Hydrobiologia (2024) 851:585–600
https://doi.org/10.1007/s10750-023-05346-9

PRIMARY RESEARCH PAPER

Acidification of freshwater lakes in Scandinavia: impacts and recovery of chironomid communities under accelerating environmental changes

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Received: 30 March 2023 / Revised: 31 July 2023 / Accepted: 11 August 2023 / Published online: 19 September 2023

Abstract We re-examined the effects of acidification on Scandinavian freshwater lakes using paleolimnological reconstructions focused on subfossil chironomids. Our study showed a widespread shift in chironomid community composition occurring at around 1960 and corresponding with the maximum fallout of anthropogenic SO_4^{2-} deposition. Results also showed that taxonomic turn-over was higher in chironomid records from nitrogen-limited lakes, likely due to the cumulative effects of acidification and eutrophication driven by atmospheric nitrogen deposition. Despite strong evidence of chemical recovery from acidification, all lake records failed to show a return to pre-acidified community compositions and most chironomid communities instead continue to follow the trajectories triggered by acidification. We hypothesized that when SO_4^{2-} deposition started to decrease after 1980, a period also marked by rapid environmental and climatic changes, the influence of pH and/or other acidification-related variables in structuring chironomid community became less important, thus, giving more relative importance to other drivers, such as brownification and climatic processes. Results, therefore, suggest the key role of acidification in shaping the response of chironomid communities to future environmental changes. Future paleolimnological studies will contribute to better manage aquatic ecosystems recovering from acidification worldwide by allowing managers to quantify the efficacy of different management actions taken to mitigate acidification as well as to redefine appropriate restoration targets.

Keywords Biodiversity · Resilience · Climate change · Acid rain · Nutrient limitations · Paleolimnology

Introduction

Anthropogenic atmospheric emissions during the last century led to increased sulphate and nitrogen depositions triggering the acidification of countless European and North American ecosystems (Mylona, 1996), and increasing the amount of excess nitrogen in nature (Galloway & Cowling, 2002). Acidification of aquatic ecosystems, one of the most severe and spatially extensive environmental issues affecting northern latitudes, resulted in numerous rapid biological changes in many lakes and rivers (and in particular in Scandinavia; Skjelkvåle et al., 2005), including effects on fish populations, invertebrate communities,

Handling editor: Jasmine Saros

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10750-023-05346-9.

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recycling of organic matter, biotic interactions within food webs and ultimately lake productivity (see also Schindler et al., 1989; Fölster et al., 2007). The effects of nitrogen deposition on aquatic ecosystems have, however, received less attention (Elser et al., 2009). In Scandinavia, strong impacts of nitrogen deposition on lake ecosystems were demonstrated in nitrogen-limited lakes as increasing nitrogen inputs induced higher development of phytoplankton (i.e. eutrophication; Bergström et al., 2005), a consequence also shown in large parts of the northern hemisphere (Bergström & Jansson, 2006). In the 1980s, atmospheric emissions control was successfully implemented, resulting in drastic reductions of SO_4^{2-} and nitrogen depositions, reaching pre-acidification levels in the late 1990s and early 2000s (Stoddard et al., 1999; Fölster et al., 2014). These measures were followed by a substantial chemical recovery, mainly characterized by an increase in pH and acid neutralization capacity, for most freshwater ecosystems (Fölster et al., 2014; Garmo et al., 2014). However, numerous studies have shown a lack of biological recovery to pre-acidified conditions (Johnson and Angeler 2010; Angeler et al., 2012; Diamond et al. 2022), suggesting that the mechanisms underlying biological recovery from acidification are still largely unknown.

The post-acidification period was also marked by rapid environmental and climatic changes in Scandinavia, characterized by increasing temperature and precipitation patterns starting in mid-1970, leading to substantial changes in aquatic communities (Blenckner et al., 2007). At the same time, monitoring data revealed increasing water organic carbon concentrations (de Wit et al., 2007). Studies have argued that organic carbon increases in surface waters may be driven by declining rates of acid deposition (Finstad et al., 2016; Redden et al., 2021), whereby decreasing soil acidity may increase the solubility of soil organic matter and consequently terrestrial organic carbon leaching (Kortelainen, 1993). Physical properties of lake catchments may, therefore, play a crucial role in terrestrial organic carbon exports (Kortelainen, 1993; Houle et al., 1995, 2020). Indeed, lakes with large catchment area to lake surface ratio and shorter retention times tend to have high water organic carbon concentrations. However, other studies have suggested that additional factors related to climate change contribute to brownification of surface waters weakly impacted by SO_4^{2-} deposition (de Wit et al., 2016; Meyer-Jacob et al., 2019), as well as changes in land use (Meyer-Jacob et al., 2015; Skerlep et al., 2020). Nevertheless, many studies have shown ecological implications of brownification, such as changes in species composition and aquatic food web structures (Creed et al., 2018). The concurrent impacts of these different stressors (e.g. accelerating environmental and climatic changes and increasing pH) and the lack of long-term data beyond traditional monitoring windows (a few decades at best), therefore, complicate identifying mechanisms underlying lake recovering from acidification.

