identify impacts of temperature rise on the long-term invertebrate community trends, as recovery from reduced acidification has presumably dominated the changes in the invertebrate communities. These findings are in line with our third hypothesis, however the environmental drivers ultimately responsible for invertebrate community change were not disentangled. Accelerated climate change is predicted for the 21st century. We therefore conclude that future research should continue to focus on the complex link between acidification, and climate on biological recovery in acidified waters.

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APPENDIX 1: OVERVIEW TAXA

Table 1: Overview of taxa identified with taxonomic order and Raddum score. Raddum score: Index 1 = extinct at pH<5.5, index, 0.5 = extinct at pH<5.0, index 0.25 = extinct at pH<4.7, index 0 = tolerating pH>4.7, - = no index (Fjellheim & Raddum, 1990).

Taxa name	Order	Raddum score	Taxa name	Order	Raddum score
Acari indet.	*class*	-	Cyrnus trimaculatus	Trichoptera	0
Adicella reducta	Trichoptera	0	Diptera indet.	Diptera	-
Agapetus ochripes	Trichoptera	-	Diura sp.	Plecoptera	-
Agrypnia sp.	Trichoptera	-	Enallagma cyathigerum	Odonata	-
Agrypnia obsoleta	Trichoptera	0	Ephemerella aurivillii	Ephemeroptera	1
Agrypnia varia	Trichoptera	-	Ephemeroptera indet.	Ephemeroptera	-
Ameletus sp.	Ephemeroptera	-	Erpobdella octoculata	Arhynchobdellida	-
Ameletus inopinatus	Ephemeroptera	0.5	Erpobdella testacea	Arhynchobdellida	-
Amphinemura sp.	Plecoptera	-	Glossosoma sp.	Trichoptera	-
Amphinemura borealis	Plecoptera	0	Glossosoma intermedium	Trichoptera	1
Amphinemura standfussi	Plecoptera	0	Glossosomatidae indet.	Trichoptera	-
Amphinemura sulcicollis	Plecoptera	0	Glyphotaelius sp.	Trichoptera	-
Anisoptera indet.	Odonata	-	Gyraulus acronicus	Hygrophila	-
Apatania sp.	Trichoptera	-	Halesus sp.	Trichoptera	-
Athripsodes sp.	Trichoptera	-	Halesus radiatus	Trichoptera	0
Baetidae indet.	Ephemeroptera	-	Harpacticoidea indet.	Cyclopoida	-
Baetis sp.	Ephemeroptera	-	Helobdella stagnalis	Hirudinea	0.5
Baetis fuscatus	Ephemeroptera	1	Heptagenia sp.	Ephemeroptera	-
Baetis muticus	Ephemeroptera	1	Heptagenia sulphurea	Ephemeroptera	0.5
Baetis rhodani	Ephemeroptera	0.5	Hirudinea indet.	Hirudinea	-
Baetis subalpinus	Ephemeroptera	1	Holocentropus dubius	Trichoptera	0
Bivalvia indet.	*class*	-	Holopedium gibberum	Cladocera	-
Bosmina sp.	Diplostraca	-	Hydra sp.	Anthomedusae	-
Brachyptera risi	Plecoptera	0	Hydrophilidae indet.	Trichoptera	-
Caenis horaria	Ephemeroptera	1	Hydropsyche sp.	Trichoptera	-
Calanoida indet.	Calanoida	-	Hydropsyche angustipennis	Trichoptera	0.5
Capnia sp.	Plecoptera	-	Hydropsyche pellicidula	Trichoptera	0.5
Capnia atra	Plecoptera	0.5	Hydropsyche siltalai	Trichoptera	0.5
Capnia pygmaea	Plecoptera	0.5	Hydroptila sp.	Trichoptera	-
Centroptilum sp.	Ephemeroptera	-	Hydroptilidae indet	Trichoptera	-
Ceraclea sp.	Trichoptera	-	Isoperla sp.	Plecoptera	-
Ceraclea nigronervosa	Trichoptera	-	Isoperla spp .	Plecoptera	-
Ceratopogonidae indet.	Diptera	-	Isoperla grammatica	Plecoptera	0.5
Chaetopteryx villosa	Trichoptera	0	Isoperla obscura	Plecoptera	0.5
Chaoborus sp.	Diptera	-	Ithytrichia lamellaris	Trichoptera	0.5
Chironomidae indet.	Diptera	-	Kageronia fuscogrisea	Ephemeroptera	-
Chydoridae indet.	Diplostraca	-	Lepidostoma hirtum	Trichoptera	0.5
Cloeon sp.	Ephemeroptera	-	Leptoceridae indet.	Trichoptera	-
Cloeon dipterum	Ephemeroptera	-	Leptophlebia sp.	Ephemeroptera	-
Cloeon simile	Ephemeroptera	-	Leptophlebia marginata	Ephemeroptera	0
Coleoptera indet.	Coleoptera	-	Leptophlebia vespertina	Ephemeroptera	0
Collembola indet.	*class*	-	Leptophlebia indet.	Ephemeroptera	-
Cordulegaster boltoni	Odonata	-	Leuctra sp.	Plecoptera	-
Corixidae indet.	Hemiptera	-	Leuctra spp.	Plecoptera	-
Crenobia alpina	Turbellaria	0.5	Leuctra digitata	Plecoptera	-
Crunoecia irrorata	Trichoptera	-	Leuctra fusca	Plecoptera	0
Crustacea indet.	subphylum	-	Leuctra hippopus	Plecoptera	0
Cyclopidae indet.	Cyclopoida	-	Leuctra nigra	Plecoptera	0
Cyrnus flavidus	Trichoptera	0	Limnephilidae indet.	Trichoptera	-
Diura bicaudata	Plecoptera	0.5	Limnephilus sp.	Trichoptera	-
Diura nanseni	Plecoptera	0.5	Limnephilus extricatus	Trichoptera	0
Ecnomus tenellus	Trichoptera	-	limnephilus flavicornis	Trichoptera	0
Cyrnus insolutus	Trichoptera	-	limnephilus lunatus	Trichoptera	0

Table 1 (continued)

Taxa name	Order	Raddum score	Taxa name	Order	Raddum score
Limnephilus rhombicus	Trichoptera	0	Phryganidae indet	Trichoptera	-
Lymnaea truncatula	Pulmonata	-	Pisidium sp.	Bivalia	0.25
Lype reducta	Trichoptera	-	Plecoptera indet.	Plecoptera	-
Micrasema sp.	Trichoptera	-	Plectrocnemia conspersa	Trichoptera	-
Micrasema gelidum	Trichoptera	-	Polycentropodidae indet.	Trichoptera	-
Micropterna lateralis	Trichoptera	0	Polycentropus sp.	Trichoptera	-
Micropterna sequax	Trichoptera	-	Polycentropus flavomaculatus	Trichoptera	0
Molanna albicans	Trichoptera	-	Polycentropus irroratus	Trichoptera	0
Molannidae indet.	Trichoptera	-	Potamophylax sp.	Trichoptera	-
Molannodes tinctus	Trichoptera	0	Potamophylax cingulatus	Trichoptera	0
Mystacides sp.	Trichoptera	-	Potamophylax latipennis	Trichoptera	0
Mystacides azurea	Trichoptera	0	Protonemura meyeri	Plecoptera	0
Mystacides longicornis	Trichoptera	-	Radix balthica	Hygrophila	-
Nematoda indet.	*phylum*	-	Rhyacophila nubila	Trichoptera	0
Nemoura sp.	Plecoptera	-	Sericostoma personatum	Trichoptera	0.5
Nemoura avicularis	Plecoptera	0	Sialis lutaria	Megaloptera	-
Nemoura cinerea	Plecoptera	0	Sididae indet.	Cladocera	-
Nemouridae indet.	Plecoptera	-	Simuliidae indet.	Diptera	-
Nemurella pictetii	Plecoptera	0	Siphlonuridae indet.	Ephemeroptera	-
Neureclipsis bimaculata	Trichoptera	0	Siphlonurus sp.	Ephemeroptera	-
Nigrobaetis niger	Ephemeroptera	-	Siphlonurus lacustris	Ephemeroptera	-
Notidobia ciliaris	Trichoptera	0	Siphonoperla burmeisteri	Plecoptera	0
Oecetis sp.	Trichoptera	-	Stenophylax permistus	Trichoptera	-
Oecetis testacea	Trichoptera		Taeniopteryx nebulosa	Plecoptera	0
Oligochaeta indet.	*subphylum*	-	Tinodes waeneri	Trichoptera	0.5
Ostracoda indet.	*subphylum*	-	Tipulidae indet.	Tipulida	-
Otomesostoma auditivum	Turbellaria	0.5	Trichoptera indet.	Trichoptera	-
Oxyethira sp.	Trichoptera	0	Turbellaria indet.	*class*	-
Perlodidae indet.	Plecoptera	-	Wormaldia sp.	Trichoptera	-
Philopotamidae indet.	Trichoptera	-	Wormaldia occipitalis	Trichoptera	-
Philopotamus montanus	Trichoptera	0.5	Wormaldia subnigra	Trichoptera	-
Phryganea sp.	Trichoptera	-	Zygoptera indet.	Odonata	-

