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Biodiversity of macro-invertebrates in acid-sensitive waters: trends and relations to water chemistry and climate

The international Cooperative Programme on Assessment and Monitoring Effects of Air Pollution on Rivers and Lakes (ICP Waters)
Convention on Long-Range Transboundary Air Pollution

LRTAP
Long-range Transboundary Air Pollution

CORRIGENDUM

Corrections to the electronic version of the ICP Waters Report 127/2016 Biodiversity of macro-invertebrates in acid-sensitive waters: trends and relations to water chemistry and climate (NIVA REPORT S.NO. 7077-2016)

Page 18: "Figure 9. Trends in quarterly air temperature, precipitation, SO4 and ANC for European river sites over the site-specific period covered by the biological data + denotes increase and – denotes decrease. Statistical significant trends are embedded in a grey circle." changed to "Figure 9. Trends in biodiversity in European rivers and lakes over the last 15 to 30 years (see Tables 1 and 2 for exact periods). + Increasing trend, – decreasing trend. Statistical significant changes in diversity are embedded in grey circles."

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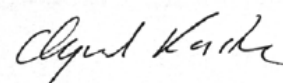
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Summary

This is a study of the international impact of acid emission reductions on vulnerable freshwater biodiversity of benthic macroinvertebrates. In order to properly attribute impacts it is necessary to also incorporate the potential effects of changes in temperature and precipitation. Most sites show an increasing number of species towards the present. This can be attributed to a decrease in acidification, while temperature has a secondary influence on diversity. We expect that the biodiversity will continue to increase in the future as acid deposition decreases. The widespread response of aquatic diversity resulting from emission reductions of acidifying components to the atmosphere demonstrates the potential of international policy for achieving positive effects on the state of the environment.

Four keywords		Fire emneord	
1.	Biodiversity	1.	Biologisk mangfold
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BIODIVERSITY OF MACRO-INVERTEBRATES IN ACID-SENSITIVE WATERS: TRENDS AND RELATIONS TO WATER CHEMISTRY AND CLIMATE

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Preface

The International Cooperative Programme on Assessment and Monitoring Effects of Air Pollution on Rivers and Lakes (ICP Waters) was established under the Executive Body of the United Nations Economic Commission for Europe (UNECE) Convention on Long-Range Transboundary Air Pollution (CLRTAP) at its third session in Helsinki in July 1985. UNECE is a catalyst in the international work aiming at reducing transboundary air emissions. Norway provides facilities for the ICP Waters Programme Centre at the Norwegian Institute for Water Research (NIVA). A programme subcentre was established at Uni Research. The Norwegian Environment Agency provides financial support to the work of the Programme Centre and with a representative leading the ICP Waters programme. In the long-term strategy for the Convention, adopted in 2010 by the Executive Body, it is stated that environmental effects of acidifying components, and its potential interaction with climate change and biodiversity, continue to be among the significant remaining problems with regard to air pollution effects on the environment. These can be addressed with the multi-pollutant/multi-effects approach of the Gothenburg Protocol.

The main aim of the ICP Waters Programme is to assess, on a regional basis, the degree and geographical extent of the impact of atmospheric pollution, in particular acidification, on surface waters. ICP Waters uses data from existing surface water biological and water chemical monitoring programmes in the participating countries, and the countries contribute to ICP waters voluntarily. The monitoring sites are generally acid-sensitive and representative of low acid-neutralising capacity (ANC) and low critical load levels. The ICP site network is geographically extensive and 30 countries in Europe and North America have partly or fully participated in the programme since its start. The Programme also promotes international harmonisation of monitoring practices. Harmonization practices include intercalibration of biological- and chemical monitoring. The participating countries submit chemical data to NIVA and biological data to Uni Research. The biological data has shown a general increase in the number of acid-sensitive taxa towards the present, indicating a recovery from acidification, in line with results from the chemical monitoring.

In this report we provide results from an extensive array of analyses on biological diversity with climatic and water chemistry drivers of the observed trends. The analysis includes about 1.8 million benthic macro invertebrates sampled from 89 European rivers and lakes collected between 1982 and 2014 at ICP Waters sites. In addition, data on water chemistry from the same sites and periods are included. Few, if any, comparable studies exist at this scale.

The report was prepared by ICP Waters subcentre in Bergen by lead Gaute Velle. Data was provided from Task Force members, and the results were discussed in several steps with the co-authors. We would like to thank all participating countries for data. In addition, we would like to thank those who contributed comments and suggestions to the draft report, especially Richard Wright, Heleen de Wit, Jens Fölster and Don Monteith.

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Bergen, August 2016

Contents

Summary

In this report, we provide results from analyses on the species diversity of benthic invertebrates from freshwater monitoring sites in the Czech Republic, Germany, Latvia, Norway, Sweden and the UK. The data includes about 1.8 million benthic macroinvertebrates from 5010 samples in 55 rivers and 34 lakes. The sampling periods cover between 12 and 29 years. In addition, data on water chemistry, precipitation and air temperature from the same sites and periods are included. The study sites were chosen as part of national monitoring programmes and most represent type-sites of nutrient poor waters that have been influenced by long-range air pollution leading to acidification. Our aim has been to find the impact of acid emission reductions on vulnerable freshwater biodiversity. In order to properly attribute impacts it is necessary to also incorporate the potential effects of changes in temperature and precipitation. To our knowledge, no comparable studies exist at this scale.

Increases in species diversity were found at 90% of the lake sites and 95% of the river sites, and with significant trends in 30% and 21% of the sites, respectively. With almost no exception, the concentration of sulphate decreased significantly. The air temperatures of most sites show increasing trends, albeit not significant for any sites during the period covered by the biological data. The amount of precipitation has increased significantly at 17% of the sites.

Most sites show a strong correlation between increasing diversity and a reduction in acidifying components. The pronounced increase in diversity at sites with the most pronounced chemical recovery and the strong correlation between sulphate and/ or ANC and diversity suggest that a reduction in acidifying components of the water has had a strong influence on species diversity of aquatic invertebrates. Most likely, sulphate and ANC have little effect on aquatic invertebrates, whereas pH and inorganic aluminium are the biological drivers.

Year-to-year variation in temperature was negatively correlated with diversity, suggesting that temperature has a secondary influence on diversity since the diversity is increasing, despite the negative correlation with temperature. The trends in warming for the periods we cover were not significant and therefore, cannot address effects from climate change. Still, the effects from temperature suggest that these communities will be sensitive to long-term climate change. There was a positive correlation between precipitation and species diversity for many river sites.

The strong correlation between acid components of the water and species diversity suggests that biodiversity will continue to increase when acid deposition decreases. However, environmental changes in the near future are expected to become less distinct for deposition and more distinct for climate, suggesting that aquatic invertebrate communities may experience stronger impacts from climate in the year to come.

The study has demonstrated that species diversity is a useful metric to accompany the acidification indices in monitoring of benthic invertebrates of acid sensitive sites, and for detection of temperature effects on biodiversity. The widespread response of aquatic diversity resulting from emission reductions of acidifying components to the atmosphere demonstrates the potential of international policy for achieving positive effects on the state of the environment.

1 Introduction

Biological diversity, or biodiversity, refers to the variety and variability of life on earth. Biodiversity as a term may include many aspects that describes the variability of life-forms, such as the variation of a specific gene within a species, the number of species at a site, the evenness of species within an ecosystem or the diversity of ecosystems in a landscape (Purvis and Hector, 2000; 2005). Earth's biodiversity has changed greatly since the initial colonisation of the land. Natural phenomena have caused five mass extinctions with an estimated 75% or more loss of species during the last 540 million years (Barnosky et al., 2011). In addition, many smaller extinction events have caused a decrease in species diversity (Zhu et al., 2006). Typically, a recovery from such events takes about 10 million years (Erwin, 2001; Kirchner and Weil, 2000). We are now facing the sixth mass extinction with an extinction rate of species that is 100 to 1000 times greater than normal background rates (Rockstrom et al., 2009; UN, 2005; Williams et al., 2015). No doubt, humans are directly or indirectly responsible for much of this most recent decline in species.

The loss of species is alarming since biodiversity has important consequences for ecosystem processes. All organisms perform functions in an ecosystem. A 'healthy' ecosystem can be defined as a system where all ecosystem functions are maintained at a natural rate. The loss of species, and also shifts in relative abundance, may halt or speed up certain ecosystem processes and cause changes that may influence the ecosystem and the ecosystem-services crucial for human well-being (Chapin Iii et al., 2000; Hooper et al., 2005).

Freshwater bodies are especially impacted by human perturbations, and freshwaters may be the most endangered ecosystems on Earth (Dudgeon et al., 2006; Sala et al., 2000). The major types of stressors that may combine to affect freshwater ecosystems adversely include over-exploitation, (water) pollution, habitat degradation, species invasion and flow modification (Dudgeon et al., 2006). Successful management of impacted ecosystems involves separation of natural phenomena from human-induced perturbations. We need to understand how biodiversity and ecosystem function have responded to past and present human influence (Condamine et al., 2013; Stendera et al., 2012). Only then can we mitigate for human influence and make predictions on the impact of future change (e.g., Markovic et al., 2014).

This is a study of the international impact of acid emission reductions on vulnerable freshwater biodiversity of benthic macroinvertebrates. In order to properly attribute impacts it is necessary to also incorporate the potential effects of changes in temperature and precipitation.

1.1 Acid deposition and effects on freshwater biota

Paleolimnological studies indicate that the pH started to decrease in surface waters already in the mid-nineteenth century, both in northern Europe and in North America (Battarbee and Charles, 1986). Surface water acidification has subsequently represented one of the major perceived drivers of biodiversity loss, as a consequence of the toxic effects of elevated hydrogen and aluminium ions particularly of a range of acid sensitive organisms. It is hard to assess the full biological impact of acidification since very few biological records exist to inform on the biological and ecological quality of surface waters prior to anthropogenic acidification. Acidification monitoring programmes were initiated only after belated recognition of the effects of acid deposition and rarely started before the 1980's. At that time, susceptible waters were heavily impacted by acidification, and the primary driver, sulphur deposition, had already peaked in most regions of concern. Declining fish populations in dilute lakes and streams were reported from the beginning of the 20th century in Norway and Sweden, and from the mid-20th century in Canada and the United States (Schofield, 1976). Detrimental effects on benthic invertebrates likely began prior to the effects on fish since some invertebrates are more sensitive than fish (Raddum et al., 1984). The threats to freshwaters accelerated during the second half of the last century, when the influence of acidification initiated biodiversity loss and alterations of ecosystem processes (Schindler, 1988).