Analysis of biological remains archived in lake sediments is a powerful approach to reconstruct the past dynamics of aquatic communities (Walker, 2001) and understand the effects of past environmental changes on lakes. Specifically, head capsules of Chironomidae larvae (Arthropoda; Diptera; Nematocera), non-biting midges with larvae living in superficial lake sediments, are morphologically well preserved in sediments. Chironomid species are good indicators of environmental change, as they have well defined ecological requirements across environmental gradients, such as temperature, nutrient and oxygen concentrations (Brodersen & Quinlan, 2006; Heiri et al., 2011; Verbruggen et al., 2011). In contrast, chironomids have usually not been regarded as sensitive indicators of acidification (Wiederholm & Eriksson, 1977; Mossberg & Nyberg, 1979; Olander, 2002), as many species of chironomid are tolerant of a wide range of pH (usually from 6.0 to 9.0). Contrasting results, however, demonstrated that pH can be a key driver of changes in chironomid communities (Raddum & Saether, 1981; Johnson & Wiederholm, 1989; Brodin, 1990; Halvorsen et al., 2001), and many chironomid species could experience difficulties with calcium and sodium regulation outside this given range (Havas, 1981). Furthermore, tolerance of acidic conditions appears to be partially related to body size (i.e. with smaller species being more sensitive to low pH; Weiderholm & Eriksson, 1977), and the presence of haemoglobin in the haemolymph (i.e. Chironomini tribe; Jernelov et al., 1981). As chironomid larvae are a keystone taxonomic group in lakes, being involved in the recycling of organic matter in sediments (Nogaro et al., 2009) and forming an important trophic link between primary producers and top predators (Wagner et al., 2012), the study of their chitinous remains will help us to elucidate the acidification-driven impacts on aquatic communities and their recovery under accelerating environmental changes.

This study aims to quantify the impacts of acidification on chironomid community composition of Scandinavian lakes and to unravel the mechanisms underlying lake recovery under accelerating environmental changes. Using subfossil chironomid remains analysed from 8 Swedish lakes: we tested the hypotheses that (i) acidification favoured the development of acid-tolerant chironomid species and its impacts should peak during the maximum fallout of SO_4^{2-} deposition, (ii) taxonomic turn-over is larger in nitrogen-limited lakes because chironomid communities respond to both increasing nitrogen deposition triggering eutrophication and acidification, (iii) lake recovery from acidification is hampered by concurrent climatic and environmental changes starting from 1980 and (iv) during the post-acidification period, lakes with larger catchment areas are subjected to larger ecological changes due to higher terrestrial organic carbon leaching.

Material and methods

Study sites and recent environmental changes

In total, eight relatively small (area range 49–505 ha) and deep (maximum water depth range 16.5–29.2 m) lakes with relatively small catchments (range 5.75–38.9 km^2) located in Sweden have been selected in this study (Table 1). Lakes lie on the Fennoscandian shield, a bedrock predominated by highly siliceous granitic and gneiss, making the water weakly conductive, slightly acidic and poorly capable of acid neutralization. Late summer water quality were retrieved from the Swedish National Monitoring Program database (https://miljodata.slu.se/mvm/), including light absorbance at 420 nm, calcium concentrations, chlorophyll *a* water concentrations, water conductivity, total organic carbon concentrations, pH, Secchi depth, nutrient concentrations, and bottom water oxygen concentrations (Table 1). Mean values were calculated using the number of years encompassed by the first cm of each sediment core given by the age-depth models (see below). The study lakes were also selected to cover a large gradient in nutrient limitations. The degree of limitations by a single

Table 1 Physical and chemical characteristics of the 8 studied lakes and their catchment areas

Lake	Agriculture (%)	CA(km^2)	Depth(m)	Area(km^2)	Abs420	Secchi (m)	Ca^{2+}	Chla	Cond25	pH	TOC	Tot_P	Tot_N	TN/TP	O2
Bysjön (BYS)	16.4	38.9	20	5.05	0.15	3.4	3.4	2.7	3.4	6.7	9.3	7.7	250	32	4.2
Försjön (FOR)	3.2	10.37	21	1.56	0.1	4.1	4.8	3.3	4.9	6.8	10.4	8.8	482	55	10.5
Holmeshultasjön (HOL)	15.8	5.75	16.5	0.64	0.1	3.3	4.8	4	6.4	6.9	10.1	7	254	36	1.3
Övre Skärsjön (OSK)	0	8.77	32	1.7	0.2	2.1	1.2	2.3	2.2	5.8	10.2	6.6	321	49	8
Rasjön (RAS)	10.4	20.77	20	3.91	0.07	4.7	16.3	1.9	12.7	7.1	11.8	4	310	78	5
Skärlen (SKA)	3.4	13.14	28	3.18	0.02	8	2	2.7	4.1	6.6	4	4	450	113	11.3
Täftesträsket (TAF)	0	12.2	17.5	2.22	0.13	2.6	2.7	5.7	3	6.6	10.5	8.8	329	37	0
Torrgårdsvatten (TOR)	0	14.8	29.2	0.49	0.01	2.4	0.7	0.9	4.7	5.5	1.8	4.5	271	60	5.5

Agriculture refers to the proportion of the catchment area used for agricultural purpose

CA catchment area, *Depth* maximum lake depth, *Area* lake area, *Abs420* absorbance at 420 nm, *Chl* chlorophyll *a* concentration (mg/L), *Cond25* specific conductance at 25 °C, *TOC* total organic carbon concentration (mg/L), *Tot_P* total phosphorus concentration (µg/L), *Tot_N* total nitrogen concentration (µg/L), *TN/TP* total nitrogen to total phosphorus concentrtaions ratios, *Secchi* water transparency as Secchi disc depth, O_2 oxygen concentrations (mg/L). Mg^{2+} Calcium ion concentrations are expressed in mg/L

Data are reported from https://miljodata.slu.se/mvm/

nutrient can be reflected by the ratios between lake water total nitrogen and total phosphorus concentrations (hereafter TN/TP ratios), where high TN/TP ratios indicate phosphorus-limited lakes and low TN/TP ratios indicate nitrogen-limited lakes (Bergström, 2010).