APPENDIX 2: TAXONOMIC CONSISTENCY

Taxa with inconsistent taxonomy through time were merged to the coarsest taxonomic unit (according to dr. Gaute Velle):

Rivers

- Agabus sp. + Agapetus sp. + Coleoptera indet. + Berosus sp. + Deronectes latus + Dytiscidae indet. + Elmidae indet. + Elmis aenea + Elodes sp. + Haliplus sp. + Helophorus sp. + Hydraena sp. + Hydraena gracilis + Hydroporus sp. + Limnius volckmari + Nebrioporus assimilis + Nebrioporus depressus + Oulimnius tuberculatus + Platambus maculatus + Stictotarsus multilineatus
- Dicranota + Limoniidae + Prionocera + Tipula + Tipulidae indet.
- Chaoborus sp. + Diptera indet + Dixidae indet. + Dixa sp. + Dolichopodidae indet. + Muscidae indet. + Pedicia rivosa + Pericoma sp. + Psychodidae indet. + Tabanidae indet.

Additional for Farsund

- Nemoura imoago + Nemoura sp.
- Potamophylax sp. + Potamophylax indet.
- Rhyacophila nubile + Rhyacophila nubile p
- Isoperla sp. + Isoperla grammatica + Isoperla obscura
- Leuctra digitala + Leuctra fusca + Leuctra hippopus + Leuctra indet.+ Leuctra sp. + Leuctra nigra

Lakes

- Diura nanseni + Diura sp.
- Halesus radiatus + Halesus sp.
- Leptophlebia marginata + Leptophlebia sp + Leptoplebia vespertina - Limnephilidae ind + Limnephilus centralis + Limnephilus marmoratus + Limnephilus rhombicus + Limnephilus sp + Limnephilus sparsus
- Nemoura avicularis + Nemoura cinerea + Nemoura sp
- Siphlonurus aestivalis + Siphlonurus alternatus + Siphlonurus lacustris + Siphlonurus sp

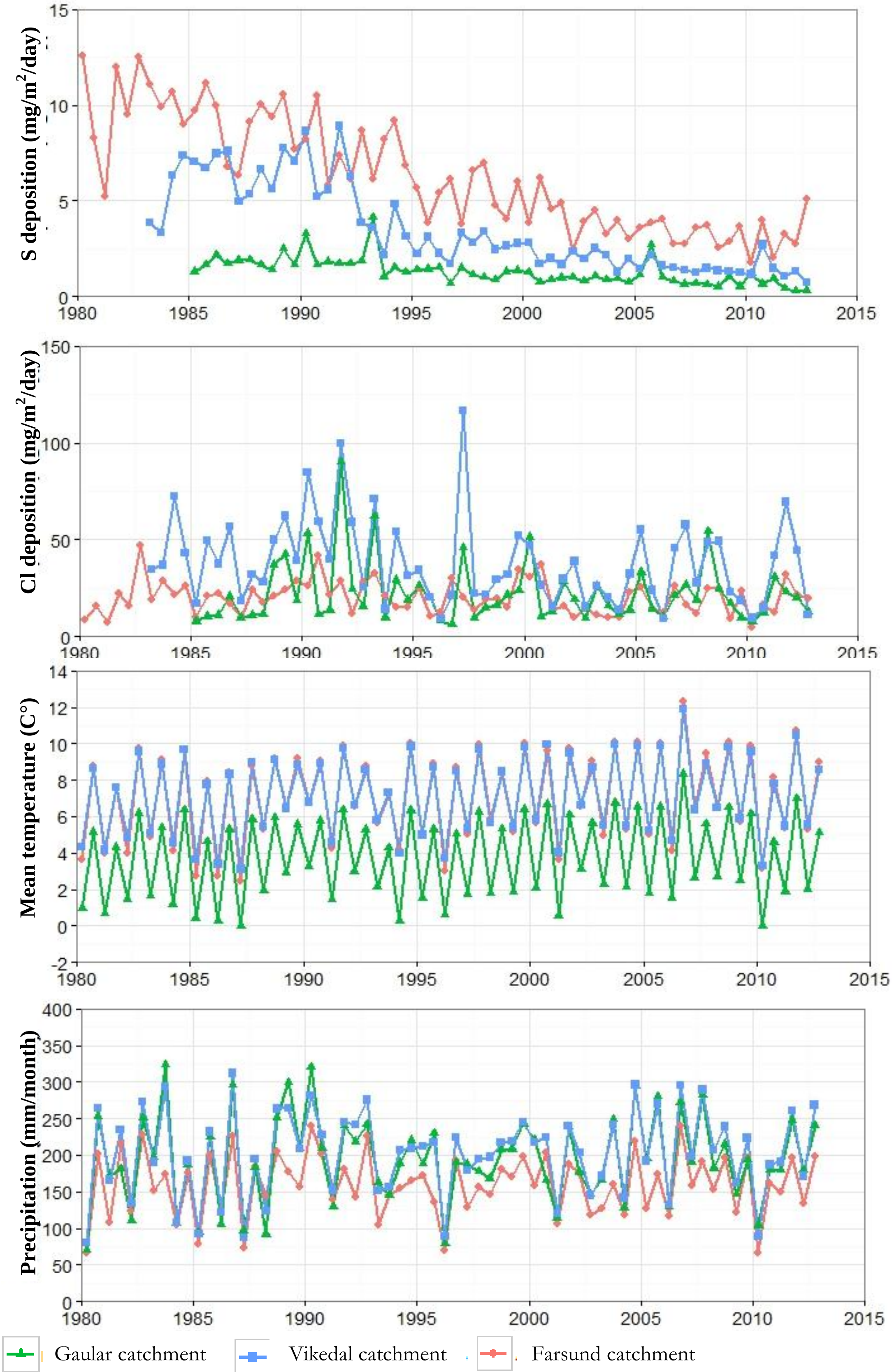

Figure 1: Non-marine sulphur and chloride deposition, temperature and precipitation averaged over January-June and July-December in the catchments: Gaular=green, Vikedal=blue, Farsund=red.