During the last 30 years, surface water chemistry and biota have been monitored in national programmes, initiated through international cooperation such as the Convention on Long-range Transboundary Air

pollution (CLRTAP) to assess the environmental and ecological impact of emissions of sulphur and nitrogen species to the atmosphere. Monitoring programmes indicate a reduction in atmospheric pollution since the late 1980's (Garmo et al., 2014; Stoddard et al., 1999) resulting in improved water quality and ecological state in a broad range of geographical areas (Evans et al., 2001; Halvorsen et al., 2003; Hesthagen et al., 2011; Johnson and Angeler, 2010; Lento et al., 2012; Monteith et al., 2005; Stendera and Johnson, 2008). However, evidence for associated recovery in biodiversity has, to date, remained largely equivocal (Angeler and Johnson, 2012; Lento et al., 2012; Monteith et al., 2005; Murphy et al., 2014). The influence of reducing the acidity of acidified waters on biodiversity and ecosystem function is particularly poorly understood (Johnson and Angeler, 2010; Ledger and Hildrew, 2005) and it remains unclear whether chemical recovery will lead to a return of biodiversity and ecological states similar to those of pre-acidified conditions or, whether alternative states will emerge. The role of a changing climate also remains unclear.

1.2 Climate change and effects of temperature and precipitation on the biota

The term "climate" normally refers to prevailing weather conditions for a region averaged over multiple years. Globally averaged combined land and ocean surface temperature have increased by 0.85 °C (0.65 to 1.06) over the period 1880 to 2012, the period over which multiple independently produced datasets have been available (IPCC, 2013). In mainland Europe, the temperature increase varies by region and season. Given a scenario for the next 50-100 years of 2°C global warming, the temperature increase during winter is expected to be largest (about 3-3.5°C) in Northern Fennoscandia available (Vautard et al., 2014). During summer, temperature increases are expected to be largest in southern Europe (about 2.5°C). Large parts of northern and central Europe are expected to experience a substantial increase in precipitation (up to 50%) during winter. During summer, the amount of precipitation is expected to increase in Fennoscandia and to decrease in southern Europe. In northern regions, diurnal temperatures ranges have changed as a consequence of minimum temperatures are increasing about twice as fast as the maximum daily temperatures (Easterling et al., 1997). As a result, periods with sub-zero temperatures are shorter causing decreased snow cover and ice extent.

Past changes in climate have been major drivers of speciation and extinctions (Mayhew et al., 2012; Sahney et al., 2010) and temperature is generally considered to be one of the main mechanisms determining species distribution patterns (Parmesan and Yohe, 2003; Quist et al., 2004). This is because many biological rates are temperature-dependent and temperature has a major impact on ecological processes (Brown et al., 2004). Warmer water temperatures will speed up physiological processes (Buisson et al., 2012; Parmesan and Yohe, 2003), and could cause variations in the number of generations a population of a species produces per year (Knell and Thackeray, 2016; Raddum et al., 2008), species replacements (Sweeney, 1984; Velle et al., 2010b), a shift in competitive advantages of communities (Isaak and Hubert, 2004) and changes in the relative timing of life cycles of species occupying different trophic levels (Thackeray et al., 2016). Thermal regimes also indirectly govern the habitat since temperature is a key factor for processes within lake, stream and terrestrial ecosystems.

In sum, the result will be altered relative abundances of taxa and altered species diversity. However, the direction and rate of change in biodiversity caused by the present climate change is known only to some extent (Heller and Zavaleta, 2009; Mantyka-pringle et al., 2012). We can expect the most pronounced changes in biodiversity to occur where the warming is large, such as in high latitudes on the Northern hemisphere, and the smallest changes in biodiversity to occur where the warming is small, such as the mid-southern hemisphere. It is difficult to assess the influence that precipitation has on biodiversity in freshwaters since the effects are not direct, unless availability of water is a limiting factor or causes flooding. In addition to direct impacts of flow, such as scouring energy, changes in precipitation may affect habitat and water quality, particularly with respect to the frequency and intensity of acid episodes.

1.3 Aims of study

The high quality biological and chemical data available from the national monitoring networks participating in ICP Waters cover a period of major reductions in acid deposition. This provide conditions

for a hemispheric-scale natural experiment with which to assess, for the first time, the impacts of emission reductions on freshwater biodiversity, and the possible confounding or amplifying effects of climate change. In the present study, we have used extensive monitoring data on benthic macro invertebrates (Figure 1.) and water chemistry in streams and lakes sampled from mid-1980s and to 2014. These data are supported by estimates of average monthly modelled air temperature and precipitation for the 0.5° x 0.5° grid squares within which each site occurs, to provide some control for possibly influential long-term change in either water temperature or flow. Participating countries in this study include the Czech Republic, Germany, Latvia, Norway, Sweden and the UK. All countries participate in both hydrochemical- and macro-invertebrate intercalibrations that ensure international comparability of methods and taxonomy.

Our primary aims have been to:

1. Identify significant trends in the species diversity of benthic macroinvertebrates from the beginning of the monitoring period and to the present
2. Test, and quantify, the extent to which such biological changes can be explained by changes in water chemistry, temperature and precipitation

In this study, we have used the species richness of Ephemeroptra, Plecoptera and Trichoptera, so-called EPT-taxa (hereby referred to as species diversity) as a measure of diversity. We have chosen to include EPT-taxa only and not the full species assemblage since the taxonomic resolution is generally to species level for EPT, whereas most other taxa are identified at a coarser taxonomic resolution. We can expect the response curves to environmental variables to be narrower for individual species than for a coarser taxonomic entity, thereby reducing noise. EPT taxa are known to be sensitive to acidification (Raddum et al., 1988; Raddum and Fjellheim, 1995), in addition to other pressures, e.g. organic pollution.
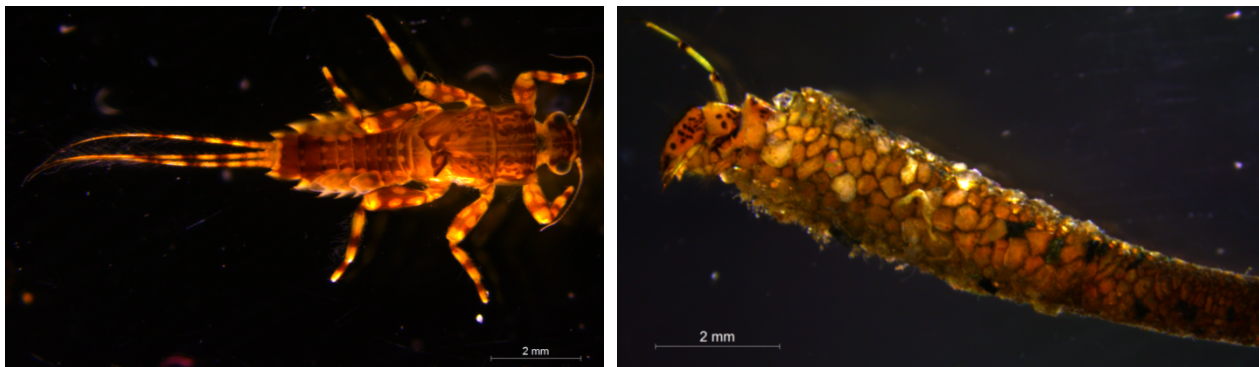

Figure 1. Benthic invertebrates from Norwegian rivers. From left to right the mayfly *Ephemerella aurivilli* and the caddisfly *Athripsodes aterrimus*. Photos by G. Velle (Uni Research).

2 Methods

2.1 Study sites

Our study sites include lakes and rivers from the Czech Republic, Germany, Latvia, Norway, Sweden and UK (Table 1 and 0). The data were collected between 1982 and 2014 and includes about 1.8 million benthic macro-invertebrate individuals from 3671 samples in 53 rivers and 1570 samples in 34 lakes (Table 1, Table 2, Figure 2). In addition, the data include about 26 000 samples of water analysed for chemistry. The sites form part of national biological- and chemical monitoring programmes in running and standing freshwaters (Halvorsen et al., 2002; Horecký et al., 2002; Horecký et al., 2006; Horecký et al., 2013; Johnson and Goedkoop, 2007; Kernan et al., 2010; Schaumburg et al., 2008).

Table 1. Samples from rivers with number of biological samples, number of sub-samples, average sample size, number of paired chemistry samples and sampling period. All biological samples have been taken by kick-sampling. *The Norwegian rivers include a total of 59 sampling stations. Full details on the sites are given in Velle et al. (2013).

	Number of Rivers	Biological samples	Sub-samples	Average sample size	Chemical samples	Sampling period
Czech Republic	3	35	1	1102	117	1999-2011
Germany	28	1037	1	NA	7863	1982-2010
Latvia	2	48	1	150	302	1997-2014
Norway	3*	2181	1	217	2316	1987-2014
Sweden	6	104	5 or 6	236	2580	1985-2014
UK	11	266	3 or 5	1312	3015	1988-2013

Table 2. Samples from lakes with number of biological samples, number of sub-samples, average sample size, number of paired chemistry samples and sampling period. Note that the Swedish littoral, sublittoral and profundal samples were taken from the same seven lakes. Grab samples were taken by use of an Ekman grab. Full details on the sites are given in Velle et al. (2013).