The spatial distribution of the study lakes also covered large gradients in SO_4^{2-} deposition: from heavily impacted areas in southernmost Sweden (i.e. Lake Torrgårdsvatten and Lake Skärlen) to moderately impacted areas in North-Eastern Sweden (i.e. Lake Täftesträsket and Lake Övre Skärsjön) inducing various deviations in their pH from pre-acidification conditions (as suggested by outputs of the MAGIC model; Moldan et al., 2020). For these systems, no management actions (i.e. liming) have been taken to counteract the effects of acidification (https://kalkdatabasen.lansstyrelsen.se); thus, the lakes represent only natural recovery after acidification.

Sediment coring and dating techniques

In June–July 2020, surface sediment cores were retrieved from the deepest point of the lakes using a gravity corer (9 cm in diameter: UWITEC). All sediment cores were also vertically split into two halves in the lab, and the uppermost 1 cm thick sediment layer of each core was immediately collected and stored at − 20 °C or + 4 °C. Sediment cores were dated by ^{210}Pb and ^{137}Cs at Liverpool University´s Environmental Radioactivity Laboratory. Sub-samples were analysed for ^{210}Pb, ^{226}Ra, and ^{137}Cs by direct gamma assay, using Ortec HPGe GWL series well-type coaxial low background intrinsic germanium detectors (Appleby et al. 1986). ^{210}Pb was determined via its gamma emissions at 46.5 keV, and ^{226}Ra by the 295 keV and 352 keV γ-rays emitted by its daughter radionuclide ^{214}Pb, following 3 weeks storage in sealed containers to allow radioactive equilibration. ^{137}Cs was measured by its emissions at 662 keV. The absolute efficiencies of the detectors were determined using calibrated sources and sediment samples of known activity. Corrections were made for the effect of self-absorption of low-energy γ-rays within the sample (Appleby & Oldfield, 1992). Dates were calculated using the CRS model (Appleby & Oldfield, 1978). Discrepancies with any clearly defined ^{137}Cs dates were resolved using the methods outlined in Appleby (2002).

Chitinous remains analysis

Between 9 and 18 sediment samples per core were analysed for chironomid remains. Chironomid head capsules were hand sorted from each sample of wet sediment (*ca.* 15 g WW) following Walker (2001) and mounted between microscopes slides. Chironomid community composition was identified under a microscope using Brooks et al. (2008) and Rieradevall & Brooks (2001). Data are expressed as relative abundances, and only taxa occurring in at least two samples, with a minimum relative abundance of more than 2%, were included in further analysis. Reliable information regarding affinities of chironomid morphotypes to pH are scarce (Henrikson et al., 1982; Brodin & Gransberg, 1993; Orendt, 1999; Olander, 2002; Kubovčík & Bitušík, 2006), but overall, a few chironomid taxa could be considered as acid-sensitive taxa (*Tanytarsus lugens* type; *Dicrotendipes nervosus* type; *Microtendipes pedellus* type; *Polypedilum nubeculosum* type), and acid-tolerant taxa (*Sergentia coracina* type; *Chironomus anthracinus* type; *Chironomus plumosus* type; *Zalutschia zalutshicola* type; *Heterotrissocladius maeaeri* type-2). Other chironomid taxa likely showed various tolerance or sensitivity to pH but could not be reliability classified into these two categories (Fig. 1).

Data analysis

To study how acidification impacted chironomid communities, constrained hierarchical cluster analysis using a Bray–Curtis distance and a CONISS linkage method (“Rioja” package for R; Juggins 2020) was applied on each chironomid community record to identify differences between periods of uniform chironomid communities (see also ESM 1). Detrended correspondence analysis (DCA) was also performed on chironomid community data to summarize temporal patterns in chironomid community composition. DCA produces scores for both samples (i.e. sediment layers) and chironomid taxa for ordination axes, corresponding to the locations of the samples and morphotypes along the DCA axes. Sample scores of the first axis of the DCA (DC1 axis) were extracted and grouped according to the following three periods: up to 1960 (i.e. increasing acidification period), 1960–1980 (i.e. peak in SO_4^{2-} deposition), and after 1980 (i.e. natural recovery under accelerating