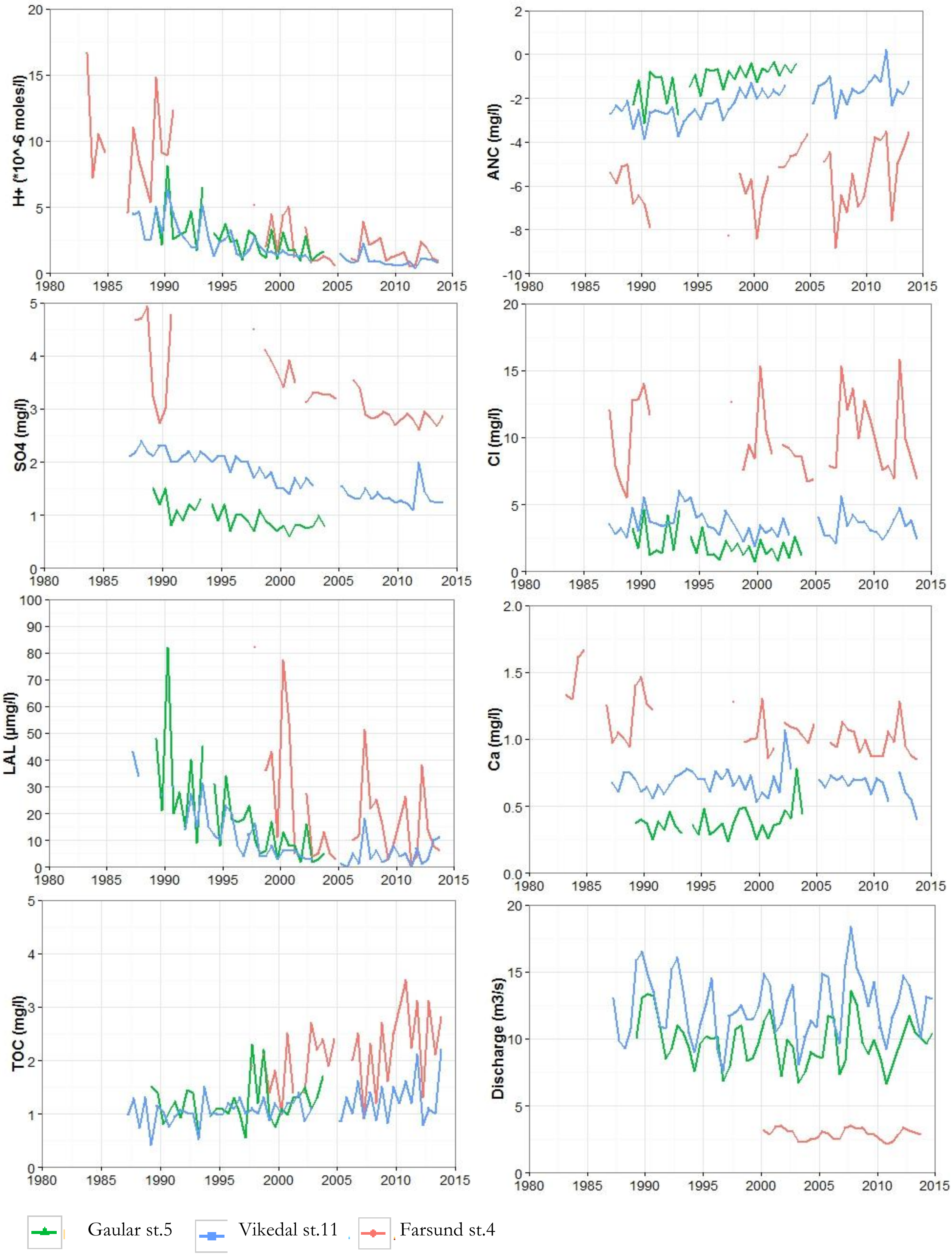

Figure 2: Hydro-chemistry variables in river sites: Gaular st.5=green, Vikedal st.11=blue, Farsund st. 4=red. Displaying variables: H^+, Labile Aluminium (LAL), Acid Neutralizing Capacity (ANC), Chloride (Cl), Sulphate (SO_4), Calcium (Ca), Total Organic Carbon (TOC), and discharge which is multiplied by 10 for Farsund st. 4.

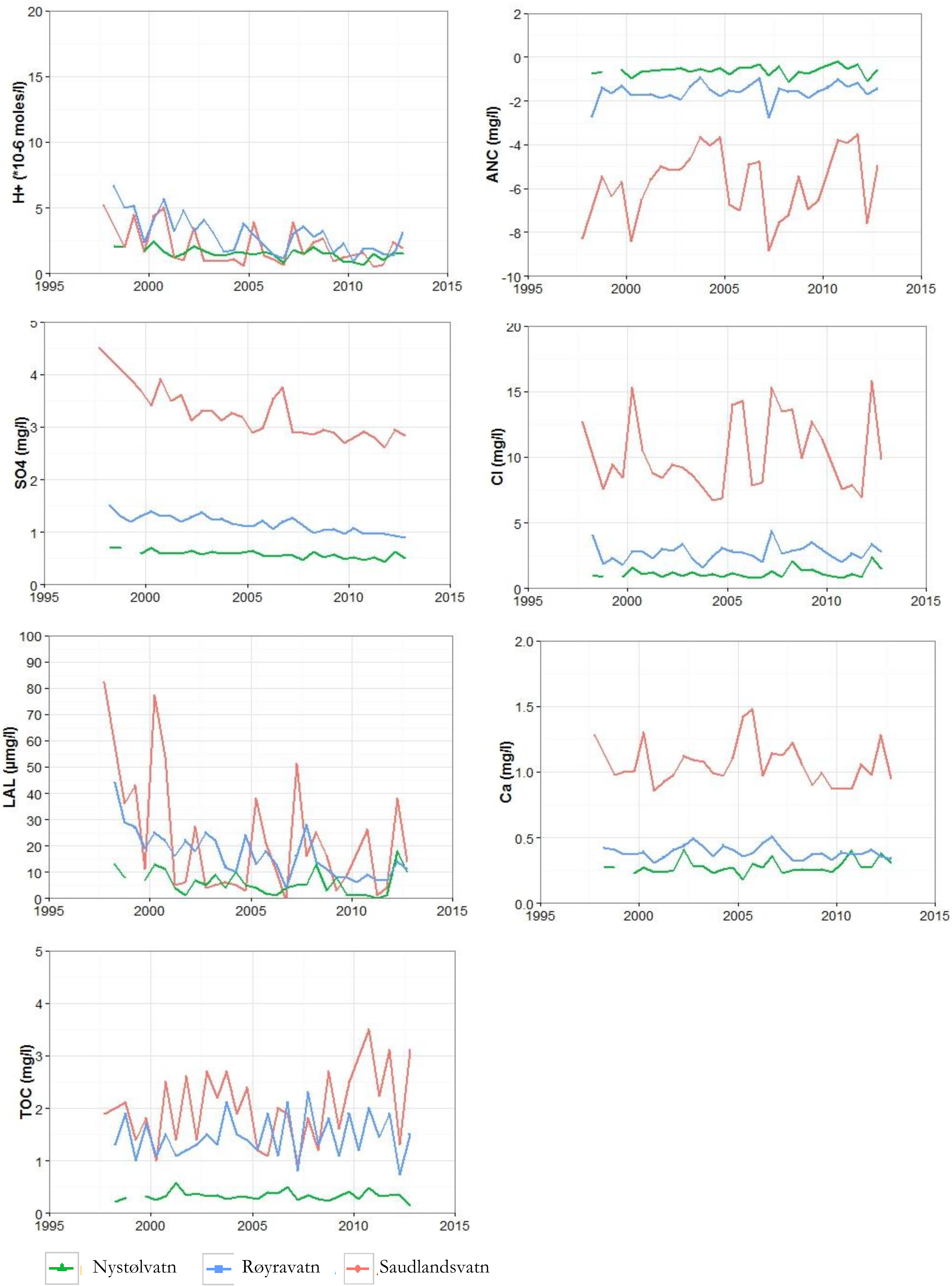

Figure 3: Chemistry variables in the lake sites: Nystølvatn=green, Røyravatn=blue, Saudlandsvatn=red. Displaying variables: H^+, Labile Aluminium (LAL), Acid Neutralizing Capacity (ANC), Chloride (Cl), Sulphate (SO_4), Calcium (Ca), and Total Organic Carbon (TOC)

Table 1: Spearman Rank Correlation matrix of environmental variables in river Gaular (N=29; year 1989-2003; upper panel) and lakes Nystølvatn (N=29; year 1998-2012; lower panel). Significance level of the two tailed tests reported as p<0.5 = *; p<0.01 = **. Strong negative correlation (r<-0.6) printed in red and strong positive correlation (r>0.6) printed in green.