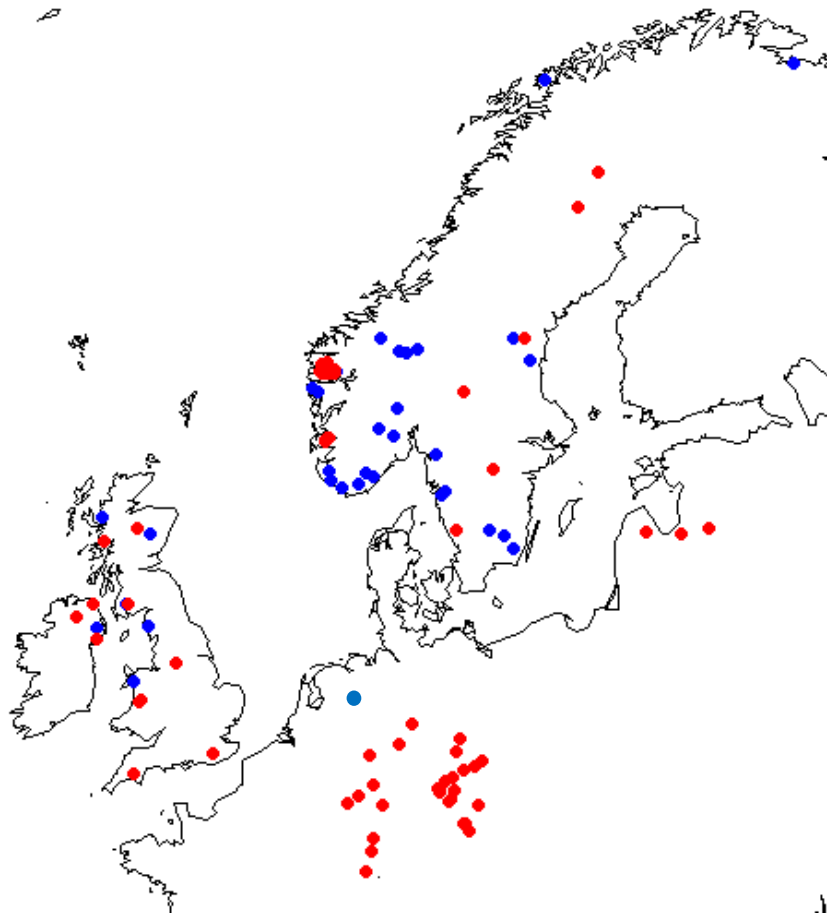|	Lakes	Biological samples	Sub-samples	Sampling method	Average sample size	Chemical samples	Sampling period
Germany	1	37	1	Kick	NA	1179	1997-2009
Norway	20	473	1	Kick	282	3051	1997-2013
Sweden littoral	7	284	5	Kick	195	1905	1986-2013
Sweden sublittoral	7	261	5	Grab	227	1650	1989-2013
Sweden profundal	7	357	5	Grab	183	1636	1986-2013
UK	6	158	3-7	Kick	442	600	1988-2013

Figure 2. Sampling sites. Red dots denote rivers and blue dots denote lakes. *There are a total of 112 sampling sites in rivers and 48 sampling sites in lakes.*

The chemical sensitivity of catchment bedrock varies among sampling regions, but apart from Latvia, most sites are in acid-sensitive bedrock consisting of gneiss, granite or quartzite. The Latvian sites are situated on claystone including smaller fractions of dolomite and gypsum. The northernmost catchments are characterised by boreal vegetation, while the southernmost sites are situated in cool temperate vegetation. Some of the sites, especially in Germany and Latvia, are in small stands of forest surrounded by farmland.

Figure 3. Sampling for benthic invertebrates in Norwegian rivers. Photo by G.Velle (Uni Research).

Most invertebrates were collected by kick sampling (Figure 3) Figure 3. (Frost et al., 1971), following the ICP Waters manual (Wathne et al., 2010). In this procedure, the substrate is disturbed and collected in a 0.25 mm mesh net. An Ekman grab was used in the Swedish sublittoral- and profundal lake sites. The sampling interval varied among sites and years with an average of about 1.5 samples per sampling station per year from the time most monitoring programmes opened in 1987 and up to the present. Each sample was sorted under a stereo microscope in the laboratory, and macroinvertebrates subsequently identified. The consistency of the taxonomic resolution through the 30-year sampling period was checked and corrected for by methods described in Velle et al. (2013). In short, data from sites with inconsistent taxonomic resolution were reduced to a coarser taxonomic level prior to numerical analysis.

Chemical variables include pH, conductivity, alkalinity, calcium (Ca^{2+}), magnesium (Mg^{2+}), potassium (K^+), sodium (Na^+), chloride (Cl^-), sulphate (SO_4^{2-}), total nitrogen (TotN), nitrate (NO_3^-), total organic carbon (TOC), hydrogen (H^+) and labile aluminium (LAL). Acid-neutralizing capacity (ANC) was calculated as $(Ca+Mg+Na+K+NH4) - (Cl+SO4+NO3)$ with units in µEq/l. For a detailed description of measured water chemistry, see Skjelkvaale and de Wit (2011).

Climate variables include monthly data for total precipitation, mean daily minimum air temperature, mean daily maximum air temperature and mean average daily air temperature. These are modelled gridded data for the 0.5-0.5 degree grid cells within which each site is located, obtained from the Climate Research Unit CRU TS3.21 (Harris et al., 2014). The data covers the period 1901-2014 and is modelled from measurements provided by national meteorological networks. In the absence of direct measurements of water temperature, we use air temperature as a surrogate. The relationship between water and air temperature is, however, by no means straightforward. As a general rule of thumb, water temperatures tend to vary spatially and seasonally in a similar manner to air temperatures, as the energy balance of both media is dominated by a similar set of factors (Layden et al., 2015; Livingstone and Lotter, 1998; Toffolon et al., 2014). However, factors such as riparian shading, effects of ice cover, snowmelt and thermal stratification etc., can also lead to significant differences in both space and time.

2.2 Numerical analyses

We first tested for linear trends in species diversity for the sites and periods covered by the biological data, and then tested for correlations between environmental variables and species diversity. Several environmental variables are presently changing concurrently in European freshwaters. The major potential drivers at the sites in this database are acid deposition (Stoddard et al., 1999; Velle et al., 2013) and climate (IPCC, 2013). The sites were specifically chosen to be free from pollution by nutrients (eutrophication).

As a consequence of the dominant effect of deposition chemistry on these systems, temporal variation in many of the chemical variables measured in water are closely correlated, such as some major ions, and some chemical variables are derivatives of others, such as alkalinity and pH. In addition, not all chemical variables were measured at every site. In order to reduce collinearity and noise, we retained sulphate (SO_4), acid neutralizing capacity (ANC), mean monthly air temperature and precipitation in the analyses of environmental drivers. ANC is the overall buffering capacity against acidification and effects from acid rain, and sulphate is the main acidifying component of acid rain. Both chemical variables have previously been found to correlate with diversity.

Biological sensitivity to acidification or climate varies according to site and region (Moe et al., 2010; Raddum and Skjelkvale, 2001). We can also expect that the response to acidification may override the response to climate for sites with a dominating change along the acidification axis. Hence, in an attempt to reduce noise and ease interpretation of results, the sites were clustered into four groups based on likely sensitivity to acidification. Here, pH 5.5 was chosen as clustering basis since the inflection point in the titration curve of pH versus ANC is at pH 5.4-5.6 (Figure 4). A small change of ANC in this pH region will cause a large change in pH. The clusters of sites are:

Group 1. All sites
Group 2. Sites where pH always has remained above 5.5 (least acidified sites)
Group 3. Sites where pH has crossed 5.5 one or multiple times (transition sites)
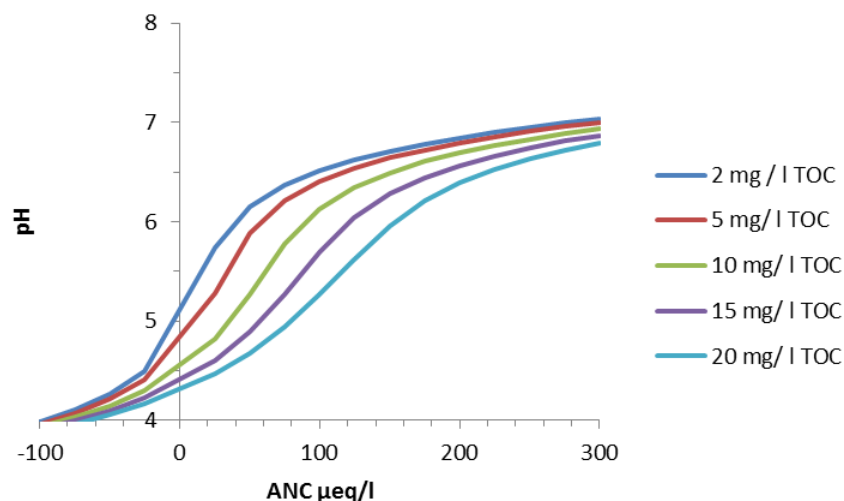Group 4. Sites where pH always has remained below 5.5 (acidified sites)

Figure 4. The change in pH given changes in ANC in freshwaters. Shown are the theoretical curves for several levels of TOC in the water calculated assuming pCO_2 of four times atmospheric and negligible concentrations of labile aluminium (after Fölster et al., 2007).

Biological data inevitably involves noise and random effects, such as clustering of species and specimens within the habitat and changes in species identification (taxonomy) through time. Also, separating the influence of multiple environmental variables on the biological communities is challenging since the effects can overlap and or/ be cumulative and/ or be masked and distorted by each other or confounding variables. Other numerical pit-falls include (1) auto-correlation, (2) pseudo replication, (3) difference in

time-scales, or sampling interval, (4) un-known delayed response in the biological communities where animals sampled at a certain time have not responded to the chemical and climate variables at this time but rather at a previous unknown time, and (5) multiple testing.

In an attempt to correct for potential pit-falls, we have used Markov Chain Monte Carlo generalized mixed effects model (MCMCglmm; Hadfield, 2010), which is a method for analysing multi-responses in the family of Bayesian statistics. MCMCglmm allows the incorporation of random effects, such as site and country, which are sources of pseudo-replication and local effects (Bolker et al., 2009). In addition, the data used in this study have significant over dispersion (residual deviance/degrees of freedom > 2), which can be accounted for using MCMCglmm (Hadfield, 2010). We used an indiscriminate priori that results in approximations similar to the Laplace approximation used in other mixed modelling packages. The model included fixed and random effects and a Poisson distribution, and assumed linearity, but not necessarily a straight line. Interaction among explanatory variables was not tested directly. However, the analysis quantifies the effect of specific explanatory variables on species diversity individually, while taking into account variation in other potentially important variables.