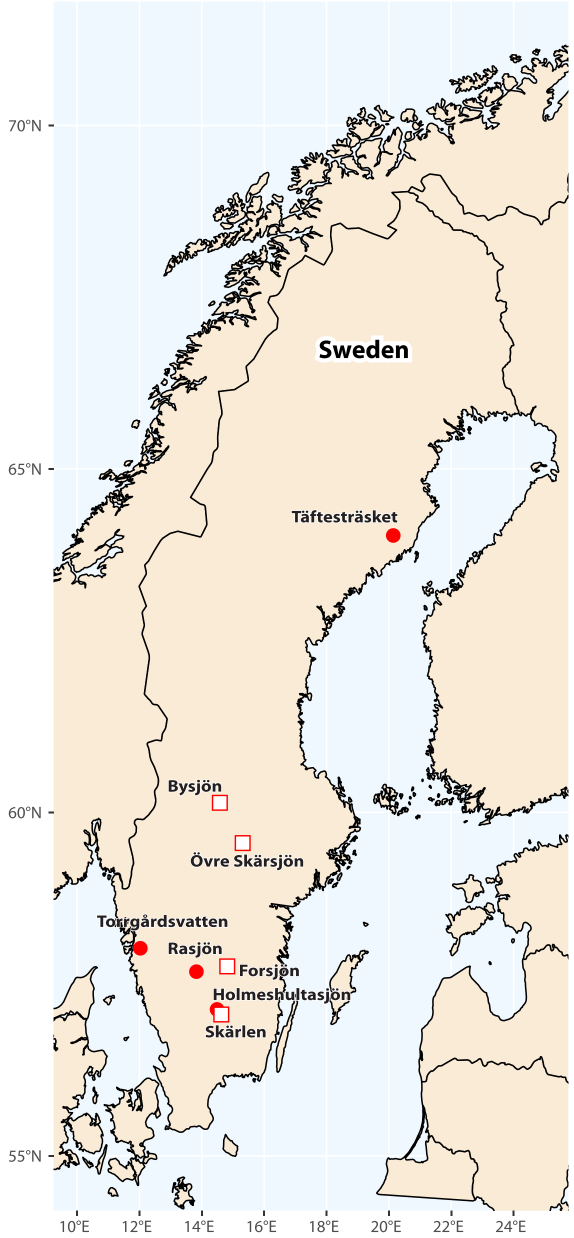


Fig. 1 Location of the study region showing the sampling sites. Circles refer to the lake with a forward trajectory after 1960, whereas squares represent lakes showing slight backward trajectory (see results for further details)

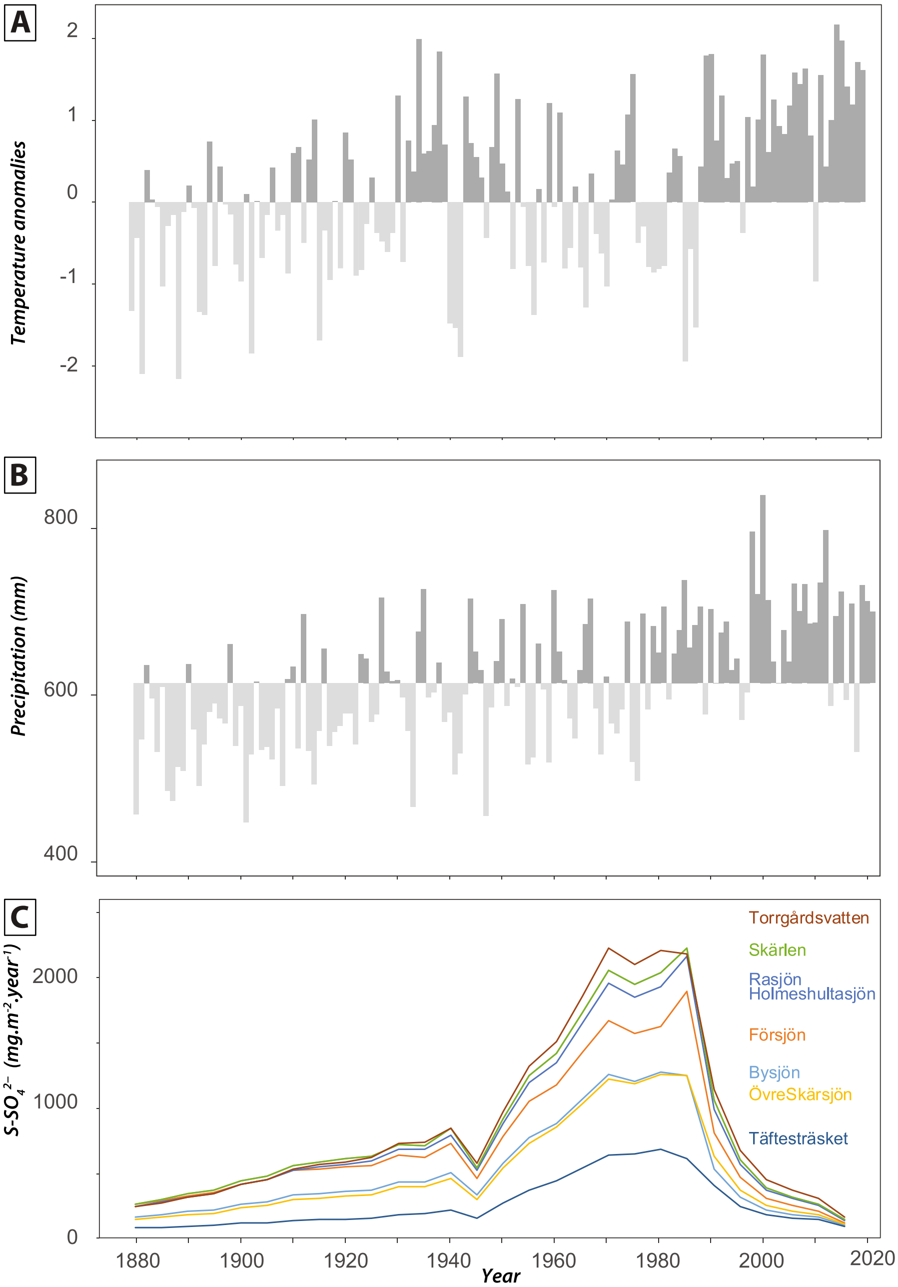
environmental changes). The number of periods was selected to capture the key moments of the recent ecological trajectories, and to have a sufficient number of samples within each period. Temporal patterns in DC1 scores will help summarize taxonomic turnover and quantify whether chironomid community composition recovered from acidification. Chironomid taxa scores of DC1 axis were also extracted to characterize temporal patterns in indicator chironomid morphotypes and infer past changes in environmental conditions. Finally, we explored the relationships between the gradient length of DC1 axis and environmental variables and physical properties of the catchment using generalized additive models to test whether nutrient limitations, land-use and associated processes (i.e. increased organic carbon export) explain observed temporal trends in chironomid communities. All statistical analyses and plots were performed using the R 4.1.1 software (R Core Team, 2021).