River / **Lake**	H+	ANC	SO_4	Cl	LAL	Ca	TOC	Disch	Dep S	Dep Cl	Temp	Prec
H+		-0.82**	0.47**	0.77**	0.83**	-0.13	-0.25	-0.27	0.59**	0.75**	-0.39*	0.68**
ANC	-0.55**		-0.77**	-0.92**	-0.77**	-0.06	0.20	0.38*	-0.60**	-0.80**	0.51**	-0.78**
SO_4	0.61**	-0.69**		0.65**	0.65**	0.22	-0.03	-0.45*	0.58**	0.50**	-0.46*	0.59**
Cl	0.37*	-0.78**	0.35		0.62**	0.24	-0.06	-0.53**	0.36	0.90**	-0.63**	0.73**
LAL	0.69**	-0.71**	0.66**	0.57**		-0.13	-0.24	-0.25	0.71**	0.63**	-0.35	0.57**
Ca	0.00	0.31	-0.05	-0.08	0.06		0.60**	-0.39*	-0.32	0.14	-0.21	0.25
TOC	-0.43*	0.50**	-0.26	-0.42*	-0.40*	0.23		-0.02	-0.28	-0.16	0.05	-0.05
Disch	-	-	-	-	-	-	-		0.22	-0.52**	0.86**	-0.20
Dep S	-0.03	0.44*	-0.02	-0.56**	-0.29	-0.01	0.43*	-		0.33	0.15	0.53**
Dep Cl	0.25	-0.53**	0.31	0.60**	0.36	0.01	-0.08	-	-0.27		-0.64**	0.62**
Temp	0.26	-0.65**	0.55**	0.54**	0.35	0.02	-0.30	-	-0.43*	0.73**		-0.25
Prec	0.37*	-0.49**	0.32	0.46*	0.34	-0.12	-0.17	-	-0.16	0.78**	0.57**	

** ANC=Acid Neutralizing Capacity calculated as (Ca+Mg+K+Na) - (Cl+SO_4+NO_3); LAL= Labile Aluminum; TOC=Total Organic Carbon; Disch=Discharge; Dep S=Non-marine sulphur deposition; Dep Cl=Chloride deposition; Temp=Temperature; Prec=Precipitation.*

Table 2: Spearman Rank Correlation matrix of environmental variables in river Vikedal (N=42; year 1987-2012; upper panel) and lake Røyravatn (N=30; year 1998-2012; lower panel). Significance level of the two tailed tests reported as p<0.5 = *; p<0.01 = **. Strong negative correlation (r<-0.6) printed in red and strong positive correlation (r>0.6) printed in green.

River / **Lake**	H+	ANC	SO_4	Cl	LAL	Ca	TOC	Disch	Dep S	Dep Cl	Temp	Prec
H+		-0.78**	0.84**	0.39*	0.78**	-0.05	-0.34*	0.17	0.76**	0.36*	-0.14	0.06
ANC	-0.57**		-0.79**	-0.77**	-0.76**	-0.27	0.50**	-0.33*	-0.61**	-0.61**	0.34*	-0.30
SO_4	0.58**	-0.38*		0.34*	0.74**	0.22	-0.31*	0.00	0.81**	0.32*	-0.26	0.02
Cl	0.26	-0.82**	-0.04		0.36*	0.43**	-0.63**	0.51**	0.13	0.68**	-0.39*	0.50**
LAL	0.84**	-0.49**	0.68**	0.18		0.01	-0.24	0.09	0.74**	0.31*	-0.16	-0.04
Ca	-0.06	-0.07	0.32	0.03	0.07		-0.34*	-0.10	-0.07	0.13	-0.47**	0.20
TOC	-0.09	0.55**	-0.09	-0.46**	-0.16	-0.10		-0.44**	-0.22	-0.69**	0.52**	-0.45**
Disch	-	-	-	-	-	-	-		0.01	0.61**	-0.12	0.82**
Dep S	0.49**	-0.13	0.68**	-0.20	0.55**	0.04	0.03	-		0.27	-0.07	-0.04
Dep Cl	-0.15	-0.26	-0.07	0.28	-0.04	-0.15	-0.67**	-	-0.11		-0.50**	0.67**
Temp	0.07	0.10	0.02	-0.03	0.01	-0.10	0.67**	-	0.05	-0.65**		-0.23
Prec	-0.03	-0.37*	0.03	0.36	0.13	-0.09	-0.58**	-	-0.03	0.90**	-0.45*	

** ANC=Acid Neutralizing Capacity calculated as (Ca+Mg+K+Na) - (Cl+SO_4+NO_3); LAL= Labile Aluminum; TOC=Total Organic Carbon; Disch=Discharge; Dep S=Non-marine sulphur deposition; Dep Cl=Chloride deposition; Temp=Temperature; Prec=Precipitation.*

Table 3: Spearman Rank Correlation matrix of environmental variables in river Farsund (N=23; year 2000-2012; upper panel) and lake Saudlandsvatn (N=29; year 1997-2000; lower panel). Significance level of the two tailed tests reported as p<0.5 = *; p<0.01 = **. Strong negative correlation (r<-0.6) printed in red and strong positive correlation (r>0.6) printed in green.

River / **Lake**	H+	ANC	SO_4	Cl	LAL	Ca	TOC	Disch	Dep S	Dep Cl	Temp	Prec
H+		-0.68**	0.15	0.65**	0.94**	0.05	-0.29	0.38	0.06	0.46*	-0.08	0.43*
ANC	-0.70**		-0.13	-0.95**	-0.59**	-0.28	0.57**	-0.45*	0.11	-0.46*	0.24	-0.46*
SO_4	0.22	-0.04		-0.09	0.17	0.04	-0.14	-0.10	0.52*	-0.07	-0.19	-0.34
Cl	0.60**	-0.91**	-0.22		0.57**	0.33	-0.47*	0.40	-0.26	0.47*	-0.11	0.55**
LAL	0.95**	-0.67**	0.19	0.58**		0.10	-0.24	0.31	0.06	0.45*	-0.06	0.44*
Ca	0.13	-0.43*	0.01	0.48**	0.21		-0.55**	0.31	-0.28	0.16	-0.24	0.57**
TOC	-0.43*	0.72**	-0.06	-0.63**	-0.41*	-0.64**		-0.59**	0.02	-0.40	0.71**	-0.50*
Disch	-	-	-	-	-	-	-		-0.21	0.74**	-0.50*	0.58**
Dep S	0.09	0.01	0.71**	-0.24	0.09	-0.10	-0.08	-		0.00	-0.21	-0.32
Dep Cl	0.30	-0.37*	-0.13	0.38*	0.23	0.09	-0.59**	-	0.09		-0.37	0.43*
Temp	-0.12	0.10	-0.04	-0.08	-0.11	-0.03	0.47*	-	-0.31	-0.70**		-0.28
Prec	0.18	-0.30	-0.26	0.32	0.16	0.31	-0.62**	-	-0.03	0.71**	-0.59**	

** ANC=Acid Neutralizing Capacity calculated as (Ca+Mg+K+Na) - (Cl+SO_4+NO_3); LAL= Labile Aluminum; TOC=Total Organic Carbon; Disch=Discharge; Dep S=Non-marine sulphur deposition; Dep Cl=Chloride deposition; Temp=Temperature; Prec=Precipitation.*