We chose $p < 0.05$ as the determinate of statistical significance. All numerical analyses were performed in R (R development core team 2010) using several statistical packages (RODBC, vegan, maps, mapdata, mgsv, MASS, MCMCglmm and nlme). Data analyses were done in three steps:

Step 1. Quantify trends and significant changes in species diversity over the sampling period covered by the biological data.

First, we calculated the species richness (N) of Ephemeroptera, Plecoptera and Trichopthera (our biodiversity metric) for all samples and all available seasons at all sites. Then, linear trends in diversity for each were assessed by use of linear mixed effect models (lme) with random intercept and slope, and tested for statistical significance. The species diversity trends (negative or positive) for each site were also plotted on a map.

Step 2. Quantify trends and significant changes in environmental data

Because environmental variables did not always occur at the time of biological sampling, we calculated the mean environmental condition over the quarter in which biological sampling took place (Q1: January – March, Q2: April – June, Q3: July – September, Q4: October – December). Trends in environmental variables were analysed by using the mean quarterly environmental value across the time span covered by the biological data at the site and with lme with random intercept and slope to test for significant changes.

Step 3. Test for correlations between environmental variables and species diversity

In order to investigate the relationships between species diversity and environmental variables, we analysed the correlation between species diversity and ANC, sulphate, temperature and precipitation. The two rivers from Latvia were excluded from this analysis because they are considered non-sensitive towards acidification and have a very high ANC compared to the other sites. In the analyses, we used a MCMCglmm, with: $N_g \sim ANC_g + SO4_g + Precipitation_g + Temperature_g$ where the subscript g denotes the pH-group.

3 Results

3.1 Environmental variables

The analyses were performed on all sites (Group 1) and on sites split into one of three pH classes (Groups 2-4) (Figure 5 and Figure 6). Water pH increased significantly during the sampling period at most sites (Table 3), while pH fluctuated more in rivers than in lakes. Most sites showed significant decreases in the concentration of SO_4 during the last 30 years, while ANC increased at most sites (Figure 7 and Figure 8). Mean quarterly air temperatures did not increase over the period covered by the biological data in any of the grid cells in which sites were located (Figure 7 and Figure 8). Eight of the 38 lake sites and 8 of the 54 river sites were situated in cells where quarterly precipitation increased.

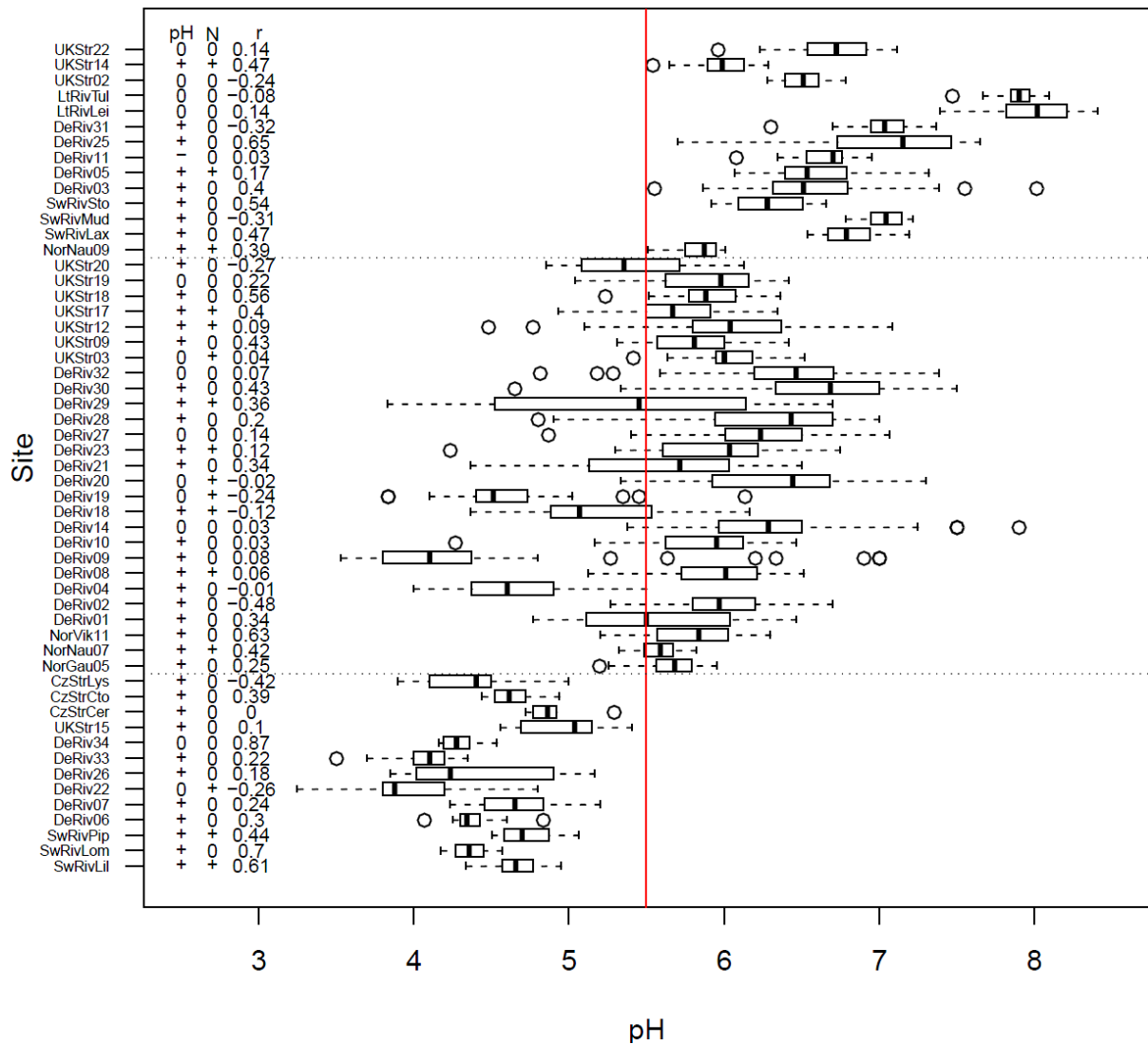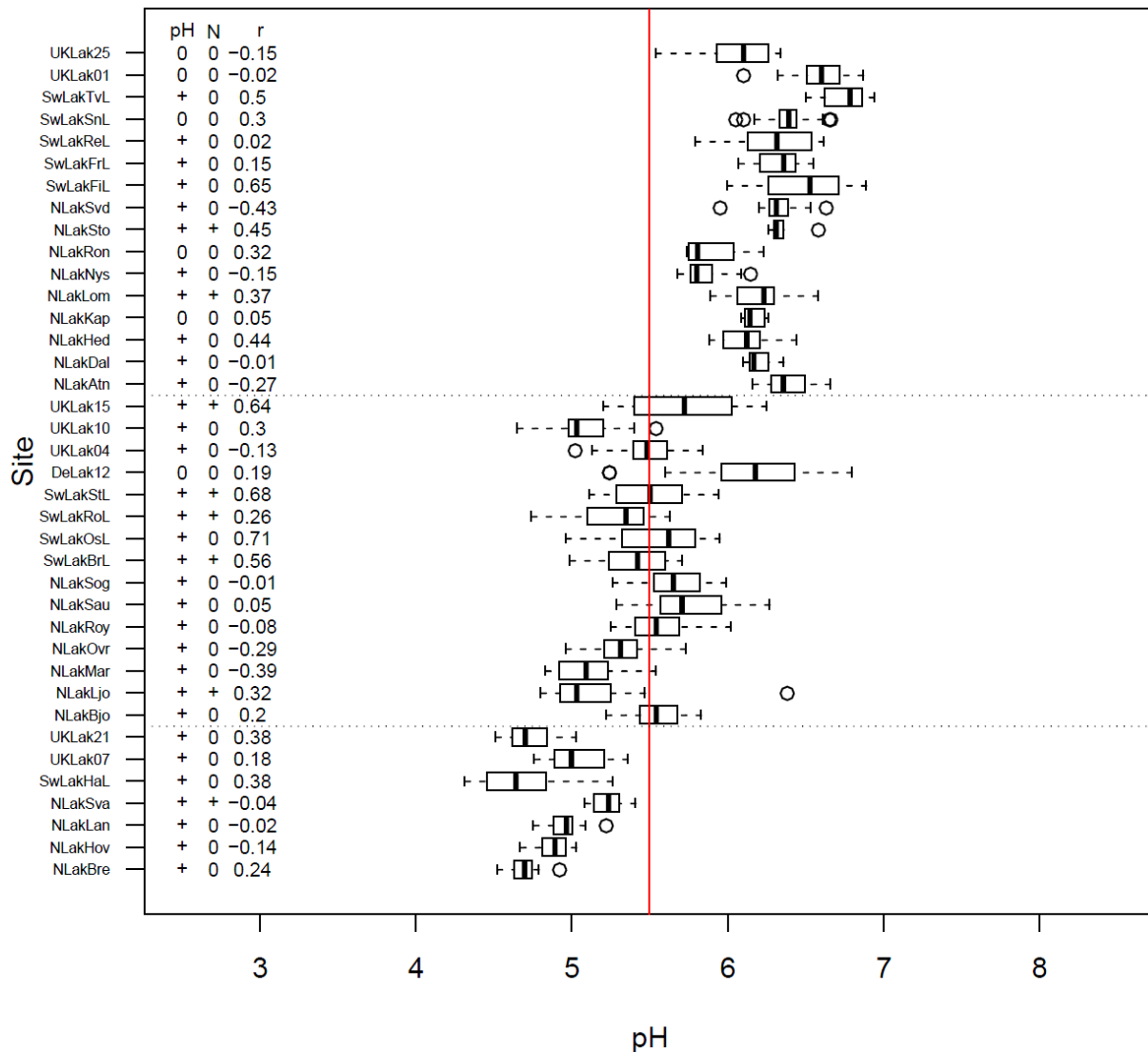**Figure 5.** All river sites are divided into four groups based on their pH-range. Group 1 are all sites, Group 2 are sites where pH < 5.5, Group 3 are sites where pH has crossed 5.5 and Group 4 are sites where pH > 5.5. The columns on the left hand side indicate sites with a significant (p<0.05) increase (+), decrease (-) or no change (0) in pH and species diversity (N).