Results

Modelled SO_4^{2-} deposition data for the 1880–2020 period were available from the European Monitoring and Evaluation Program (EMEP) and showed a sharp increase in deposition from 1940 to peak at *ca*. 1960, and deposition remained constant until 1980 (Fig. 2C). The onset and maximal imprint of acidification was also characterized by low variability in temperature fluctuations and precipitations pattern (Fig. 2A and B). Then, the SO_4^{2-} deposition followed a steady decrease to pre-acidification levels around 2000, but the post-acidification period was also marked by a warming climate starting in the 1980's (Fig. 2A) and increasing precipitation after mid-1970's (Fig. 2B).

Subfossil chironomids analysed from the 8 sediment records, spanning from 1880 to 2020, in a total of 8141 chironomid remains were identified in 111 sediment samples, with sample counts ranging from 26 to 110 (but six samples had counts between 40 and 50 and only six samples with counts < 40). Constrained hierarchical cluster analysis applied on chironomid community data revealed substantial changes in chironomid community composition over time (Fig. 3A). Although the study lakes covered large spatial gradients in SO_4^{2-} deposition (Fig. 1), dendrograms showed widespread shifts in community composition occurring around 1960 in all sediment records (Fig. 3B). The 1960 taxonomic shift also marked the difference between the two main clusters of samples sharing the most similar taxonomic composition, expect for Lake Övre Skärsjön for which

Fig. 2 **A** Temporal patterns of mean annual temperature in Sweden during the period 1860–2020. All data are shown as anomalies from the respective mean values over the entire time series (SMHI). **B** Temporal patterns of mean annual precipitation in Sweden during the period 1860–2020. **C** Atmospheric sulphate sulphur (S-SO_4^{2-}) deposition time series (1880–2015) for each of the studied lakes from the European Monitoring and Evaluation Program



three clusters were observed (Fig. 3A). Most differences in ages of these major taxonomic changes can be explained by uncertainties in age-depth models, as the different probability distributions largely overlapped (Fig. 3B). Furthermore, these synchronic changes corresponded with peak in anthropogenic SO_4^{2-} deposition in Sweden (Fig. 2).

Sample scores of DC1 axis performed on chironomid community data were grouped according to three periods corresponding to increasing acidification (up to 1960), peaks in SO_4^{2-} deposition (1960–1980), and natural recovery under accelerating environmental changes (after 1980). Temporal patterns in DC1 scores showed high temporal turn-over in chironomid community composition, and continuous temporal changes between the different periods (Fig. 4). Sample scores of DC1 axis showed consistent increase or decrease over time for four lakes (Fig. 4 lower panel),