APPENDIX 4: SEASONAL MANN-KENDALL TEST FOR ALL SAMPLE STATIONS

Table 1: Results of the Seasonal Mann-Kendall test of trends for the invertebrate indices in the river- and lake stations with seasons (spring and autumn) computed separately. The relative change (Rel. change) is the Sen slope divided by the mean. The significance level is reported as p<0.5=, p<0.01=**, p<0.001=***, and the p value is reported if not significant. Significant positive trends are reported in green, significant negative trends in red, and non-significant trends in black.*

	Richness all taxa		**Richness EPT taxa**		**Richness acid-sensitive taxa**		**% Ephemer-optera**		**% Plecoptera**		**% Trichop-tera**		**% EPT**		**% Acid-sensitive taxa**		**Diversity**		**Stability**	
	Rel. change (%)	p value	Rel. change (%)	p value	Rel. change (%)	p value	Rel. change (%)	p value	Rel. change (%)	p value	Rel. change (%)	p value	Rel. change (%)	p value	Rel. change (%)	p value	Rel. change (%)	p value	Rel. change (%)	p value
River Gaular (1987-2014)																				
Gau01	2.69	***	5.24	***	0.00	**	0.00	1.00	2.14	*	5.93	***	3.73	**	0.00	**	-0.87	0.24	1.30	*
Gau02	1.61	***	2.68	***	0.00	0.36	0.00	***	-1.16	0.45	5.63	***	0.57	0.66	-1.11	0.34	-0.89	0.20	0.75	0.10
Gau03	0.97	*	1.55	*	7.60	***	4.11	***	0.04	0.99	1.29	0.21	2.16	*	5.93	***	0.31	0.43	-0.08	0.81
Gau04	1.88	***	2.61	***	7.44	***	4.29	***	1.30	0.13	1.52	0.28	2.34	**	7.51	***	0.58	0.39	0.17	0.75
Gau05	1.93	***	2.52	**	8.33	***	4.86	***	-3.56	**	0.75	0.59	-0.01	1.00	5.28	***	-0.33	0.59	0.67	0.17
Gau06	0.40	0.30	0.00	0.27	3.14	***	1.42	0.27	-2.16	0.07	1.05	0.32	0.47	0.54	3.42	*	-0.97	*	0.60	0.29
Gau07	2.10	***	2.34	***	2.58	***	5.22	***	-0.56	0.49	0.00	0.97	1.53	*	5.11	***	0.91	0.19	0.39	0.42
Gau08	1.45	**	2.00	**	6.77	***	2.34	***	-0.90	0.32	0.00	0.80	0.89	0.20	3.89	***	0.75	0.30	-0.10	0.87
Gau09	2.08	***	3.13	***	6.72	***	0.00	*	0.93	0.30	3.22	*	1.58	*	5.71	***	1.43	*	-0.75	0.16
Gau10	0.88	0.22	0.79	0.26	6.73	***	2.37	*	3.42	**	2.84	0.08	4.20	***	6.50	***	0.17	0.88	-1.78	*
Gau11	1.50	***	1.73	***	4.09	***	5.52	***	-0.20	0.71	1.52	0.11	1.18	0.08	4.19	***	1.27	**	-0.73	0.21
Gau12	0.87	0.09	0.76	0.14	2.61	***	-0.65	0.53	-5.23	***	3.18	**	-0.03	0.99	-0.17	0.85	-1.91	**	0.99	**
Gau13	1.38	***	1.13	*	4.00	***	1.33	0.33	-1.92	0.15	2.96	***	0.50	0.64	3.95	**	-1.09	*	0.35	0.42
Gau14	0.37	0.31	0.00	0.66	6.16	***	0.00	0.18	2.98	*	0.33	0.77	3.54	**	5.87	***	0.02	1.00	-0.17	0.81
Gau15	1.32	**	1.89	***	5.02	***	3.72	***	1.48	0.33	-0.38	0.65	1.45	0.24	3.76	**	0.45	0.39	-0.63	0.25
Gau16	0.60	*	1.24	**	3.62	***	1.07	0.14	-1.35	0.18	1.52	0.05	0.71	0.13	2.59	*	-1.04	0.14	-0.23	0.56
Gau17	1.33	**	1.08	0.08	4.32	***	2.91	0.06	-2.85	*	-0.28	0.85	-0.58	0.43	3.18	*	-0.39	0.47	1.67	***
+ trend	**13**		**12**		**15**		**8**		**2**		**5**		**7**		**14**		**1**		**3**	
- trend	**0**		**0**		**0**		**0**		**3**		**0**		**0**		**0**		**3**		**1**	
no trend	**4**		**5**		**2**		**9**		**12**		**12**		**10**		**3**		**13**		**13**	

River Vikedal (1989-2014)																				
Vik01	1.39	***	1.46	***	4.03	***	6.94	***	-0.05	0.92	-0.13	0.87	2.04	***	6.54	***	0.50	0.21	1.08	*
Vik03	1.23	***	1.49	***	0.00	***	0.00	0.12	0.86	0.09	-2.03	*	0.51	0.20	3.74	***	-0.51	0.13	-0.08	0.85
Vik04	0.70	*	0.82	*	0.00	***	0.00	***	1.01	0.31	-2.08	0.06	0.85	0.13	0.00	***	-0.35	0.61	0.56	0.14
Vik05	1.29	***	1.78	***	7.27	***	4.26	***	2.12	*	-0.75	0.52	1.50	*	6.57	***	0.88	0.07	-0.31	0.47
Vik07	0.83	**	1.51	***	3.03	***	1.42	0.13	0.99	0.15	0.53	0.55	1.33	**	2.46	**	0.27	0.38	-0.14	0.61
Vik09	0.37	0.19	0.78	*	5.74	***	5.55	***	0.77	0.18	-2.17	*	2.39	***	5.40	***	-0.54	0.16	-0.10	0.78
Vik10	2.61	***	3.66	***	7.39	***	4.16	***	1.21	0.28	-1.20	0.26	-0.13	0.92	9.59	***	1.45	**	0.40	0.17
Vik11	1.31	***	1.78	***	9.26	***	8.81	***	-1.75	*	2.73	***	1.98	***	10.40	***	0.95	0.09	-0.19	0.47
Vik12	1.52	***	2.06	***	6.62	***	0.00	0.27	2.46	*	0.54	0.58	2.20	**	2.59	***	1.34	*	-0.65	0.13
+ trend	8		9		7		5		2		1		6		8		2		1	
- trend	0		0		0		0		1		2		0		0		0		0	
no trend	1		0		2		4		6		6		3		1		7		8	
River Farsund (1981-2013)																				
Far04	1.28	***	2.16	***	0.00	***	-0.70	**	4.59	***	-0.18	0.85	-0.20	0.76	0.00	***	0.49	0.26	0.14	0.78
Far05	0.00	0.27	1.92	***	6.10	***	-2.58	***	5.78	***	-0.65	0.36	0.49	0.45	5.00	***	-0.60	0.18	0.76	**
Far06	0.87	*	0.88	*	6.21	***	0.00	**	1.63	0.07	-1.61	0.06	-0.23	0.80	4.16	***	-0.73	0.15	0.62	0.06
Far07	0.82	*	1.68	***	6.63	***	-3.24	***	3.4	**	-0.86	0.19	-0.59	0.37	4.38	***	-0.68	0.24	0.51	0.13
+ trend	3		4		3		0		3		0		0		3		0		1	
- trend	0		0		0		3		0		0		0		0		0		0	
no trend	1		0		1		1		1		4		4		1		4		3	
Lake Nystølvatn (1997-2012)																				
Nys	0.00	0.22	0.00	0.30	0.00	1.00	0.00	1.00	0.00	**	5.92	0.12	-0.11	0.92	0.00	1.00	-2.95	*	1.84	**
Lakes Røyravatn (1998-2012) and Botnavatn (1987-2014)																				
Røy	0.00	0.45	4.46	*	0.00	0.61	4.43	*	1.76	0.30	0.00	0.54	4.31	0.07	0.00	0.47	0.58	0.51	-0.86	0.26
Bot	0.42	0.14	2.09	**	0.00	0.07	1.45	0.13	0.00	0.12	2.13	0.07	2.01	*	0.00	0.08	-0.23	0.71	-0.74	0.06
Lake Saudlandsvatn (1997-2012)																				
Sau	0.00	0.67	0.00	0.38	0.00	0.34	-4.13	0.17	0.00	0.20	0.00	0.89	-2.53	0.16	0.00	0.42	-3.85	**	0.66	0.40

APPENDIX 5: DETAILS CHANGE POINT ANALYSIS

Table 1: Overview Change Point Analysis of invertebrate indices. Indicating the moment of change with confidence-interval (season-year), confidence level that change took place (%), and the amount of change (from – to). Confidence level for inclusion in the table was 90% and confidence-interval was 95% (standard settings).