Figure 6. All lakes are divided into four groups based on their pH-range. Group 1 are all sites, Group 2 are sites where pH < 5.5, Group 3 are sites where pH has crossed 5.5 and Group 4 are sites where pH > 5.5. The columns on the left hand side indicate sites with a significant (p<0.05) increase (+), decrease (-) or no change (0) in pH and species diversity (N), and the correlation between pH and N.

3.2 Species diversity

Most sites show a positive trend in the number of EPT taxa (N) over time (Figure 9). The species diversity increased at all river sites, except three, and at all lake sites, except six. The increase was statistically significant in 30% of the river sites and 21% of the lakes. There was a non-significant decrease in diversity in one river and six lakes. A larger fraction of sites within the group deemed to be sensitive to acidification (Group 3) showed a significant increase in diversity compared to the other groups (Table 3, Figure 10). Diversity also increased significantly at some of the sites deemed to be least influenced by acidification (Group 2), but only at sites where there has been a significant increase in pH (Figure 5 and Figure 6). It should be noted that while a relatively smaller proportion of Group 2 rivers and lakes showed significant trends, this still amounted to around two thirds of all sites in these groups.
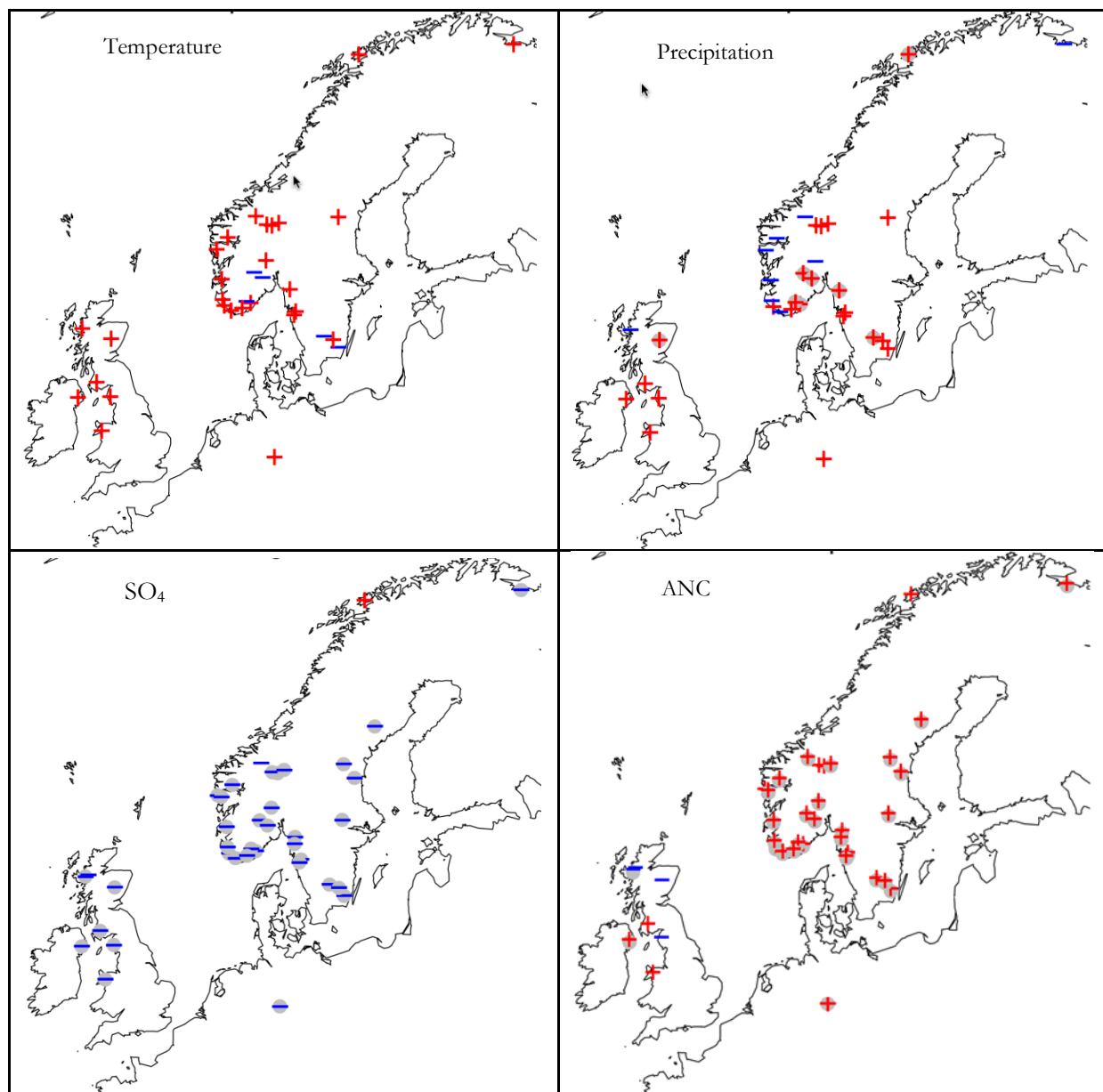
Figure 7. Trends in quarterly air temperature, precipitation, SO₄ and ANC for European lakes over the site-specific period covered by the biological data. + denotes increase and – denotes decrease. Statistical significant trends are embedded in a grey circle.

Figure 8. Trends in quarterly air temperature, precipitation, SO4 and ANC for European river sites over the site-specific period covered by the biological data. + denotes increase and – denotes decrease. Statistical significant trends are embedded in a grey circle.
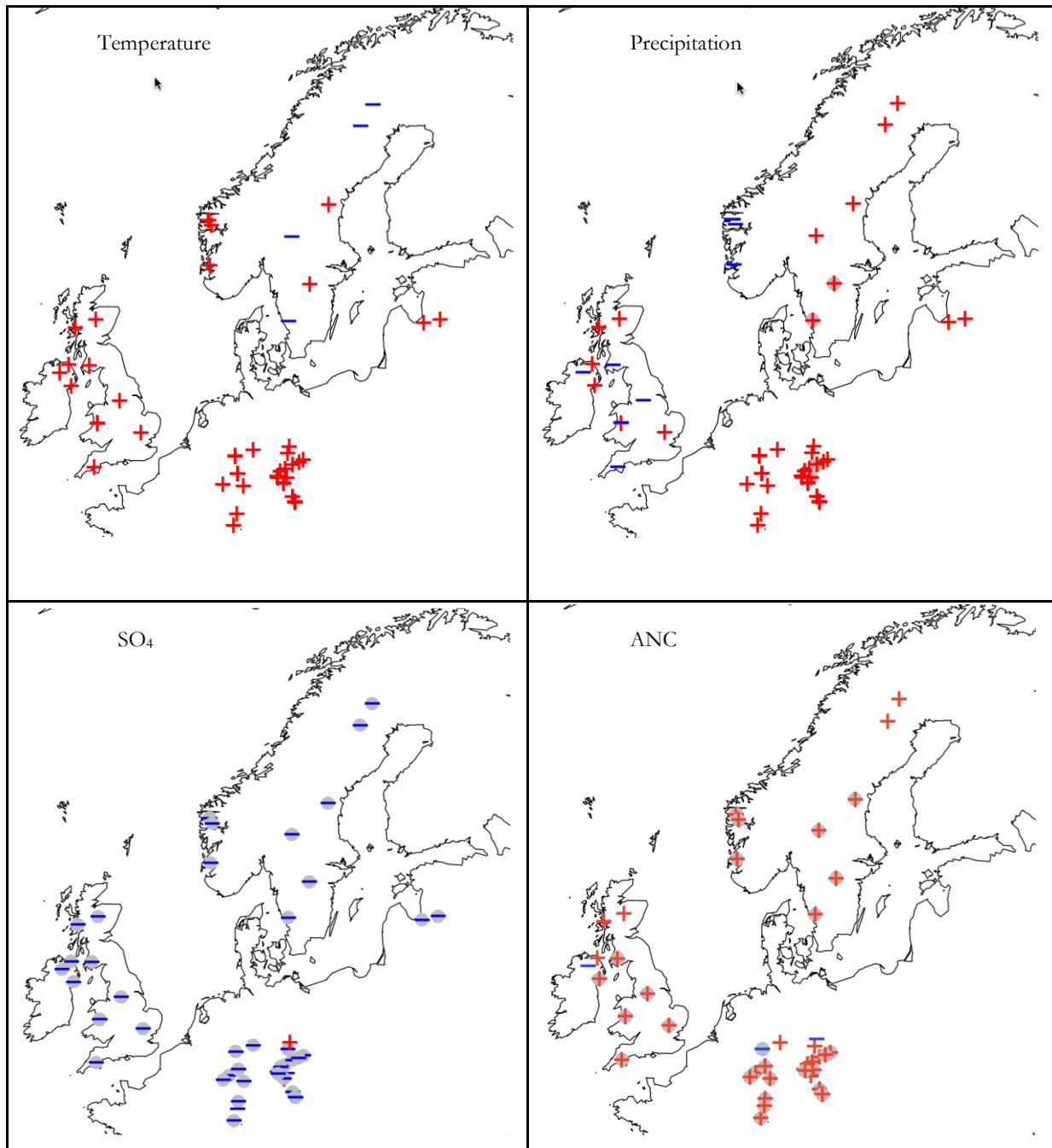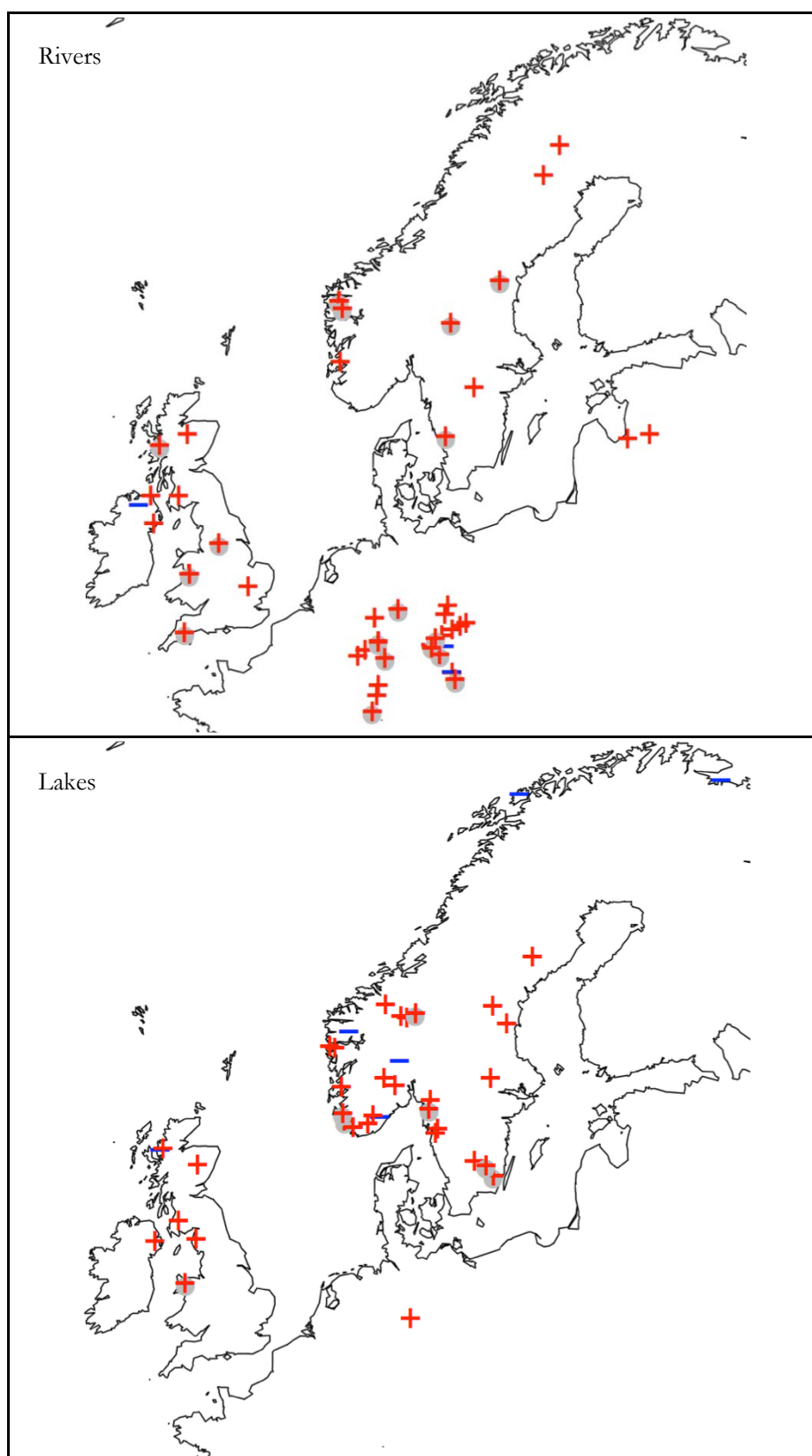
Figure 9. Trends in biodiversity in European rivers and lakes over the last 15 to 30 years (see Tables 1 and 2 for exact periods). + Increasing trend, – decreasing trend. Statistical significant changes in diversity are embedded in grey circles.