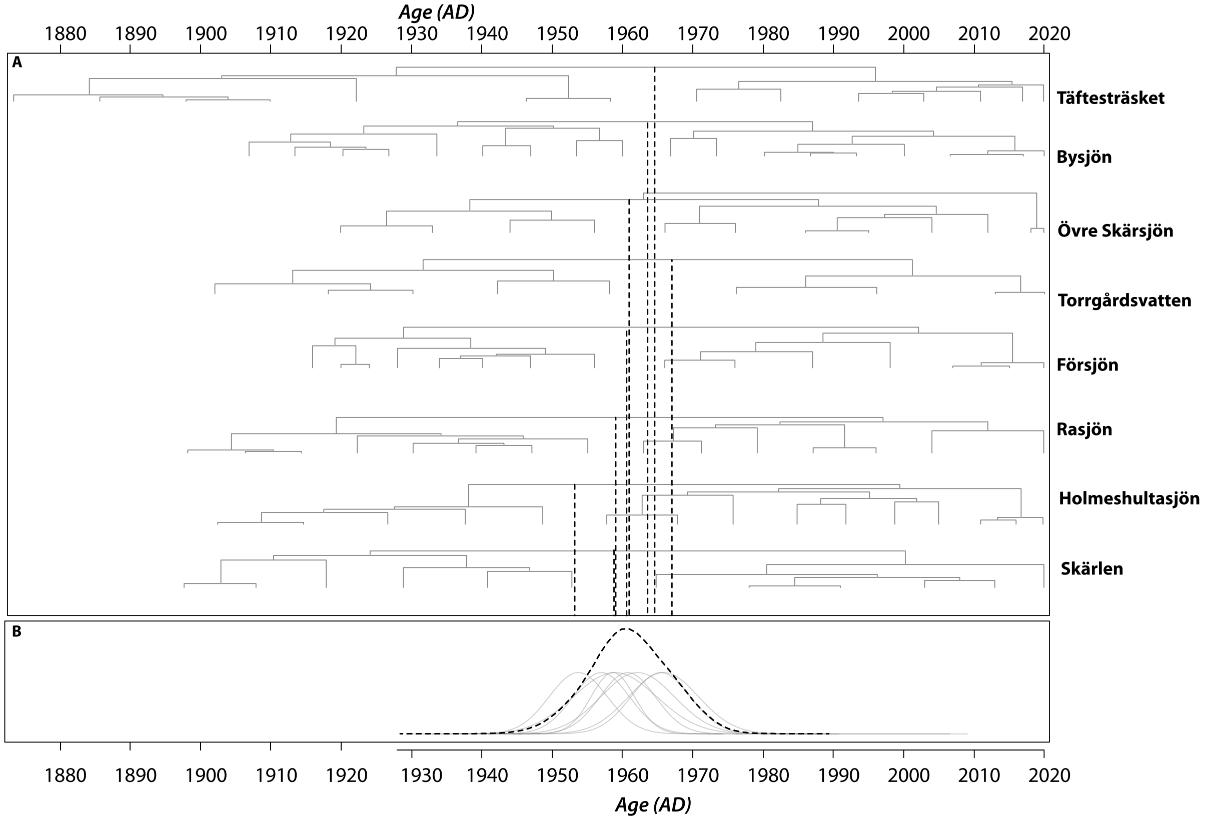


Fig. 3 Cluster plots showing temporal changes in chironomid taxonomic composition reported in 8 Swedish lakes over the last 150 years. Shifts in chironomid taxonomic composition occurred at *ca*. 1960 (most differences could be explained by age-depth model uncertainties), leading to potential dramatic effects on regional biodiversity. Lakes are ranked according their latitude (e.g. northern sites towards the top)

where DC1 scores reached maximum or minimum values during the most recent period. In contrast, only four lakes exhibited a slight backward trajectory, where DC1 scores reached maximum or minimum values during the 1960–1980 period (Fig. 4 upper panel), and more pronounced backward trends were observed in Lake Försjön and Lake Övre Skärsjön records (see also ESM1 C and E). Furthermore, the grouping into forward (Fig. 4 lower panel) and backward (Fig. 4 upper panel) trajectories cannot be explained either by differences in anthropogenic land-use (forested vs. agricultural landscapes; Table 1 and Fig. 4) or SO_4^{2-} deposition levels (Fig. 2C).

Chironomid taxa scores of DC1 axis were also extracted to infer past changes in environmental conditions, and to classify the chironomid morphotypes into acid-sensitive or acid-tolerant morphotypes. Out of 53 chironomid morphotypes identified in the sediment records, only nine chironomid morphotypes had sufficient background information to define their pH affinities, thus, corresponding to only 17–33% of the total chironomid diversity of each lake. However, these nine indicator taxa comprised the predominant morphotypes in each of the chironomid communities. Acid-sensitive and acid-tolerant morphotypes were, in most cases, located towards opposite ends of DC1 axis (red vs. green dots in Fig. 5), suggesting contrasted responses to pH and environmental changes. Overall, sample and chironomid scores of DC1 axis illustrated higher development of acid-tolerant chironomid morphotypes after 1960 and conversely, lower development of acid-sensitive morphotypes (Figs. 4 and 5), thus, showing a good agreement with the expected acidification history (Fig. 2C). Interestingly, chironomid communities of Lake Holmeshultasjön also showed a strong taxonomic shift at *ca*.