Location	Index	Moment of change	Confidence-interval		Conf. level (%)	From - to	
Gaular	Richness all taxa	autumn-1993	autumn-1990	spring-2003	94	11.4	14.0
		autumn-2003	autumn-2001	autumn-2007	100	14.0	19.0
	Richness EPT taxa	autumn-2003	spring-2001	autumn-2007	100	8.2	12.6
	Richness acid-sensitive taxa	autumn-2003	autumn-2002	autumn-2007	100	0.7	2.7
	% EPT taxa	autumn-1998	autumn-1989	autumn-2004	93	35.8	24.2
	% acid-sensitive taxa	autumn-2008	spring-2008	autumn-2014	100	2.3	17.8
	Stability	autumn-1994	spring-1990	spring-1995	94	0.6	0.7
		spring-1997	spring-1997	autumn-1997	94	0.7	0.3
		autumn-1998	spring-1998	autumn-1998	100	0.3	0.7
Vikedal	Richness all taxa	spring-1992	autumn-1991	spring-1996	95	16.9	13.8
		autumn-1996	autumn-1993	autumn-1997	99	13.8	18.5
		spring-2002	autumn-1999	autumn-2003	100	18.5	21.8
		autumn-2010	autumn-2003	autumn-2014	91	21.8	20.0
	Richness EPT taxa	autumn-1996	spring-1991	spring-1998	99	9.1	12.4
		autumn-2006	autumn-2001	spring-2012	95	12.4	14.4
	Richness acid-sensitive taxa	autumn-1996	spring-1994	autumn-1999	97	0.4	1.4
		autumn-2001	autumn-2000	autumn-2001	100	1.4	3.6
		autumn-2006	autumn-2006	spring-2010	99	3.6	4.9
	% EPT taxa	spring-2007	spring-2006	spring-2007	100	32.8	54.4
		autumn-2010	autumn-2010	autumn-2014	91	54.4	39.5
	% acid-sensitive taxa	autumn-1996	spring-1996	autumn-1999	100	0.5	4.1
		autumn-2001	autumn-2001	autumn-2002	100	4.1	13.8
		autumn-2008	autumn-2007	autumn-2008	98	13.8	25.8
	Diversity	spring-2007	spring-2006	autumn-2007	99	6.9	10.7
		autumn-2010	autumn-2009	autumn-2013	100	10.6	7.4
	Stability	autumn-1991	autumn-1991	autumn-1991	99	0.8	0.6
		autumn-1995	autumn-1993	autumn-1999	99	0.6	0.7
Farsund	Richness all taxa	autumn-1986	autumn-1983	spring-2002	98	9.1	12.0
		autumn-2002	spring-1999	autumn-2005	100	12.0	15.7
	Richness EPT taxa	autumn-1989	autumn-1987	autumn-1993	98	4.7	7.0
		autumn-1995	spring-1991	spring-1997	93	7.0	4.7
		autumn-2002	spring-2002	spring-2005	100	4.7	8.8
	Richness acid-sensitive taxa	spring-2004	autumn-2003	spring-2006	100	0.1	0.9
	%EPT taxa	autumn-1986	autumn-1983	autumn-1987	91	27.1	50.4
		autumn-1991	autumn-1990	spring-1992	100	50.4	26.5
		autumn-1997	spring-1992	autumn-1998	95	26.5	18.1
		autumn-2002	autumn-2002	spring-2008	100	18.1	34.7
	% acid-sensitive taxa	spring-2004	spring-2004	autumn-2008	100	0.2	5.6
	Diversity	spring-1998	spring-1992	spring-1998	93	4.8	2.6
		spring-2002	spring-2002	spring-2005	95	2.6	5.2
	Stability	autumn-1988	autumn-1983	autumn-1992	91	0.6	0.7
		autumn-2009	autumn-2008	autumn-2012	99	0.7	0.6
Nystølvatn	Richness all taxa	autumn-2005	autumn-2000	autumn-2010	92	7.1	5.8
	Diversity	autumn-2003	spring-1999	spring-2005	96	3.6	2.4
	Stability	spring-2007	autumn-1999	spring-2007	91	0.6	0.9

APPENDIX 6: REDUNDANCY ANALYSIS OF ALL SAMPLE LOCATIONS

Table 1: Unconstrained gradient in the invertebrate community analyzed by Principle Component Analysis (PCA), and Time constrained gradient with Season as covariate analyzed by the Redundancy analysis ($RDA_{\lambda time}$). The eigenvalues and percentage between-sample variance explained are reported for both analysis. The significance level of the $RDA_{\lambda time}$ was reported as p<0.5=*, p<0.01=**, p<0.001=, and the p value is reported if non-significant.***

		Gau 01	Gau 02	Gau 03	Gau 04	Gau 05	Gau 06	Gau 07	Gau 08	Gau 09	Gau 10	Gau 11	Gau 12	Gau 13	Gau 14	Gau 15	Gau 16	Gau 17
PCA	*Eigenvalue*	7.0	4.3	6.1	5.4	6.8	5.9	5.5	8.5	6.4	10.5	5.6	5.3	4.3	6.4	5.8	4.8	6.0
	% explained	35.9	22.3	24.5	19.0	25.7	23.3	24.1	26.2	23.0	26.6	20.7	27.8	17.5	25.8	23.6	20.2	21.1
$RDA_{\lambda time}$	*Eigenvalue*	2.3	2.5	2.7	3.7	3.6	3.2	1.8	1.9	1.4	4.6	3.1	3.4	3.3	2.7	2.1	2.3	3.3
	% explained	12.0	13.8	12.0	14.1	14.2	13.4	9.1	6.9	5.5	12.9	12.3	19.1	14.2	12.2	10.0	11.2	12.0
	p-value	***	***	***	***	***	***	***	**	**	***	***	***	***	***	***	***	***

		Vik 01	Vik 03	Vik 04	Vik 05	Vik 07	Vik 09	Vik 10	Vik 11	Vik 12	Far 04	Far 05	Far 06	Far 07	Nys	Røy	Bot	Sau
PCA	*Eigenvalue*	5.2	6.8	6.8	5.1	4.0	7.8	4.2	6.5	4.8	5.5	8.1	6.1	5.3	6.3	2.7	8.0	7.0
	% explained	19.7	26.2	26.3	19.7	18.6	28.3	20.0	28.9	19.9	19.5	28.2	26.3	20.6	34.3	31.1	36.7	32.1
$RDA_{\lambda time}$	*Eigenvalue*	3.8	5.1	1.5	2.7	1.7	3.1	2.9	5.2	2.7	2.1	5.3	2.8	3.1	2.3	0.9	1.4	1.5
	% explained	15.4	20.5	6.4	11.5	9.2	13.5	14.7	24.1	11.9	7.9	19.5	12.8	12.9	13.1	6.2	7.8	9.4
	p-value	***	***	***	***	***	***	***	***	***	***	***	***	***	***	*	**	***

Table 2: Linear regression between the relative abundance of each taxa and Time, showed which taxa were most influential in driving the community change. The threshold for inclusion in the table was set at >20% of between-sample variance explained by Time, which is based on Monteith et al. (2005). Green indicates an increase in relative abundance and red indicates a decrease in relative abundance. Acid-sensitive taxa are printed in bold.