Table 3. The proportion of sites with a statistically significant increase in pH and number of EPT species (N) over the last ca 30 years. Numbers in brackets show a significant decrease. Group 1 includes all sites, Group 2 includes sites where pH < 5.5, Group 3 includes sites where pH has crossed 5.5 during the sampling period and Group 4 includes sites with pH > 5.5.

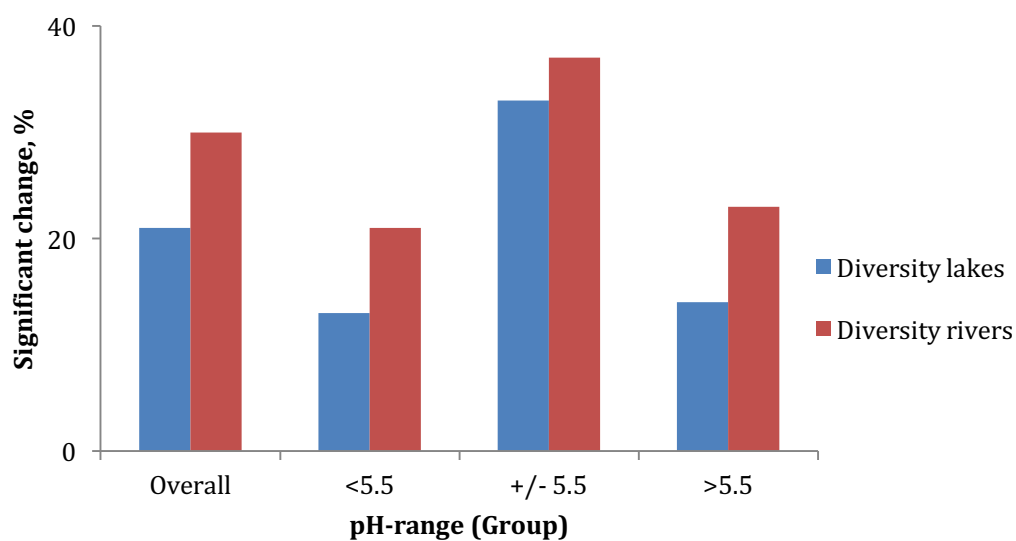|	Rivers				Lakes			
	Group 1	Group 2	Group 3	Group 4	Group 1	Group 2	Group 3	Group 4
Group size	54	14	27	13	38	16	15	7
pH	0.74 (0.02)	0.64 (0.07)	0.74	0.85	0.84	0.69	0.93	1.0
N	0.30	0.21	0.37	0.23	0.21	0.13	0.33	0.14

Figure 10. The proportion of sites with a statistically significant increase in number of EPT species (N) over the last ca 30 years.

Table 4. Correlation analyses between environmental variables and diversity, as analysed by a Markov Chain Monte Carlo generalized mixed effects model. Model outputs for rivers and lakes throughout Germany, Sweden, Latvia, Czech Republic, United Kingdom, and Norway. Post mean is the mean of the posterior distribution. The upper and lower 95% CI are credible intervals analogous to standard confidence intervals. The effective sample size (Eff. sample) is a measure of the auto-correlation within the parameter sample. Group 1 includes all sites, Group 2 includes sites where pH < 5.5, Group 3 includes sites where pH has crossed 5.5 during the sampling period, and Group 4 includes sites with pH > 5.5. *denotes significance at p<0.05. The correlation of single parameters is corrected for the influence of the other explanatory variables.