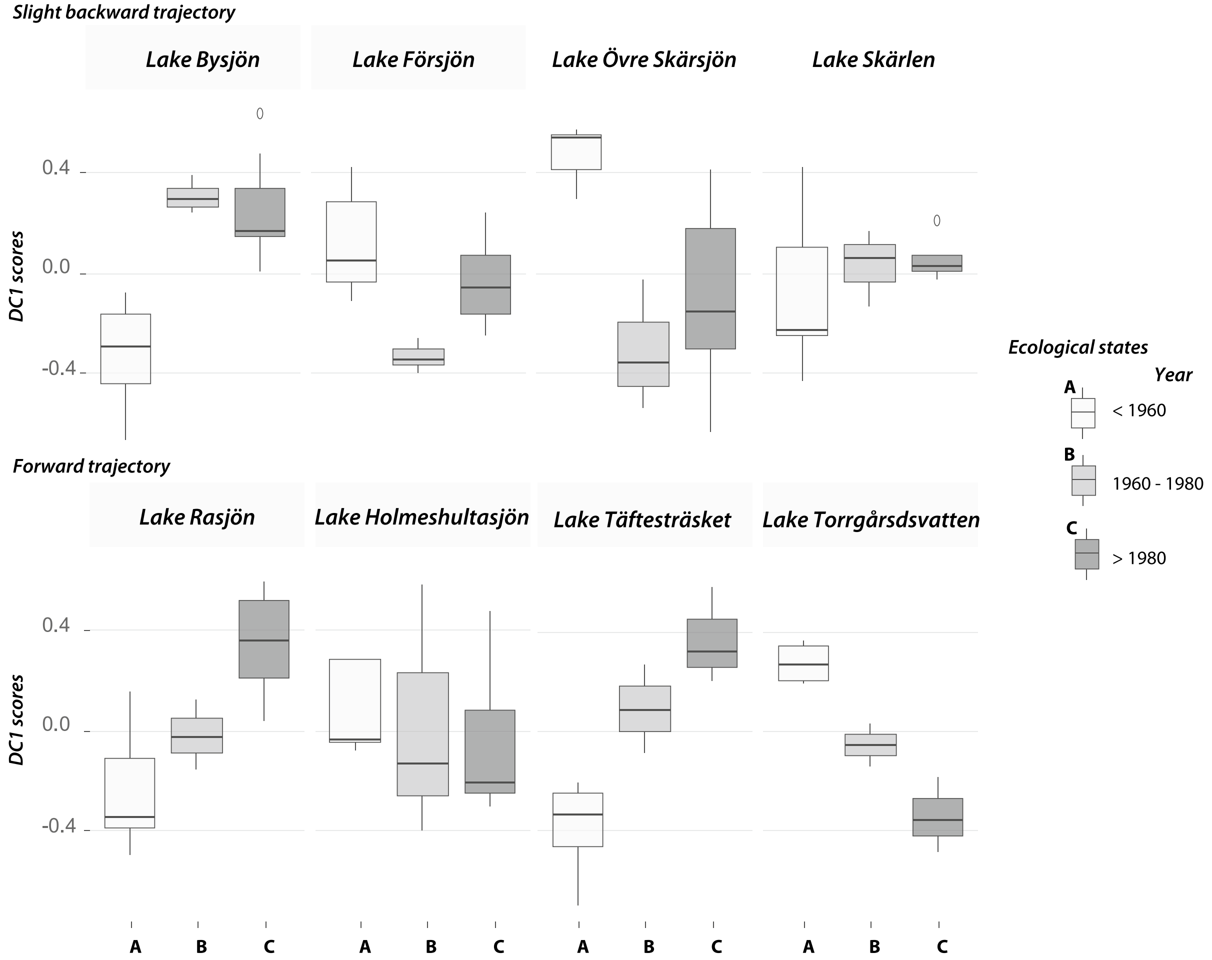


Fig. 4 Boxplots showing the scores of the first axis of a detrended correspondence analysis (DC1 scores) applied on chironomid taxonomic composition of the eight studies lakes. Each boxplot represents the three following periods: pre-acidification period (**A**; < 1960 AD), sulphate deposition peak (**B**; 1960–1980) and recovering period (**C**; > 1980 AD). Lakes are also grouped according to temporal trends in DC1 scores, showing a slightly backward trajectory (Lake Bysjön, Lake Övre Skärsjön, Lake Försjön, Lake Rasjön and Lake Skärlen), or forward trajectory (Lake Täftesträsket, Lake Torrgårdsvatten, Lake Rasjön and Lake Holmeshultasjön)

1960, but temporal trends in the main acid-tolerant and acid-sensitive morphotypes (*Sergentia coracina* type and *Tanytarsus lugens* type) differed from their responses to acidification (ESM Fig. 1G). Furthermore, beside the main change in predominant morphotypes, the 1960 taxonomic shift was also characterized by the disappearance of a few small-sized taxa: such as *Cricotopus interseptus* type and *Cladopelma lateralis* in Lake Bysjön; *Heterotrissocladius marcidus* type in Lake Täftesträsket; *Micropsectra insignilobus* type and *Cladopelma lateralis* in Lake Bysjön; *Heterotrissocladius grimshawi* in Lake Torrgårdsvatten (see also ESM Fig. 2). During the most recent period, results also showed an increase of oxygen tolerant species, warm-water taxa and morphotypes typically found in humic waters and characterizing higher trophic status (such as *Heterotanytarsus*; *Chironomus anthracinus* type; *Zalutschia zalutshicola* type; Fig. 5).

Relationships between the gradient length of DC1 axis applied on individual chironomid records and environmental variables and physical properties of the catchment showed that browner lakes tended to have higher taxonomic turn-over ($R^2 = 0.55$, P value < 0.001, Fig. 6A). Furthermore, the gradient length of DC1 axis appeared to be also negatively

Fig. 5 Scores of the main chironomid morphotypes along the first axis of a detrended correspondence analysis (DC1 scores) applied on chironomid taxonomic composition of the eight studies lakes. Acid-tolerant morphotypes are marked with red names and dots, whereas green dots and names refer to acid-sensitive morphotypes. Lakes are also grouped according to temporal trends in DC1 scores, showing a slightly backward trajectory (Lake Bysjön, Lake Övre Skärsjön, Lake Försjön, Lake Rasjön, and Lake Skärlen), or forward trajectory (Lake Täftesträsket, Lake Torrgårdsvatten, Lake Rasjön and Lake Holmeshultasjön)