	Gau01	Gau02	Gau03	Gau04	Gau05	Gau06	Gau07	Gau08	Gau09	Gau10	Gau11	Gau12	Gau13	Gau14	Gau15	Gau16	Gau17	Vik01	Vik03	Vik04	Vik05	Vik07	Vik09	Vik10	Vik11	Vik12	Far04	Far05	Far06	Far07	Bot	Nys	Roy	Sau	+ trend	- trend
Acari indet.		red		red		red						red				red	red				red	red	red		red						red	red	red		0	13
Agapetus ochripes													green				green																		2	0
Ameletus inopinatus						green																				green									1	0
Amphinemura borealis		green	green	green	green						green				green			green	green		green			green	green	green									12	0
Amphinemura sp.																		red																	0	1
Amphinemura sulcicollis																										green		green							2	0
Baetis rhodani	green	green	green	green		green				green							green			green		green	green	green											11	0
Bivalvia indet																														red					0	1
Capnia pygmaea				green																															1	0
Chironomidae indet.												green																							1	0
Coleoptera indet					green								green	green	green									green	green			red						red	6	2
Corixidae indet.																																		red	0	1
Crustacea indet.										green																									1	0
Diptera indet.														red						red												red			0	3
Diura nanseni						green																				green									2	0
Ephemerella aurivillii													green			green	green																		3	0
Erpobdella octoculata																																		green	1	0
Heptagenia sulphurea													green			green	green																		3	0
Hirudinea.indet.																												red		red					0	2
Hydropsyche pellicidula																								green	green										2	0
Hydropsyche siltalai													green												green	green	green	green	green						6	0
Hydropsyche sp.																								green											1	0
Hydroptila sp.													green											green											2	0
Isoperla grammatica			green				green	green	green	green	green		green	green		green	green	green				green			green										13	0
Isoperla sp.																red	red					red													0	3
Ithytrichia lamellaris																	green								green										2	0
Lepidostoma hirtum													green								green				green	green									4	0
Leptophlebia vespertina																												red							0	1
Leuctra digitata															green				green				green	green		green									5	0
Leuctra fusca																	red						red		red										0	3
Leuctra nigra						red																													0	1

Leuctra spp.																																			4	0
Nematoda indet.																																			0	9
Nemoura sp.																																			0	3
Nigrobaetis niger																																			1	0
Oligochaeta indet.																																			1	1
Ostracoda indet.																																			0	1
Oxyethira sp.																																			1	0
Pisidium sp.																																			2	0
Plectrocnemia conspersa																																			0	5
Polycentropus flavomaculatus																																			7	1
Protonemura meyeri																																			0	2
Radix balthica																																			1	0
Rhyacophila nubila																																			4	0
Sericostoma personatum																																			4	0
Simuliidae indet.																																			0	5
Positive (+) trend	2	3	3	4	4	4	1	1	2	3	3	3	10	2	3	4	9	2	3	1	2	3	2	7	7	6	3	4	2	1	0	1	0	1		
Negative (-) trend	2	2	0	1	1	3	0	0	0	1	0	4	3	3	0	3	3	1	1	1	1	3	3	1	5	0	0	4	1	3	1	2	2	3		

APPENDIX 7: NON-METRIC MULTIDIMENSIONAL SCALING

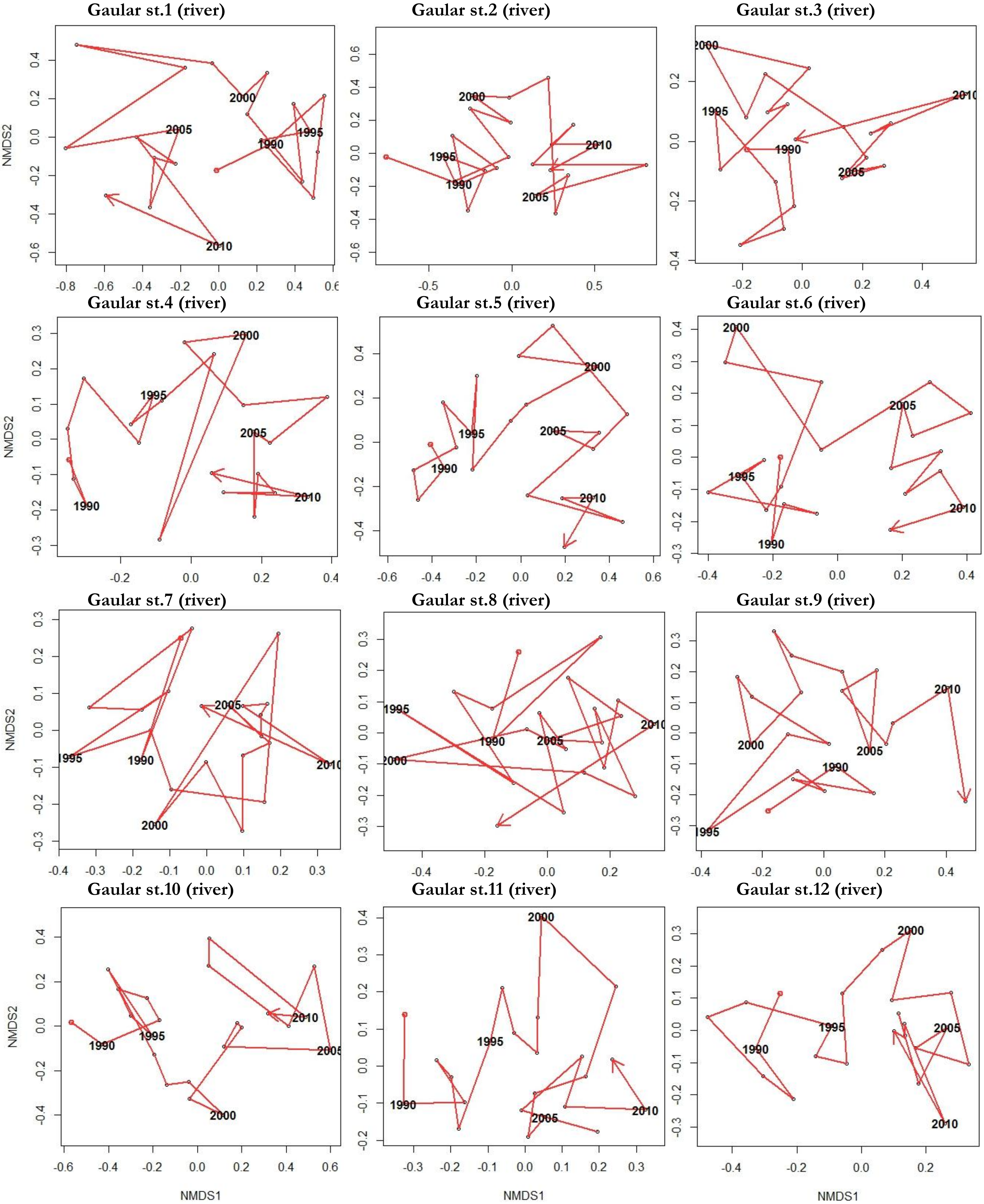

Figure 1: Non-metric multidimensional scaling (NMDS) of acid-sensitive invertebrates with time trajectories. The start of the monitoring period is indicated by a dot and the end is indicated by an arrow. Closely placed samples have similar species composition.