| Variable	Post Mean	Lower 95%CI	Upper 95%CI	Eff. sample	p-value
Rivers					
Group 1 (all sites)					
Temperature	-0.006	-0.010	0.002	40.0	0.001*
Precipitation	0	0	0.001	37.0	0.036*
ANC	0	0	0	31.8	0.001*
SO4	-0.013	-0.015	-0.009	12.3	0.001*
Group 2 (least acid)					
Temperature	-0.02	-0.009	-0.006	7.5	0.34
Precipitation	0.001	0	0.003	10.4	0.108
ANC	0	0	0001	3.6	0.932
SO4	-0.044	-0.054	-0.035	3.2	0.001*
Group 3 (sensitive)					
Temperature	-0.002	-0.008	0.005	152.3	0.606
Precipitation	0	0	0.001	247.0	0.036*
ANC	0	0	0	117.4	0.076
SO4	-0.009	-0.013	-0.005	33.4	0.001*
Group 4 (acid)					
Temperature	-0.009	-0.017	-0.002	11.5	0.004*
Precipitation	0	0	0.001	5.7	0.984
ANC	0	0	0.001	12.4	0.001*
SO4	-0.018	-0.026	-0.014	12.1	0.001*
Lakes					
Group 1 (all sites)					
Temperature	-0.034	-0.049	-0.023	7.0	0.001*
Precipitation	0.001	0	0.002	5.2	0.064
ANC	0.003	0.002	0.004	12.4	0.001*
SO4	0	-0.002	0.016	10.9	0.95
Group 2 (least acid)					
Temperature	-0.055	-0.070	-0.048	4.4	0.001*
Precipitation	0	0	0	8.2	0.006*
ANC	-0.004	-0.005	-0.003	13.3	0.001*
SO4	-0.063	-0.070	-0.034	3.5	0.001*
Group 3 (sensitive)					
Temperature	-0.040	-0.045	-0.018	4.6	0.001*
Precipitation	0.002	0	0.003	2.3	0.001*
ANC	0.001	0	0.002	5.7	0.052
SO4	0.004	-0.011	0.018	11.7	0.426
Group 4 (acid)					
Temperature	-0.034	-0.040	-0.024	21.4	0.001*
Precipitation	0	0	0.002	5.8	0.344
ANC	0.004	0.002	0.0055	15.8	0.001*
SO4	-0.023	-0.060	0.0338	1.67	0.354
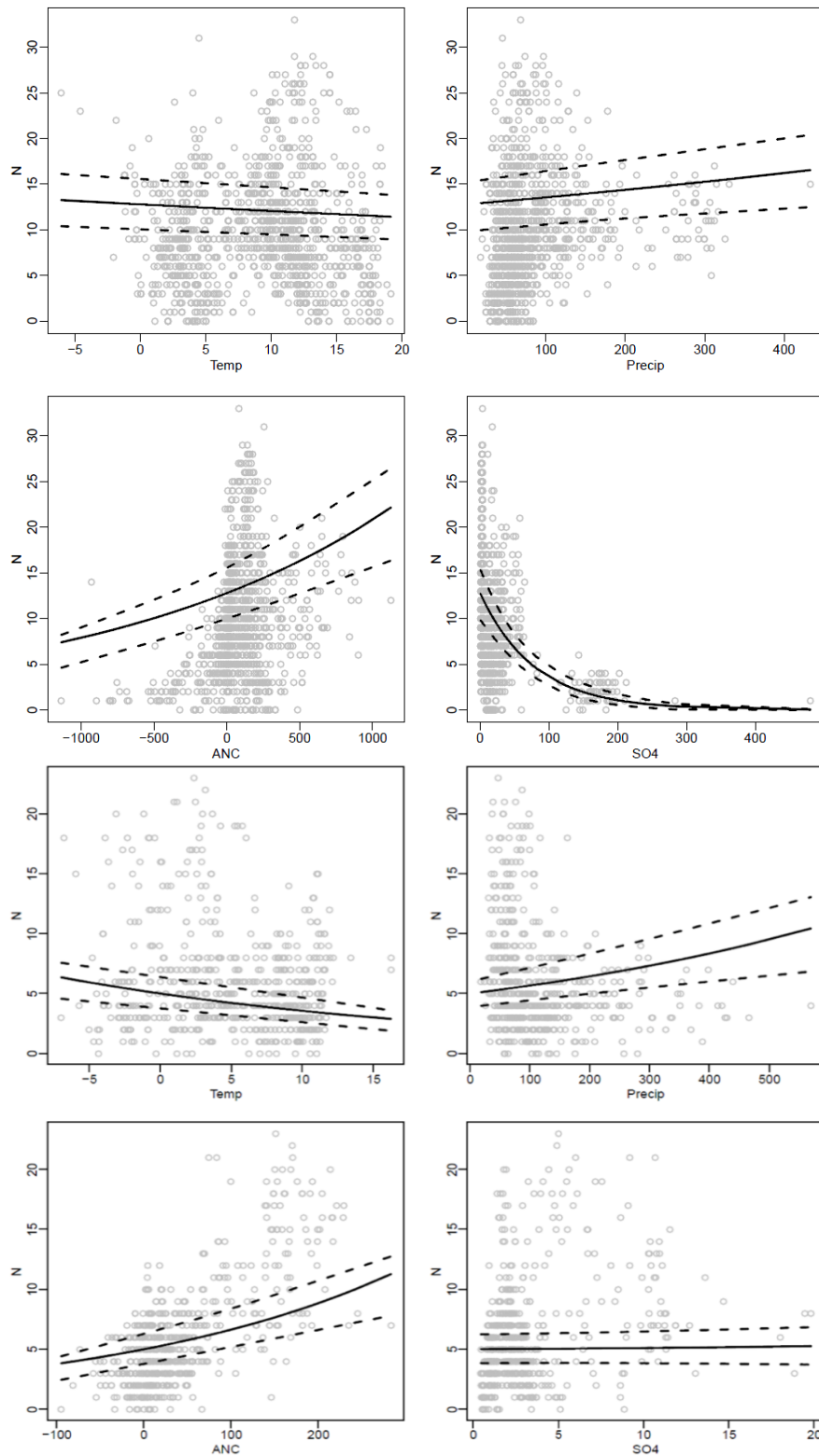
Figure 11. The relationship between environmental conditions and diversity for Group1 sites (upper four are rivers and lower four are lakes), as analysed by MCMC glmm. Temp: mean monthly temperature (˚C), Precip: mean monthly precipitation (mm), SO₄: sulphate (mg/l) and ANC: acid neutralizing capacity (µEq/l). The models include various parameters where points and lines do not need to agree in order to be significant.

3.3 Possible drivers of biodiversity

According to the MCMCglm-model, (ANC, SO$_4$; Table 4, Figure 11), the diversity of all rivers and lakes (Group 1) is significantly correlated to ANC and temperature, and SO$_4$ and precipitation is also significant for the rivers. When it comes to the subsets of rivers, SO4 is important for all three sub-groups. According to the relationship between SO$_4$ and species diversity, lower SO4 leads to higher diversity where a 10 mg/l reduction in SO$_4$ is associated with an increase of about two species (Figure 12). ANC is most important for the most acidified rivers, has perhaps a marginal effect in the sensitive rivers, and appears unimportant for the least sensitive. In addition, temperature is significant for the most acid rivers and precipitation for the sensitive rivers. For lakes, ANC appears the more important chemical variable, with changes in SO$_4$ only important for the least acid sites. Clearly, temperature is an important variable in lakes with a significant negative effect in all groups. Precipitation is significant for the least acid sites and for the sensitive sites.

There is no clear indication that the species diversity of sites with the least impact from acidification is more influenced by climate. For example, the species diversity of the least acidified rivers is correlated to SO$_4$ (Figure 11) and not to temperature or precipitation.
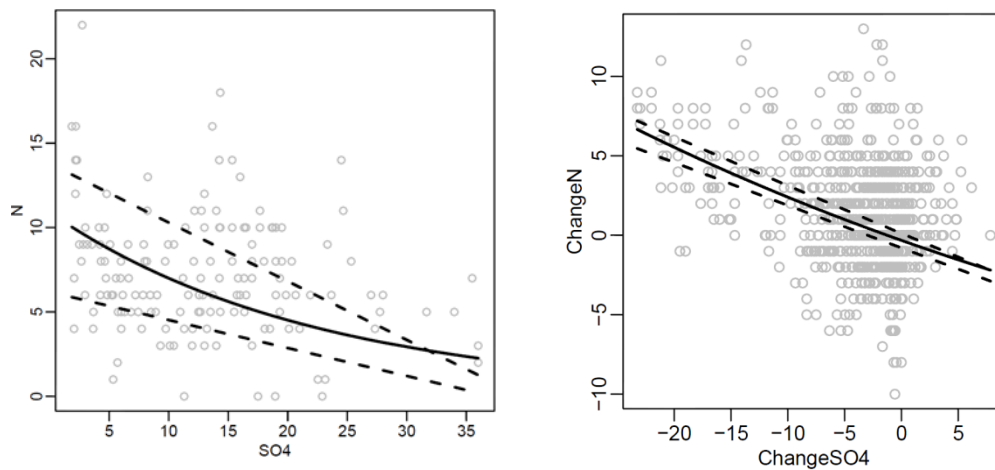

Figure 12. The relationship between sulphate (SO$_4$, mg/l) and species diversity (N) for the least-acidified rivers (Group 2) (left) and the reductions in sulphate-concentration needed in order to alter the diversity (right). The right hand figure is the change in diversity across time (T2-T1, T3-T1, T3-T2 etc.) versus the corresponding change in SO$_4$. Both relationships are analysed by a MCMC glmm.

4 Discussion

4.1 Recovery from acidification as drivers of diversity

There are very clear relationships between acid chemistry and diversity amongst rivers and lakes in ICP Waters sites. This is evident when all groups are analysed together and when they are analysed separately. The most pronounced increase in diversity is found at sites with the most pronounced chemical recovery (Table 3, Figure 10), yet all sites with an increase in diversity also show a pattern of concurrent increase in pH (Figure 5 and Figure 6). There is a clear overall significant negative correlation between diversity and sulphate, e.g., for all groups of rivers, and a significant positive correlation between ANC and diversity, e.g., for all lakes (Figure 11, Table 4), which is consistent because reduced SO_4 in acid-sensitive sites often will be associated with an increase in ANC. The correlation is evident even for sites anticipated to be least influenced by acidification. The clear relationships between acid chemistry and diversity suggest that a reduction in acidifying components of the water is having a strong influence on species diversity in remote surface waters across north-western Europe. A similar relationship between diversity and sulphate has also been documented for streams in North Eastern USA (Klemm et al., 2002).

The analysis therefore provides a clear demonstration of a regional scale impact of acid emissions reduction policy on aquatic biodiversity. The regional extent of increasing species is surprising, particularly given that not all were initially considered sufficiently acid-sensitive to have responded chemically to reductions in acid deposition. The communities may have been insensitive to mild acid deposition if the pre-disturbance community consisted of insensitive taxa, by assemblages limited by biotic interactions or other environmental variables than acidification, or if the acidification eradicated fish populations (Hesthagen, 1986), allowing invertebrates that are sensitive to fish predation to flourish (Appelberg et al., 1993; Hildrew, 2009; Layer et al., 2011). We lack information on the reference state of biodiversity for our sites and our understanding is therefore largely based on space-for-time approaches, whereby communities in acid-sensitive but un-acidified areas provide our best guide as to the likely composition of sites prior to acidification. From this approach, it is likely that acidification was accompanied by a gradual decrease in biodiversity.

Sulphate was chosen as an explanatory parameter because it has dominated the acid load in the region historically. Furthermore, in catchments with soils that have formed since the last glaciation, the majority of sites in this dataset, the SO_4 anion tends to behave relatively conservatively within catchments, so that changes in sulphate deposition have, for example, been shown to follow those in surface waters at an annual time-step in UK waters (Cooper, 2005). Changes in sulphate concentrations can therefore be assigned to changes in acid deposition in sites with no local sources of sulphate and in sites with soils that have little capacity to sorb SO_4, which is the case in formerly glaciated and acid-sensitive sites. Sulphate *per se*, however, is generally non-toxic at the concentrations measured at our sites and has little direct effect on aquatic invertebrates. Rates of change in the deposition of SO_4 tend to correlate quite closely to rates of change in ANC (Monteith et al., 2014), while influencing specific acid characteristics of surface waters in different ways depending on the history of acidification, base cation buffering potential and the availability of organic anions provided by dissolved organic matter. As ANC increases, changes in inorganic aluminium will be most marked in highly acidified waters, while pH changes are most sensitive in waters around pH 5.5.

Both pH and inorganic aluminium have been shown to exert direct toxic effects on biota. pH can influence the survival of aquatic insects, e.g., through the increase in hydrogen ion that interferes with the uptake and regulation of sodium and other ions (Havas and Rosseland, 1995; Paradise and Dunson, 1997) and by increasing aluminium toxicity (e.g., Havas and Rosseland, 1995; Sparling and Lowe, 1996). Many organisms cannot cope with high concentrations of H+ and inorganic aluminium (Raddum and Fjellheim, 1995; Raddum and Skjelkvale, 2001). When toxicity is too great for acid-sensitive taxa, local survival is only possible in refuges, perhaps downstream or in neighbouring catchments, which are less impacted by acidification. As conditions improve, the sensitive taxa reappear from the source populations. Such taxa form the basis for acidification indices and scores from these indices are now beginning to hint at

improved conditions at sites in The Czech Republic, Germany, Norway, Sweden, UK and elsewhere (Angeler and Johnson, 2012; Hesthagen et al., 2011; Monteith et al., 2005; Murphy et al., 2014).