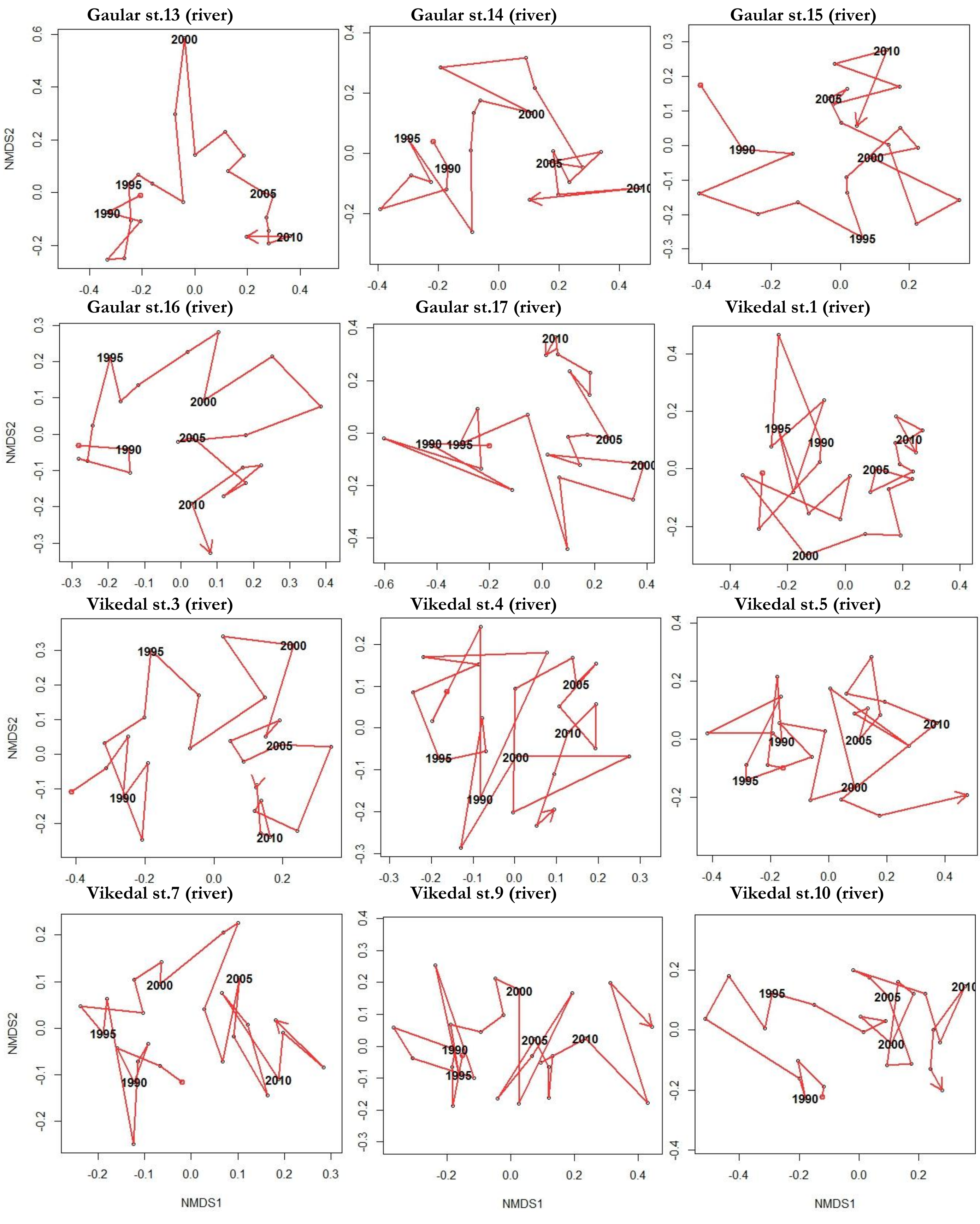

Figure 1 (continued): Non-metric multidimensional scaling (NMDS) of acid-sensitive invertebrates with time trajectories. The start of the monitoring period is indicated by a dot and the end is indicated by an arrow. Closely placed samples have similar species composition.

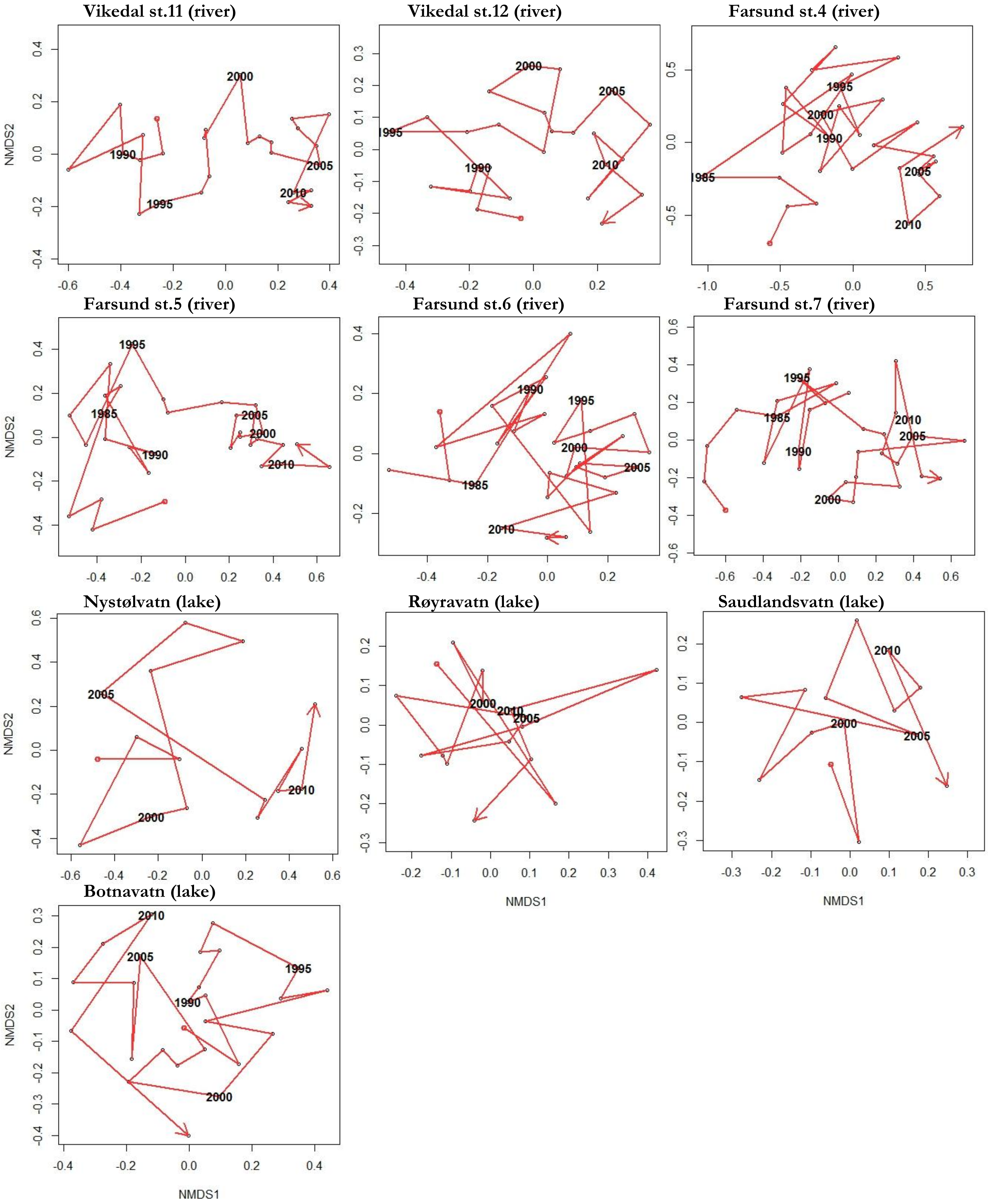

Figure 1 (continued): Non-metric multidimensional scaling (NMDS) of acid-sensitive invertebrates with time trajectories. The start of the monitoring period is indicated by a dot and the end is indicated by an arrow. Closely placed samples have similar species composition.