A continuous biotic recovery of the least impacted sites would not be evident when monitoring the sites by indices previously applied to assess trends in macroinvertebrates across the ICP Waters network. Acidification indices generally depend on the fraction of acid sensitive taxa in the species assemblage, whereas species diversity is the sum of all species in the assemblage. Many acidification indices are insensitive to pH above pH >5.5 (Fjellheim and Raddum, 1990; Raddum et al., 1988). The median tolerable pH for most sensitive species of invertebrates is between 5.2 and 6.1 (Lacoul et al., 2011), however, it is has been demonstrated that a few macroinvertebrate species are sensitive even at pH slightly below 7 (Bell, 1971; Moe et al., 2010).. This suggests that species diversity should accompany the acidification indices in monitoring of acid sensitive sites. Site-specific time series of species diversity can then act as a reference for the most recent developments in diversity.

4.2 Temperature and precipitation as drivers of diversity

There was no significant change in air temperature within the grid cells representing the ICP Waters sites over the period covered by the biological data. This may be due to small absolute changes and the large year-to-year fluctuations. Nevertheless, we observed significant, and invariably negative, correlations between temperature and species diversity for both lake and river sites. As temperature trends were lacking these correlations must therefore reflect inter-annual sensitivity of invertebrate populations to variations in temperature around the time of sampling. Whether such negative effects on temperature would be sustained over a period of ramped warming remains to be seen, but these results point to a potential threat to these surface waters from forecast changes in temperature in the region. It should also be noted that we cannot exclude the possibility that the warmer years result in earlier emergence of adults and thus lower larval catches.

In contrast to air temperatures, the amount of precipitation for grid cells representing the ICP Waters sites increased significantly for about 10% and 20% for river and lake sites, respectively. We found a positive correlation between precipitation and species diversity in rivers for all groups expect the most acid sites (Group 4). Increased precipitation may act on species diversity through at least one of four different processes: 1. by decreasing the frequency of drought events and desiccation, 2. by enhancing catchment erosion and thereby increases the level of nutrients in the ecosystem, 3. by increasing the frequency of extreme flooding events that flushed out the animals, and 4. by increasing the frequency and intensity of acid episodes. Both 1 and 2 can be expected to have a positive influence on species diversity, while 3 and 4 can be expected to have a negative effect on species diversity. The lack of correlation between precipitation and species diversity at the most acid sites may either suggest that changes in precipitation have not been sufficiently large to impact on these communities or that multiple hydraulic processes with conflicting effects (including the effect of acid episodes) may be operating.

Surface water organisms are potentially sensitive to variation in various climatological characteristics. Monthly or annual average temperature or precipitation may change, extreme values can become more intense or frequent, seasonality may be altered and the timing of specific weather events can shift (Garcia et al., 2014; Kusch, 2015). Extreme weather may influence the species diversity, e.g., through sea salt sea-salt episodes (Hindar et al., 2004). Many benthic invertebrates have an optimal water temperature and cannot survive if the temperatures are too warm or too cold (Velle et al., 2011). In cold regions, their development requires more accumulated degree-days than are available. Some species might benefit from a future climate in which the length of the growing season increases and the winters become less harsh (Iacarella et al., 2015). Increased temperatures have already resulted in range expansions, pole-ward shifts and altered species phenologies (Dingemanse and Kalkman, 2008; Hickling et al., 2006; Parmesan et al., 1999; Walther et al., 2002). In addition, the biota may be negatively influenced by river bed instability during enhanced precipitation (Lods-Crozet et al., 2001).
A continuous warming can be expected to influence species diversity negatively, e.g. as a result of a decrease in the amount of suitable areas subsequent to climate change (Domisch et al., 2013), it can have a neutral effect on species diversity (Burgmer et al., 2007), or the response can vary according to taxonomic group (Kusch, 2015; Li et al., 2014). On a millennium time scale, we might also expect warmer

temperatures to lead to more diverse communities, in accordance with patterns of species richness that often are correlated with latitudinal gradients (Hawkins et al., 2003; Wright et al., 1993). Rohde (1999) concluded that latitudinal gradients in species diversity result from effective evolutionary time modulated by several factors, such as temperature and energy input. Still, the mechanism responsible for the strong relationship between temperature and freshwater biota is not well understood (Eggermont and Heiri, 2012; Velle et al., 2010a). Complex and multidimensional ecological processes – other than simply temperature preferences – are determining the degree and direction of species distributions in aquatic systems (Velle et al., 2010a). Shifts in species response to temperature are likely to vary both spatially and temporally, depending on the nature of climate change and the setting of the aquatic environment in question (Dingemanse and Kalkman, 2008).

4.3 Stability- and length of the environmental gradients

We expected a stronger correlation between diversity and temperature for the least-acidified sites (Group 2). However, water chemistry has an overriding influence on species diversity for all groups of sites. With changes in water chemistry taken into account, temperature was found to exert a net negative effect on species diversity. It is not likely that temperature had a dominating influence on species diversity given that the diversity has increased for most sites. This can also be expected since the gradient of change along the temperature axis is short (not significant long-term change at any site) compared to the pronounced change along the ANC- and sulphate gradients (significant at most sites). The longer chemistry gradients in rivers may explain why the relationship between diversity and ANC- and sulphate is stronger for rivers than for lakes.

A differing response between rivers and lakes can also result from the dissimilar stability of the two environments. The lake thermal environment is more stable and to a lesser extent affected by shading or by short-term variations in hydrology, implying that the air temperature metric provides a more robust measure of variation in lake temperature than it does for stream sites. The same may potentially apply to the chemistry, in as much as point sampled ANC for a river is highly sensitive to short term variation in hydrology, while the ANC of a lake will be more representative of average recent chemistry. SO_4 takes up more of the variance for the rivers, because SO_4 concentration in rivers tends to be generally more stable and robust predictor of recent average chemistry than ANC. More homogenous conditions in lakes than in rivers may also suggest that the biota of lakes to a smaller is influenced by acidification. For example, lakes are less susceptible to episodic shocks events, such as acid peaks during snow-melt or sea-salt episodes. This can partly explain the observation of a more pronounced increase in species diversity of rivers than lakes. In addition, the biological resolution of rivers is higher than for lakes since the number of EPT-taxa naturally is higher in rivers. In lakes, these insects are less abundant and non-biting midges (Chironomidae) form the most abundant benthic macroinvertebrate (Armitage et al., 1995). Non-biting midges are rarely identified below family-level for monitoring purpose.

4.4 Implications for policy

As a response to global threats to biodiversity, the partners to the Convention on Biological Diversity committed themselves in 2002 to achieve, by 2010, a significant reduction in the current rate of loss of biodiversity at the global, regional and national level. This target was not met (Spyropoulou et al., 2010) and the loss of biodiversity has continued. There is now a Strategic Plan for Biodiversity 2011-2020 that aims to halt and eventually reverse the loss of biodiversity of the planet by 2020. To build support and momentum for this task, the United Nations General Assembly at its 65th session declared the period 2011-2020 to be "The United Nations Decade on Biodiversity". This is a demanding task given that worldwide, the biodiversity of freshwaters and elsewhere is declining (Barnosky et al., 2011; Sala et al., 2000).
In the context of this grim news, our evidence of an apparent hemispheric-scale response of aquatic diversity to internationally agreed acid emission reductions provides an encouraging demonstration of the potential for international action to achieve positive results in this field. Based on the correlations we have established between water acidity and diversity, even for the least-acidified sites (Figure 12), we can expect a further increase in species diversity providing levels of deposition continue to decrease. In addition, we can expect a further increase in diversity since biological recovery often is lagging improvements in

chemistry (Murphy et al., 2014). A number of hypotheses have been proposed to explain this behaviour (Monteith et al., 2005), and of these the most likely surround biological inertia, in which acid sensitive taxa struggle to re-establish functional niches that have become occupied by acid tolerant generalists (Ledger and Hildrew, 2005) and/ or the impoverished buffer capacity of the catchments that makes the assemblages vulnerable to short term acid episodes. Conversely, the effect of climate warming on species diversity may counteract the effects of reduced acid deposition in the future. The trends in warming for the periods for which biological records in the ICP Waters database exist, were not significant and therefore, this analysis cannot address whether long-term climate change affects aquatic biodiversity in acid-sensitive ecosystems. Still, temperature had effects on variation in biodiversity, suggestion that these communities will be sensitive to long-term temperature change. Continued monitoring of biological communities will be extremely valuable for detection of climate effects on biodiversity.

4.5 Perspectives

For the basic unit of biological classification, the species,   -biological diversity is expressed as a function of the number of species and their frequency, or simply the number of species (Chapin Iii et al., 2000; Tuomisto, 2010), as we have done. Nevertheless, biodiversity metrics reduce complex information on structure and abundance of communities to simple numbers. There are two main limitations to the concept of biodiversity: (1) the term is artificial implying that biodiversity not is an intrinsic property in nature and (2) biodiversity is a simplification of nature and it is necessary to consider that information is lost when complex processes are reduced to a single number (Hurlbert, 1971).

A natural next step in the analysis of long-term trends in biological communities and their relationship to environmental drivers is to analyse changes in the function of the communities. Such analyses will complement the analysis of species diversity. Function reflects the biological complexity of the ecosystem expressed by important biological traits (Heino, 2005, 2008; Schleuter et al., 2010). Such traits could include feeding mode, food source, mode of mobility, size at maturity, life cycle length etc. Changes in these traits over space or time gives direct information about ecological processes, and also are highly relevant for finding effects on ecosystem-services.

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6 Reports and publications from the ICP Waters programme

All reports from the ICP Waters programme from 2000 up to present are listed below. Reports before year 2000 can be listed on request. All reports are available from the Programme Centre. Reports and recent publications are also accessible through the ICP Waters website; http://www.icp-waters.no/

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