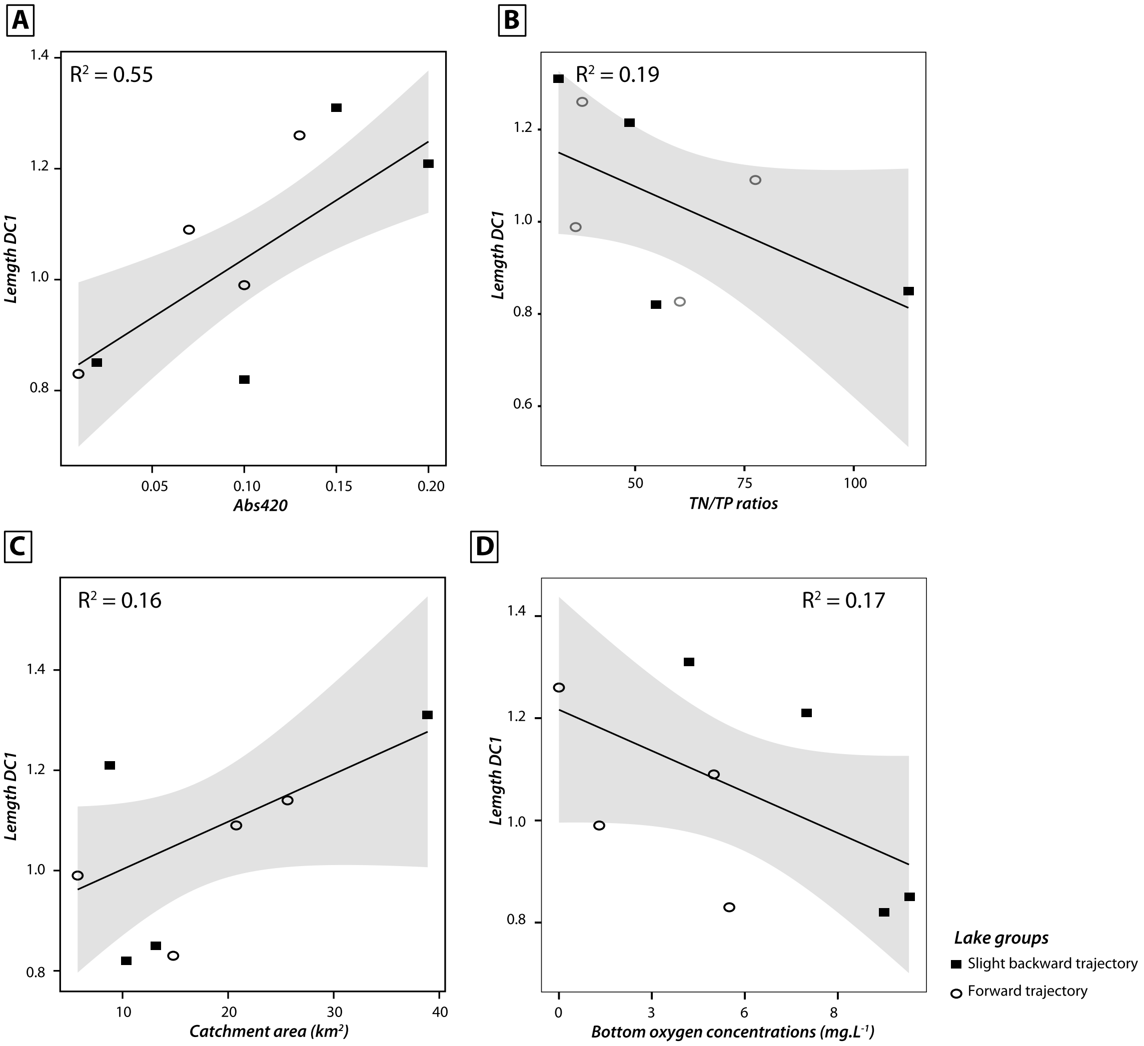


Fig. 6 Relationships between the length the first axis of a detrended correspondence analysis (DC1 length) applied on chironomid taxonomic composition and **A** water illustrated by measurements of absorbance at 420 nm, **B** present-day lake water total nitrogen to total phosphorus concentrations ratios (TN/TP ratios), **C** catchment area (km^2) and **D** bottom oxygen concentrations (mg/L)

associated with present-day TN/TP ratios (Fig. 6B), where higher taxonomic turn-over was observed in records from low TN/TP ratios (nitrogen-limited lakes). To a lesser extent, catchment area ($R^2 = 0.19$, P value = 0.12, Fig. 6C) and bottom oxygen concentrations could also be additional drivers of change in chironomid community composition, where large catchment and low oxygen levels could lead to higher taxonomic turn-over ($R^2 = 0.16$, P value = 0.12, Fig. 6C; $R^2 = 0.17$, P value = 0.10, Fig. 6D). Some of the statistical relationships were also expected to be non-linear (e.g. nitrogen deposition differentially affected nitrogen-limited and phosphorus-limited lakes), but they could not be identified to the low number of records available. Finally, the previously defined groups consisting of lakes following forward and slight backward trajectories did not show any specific locations across the water colour, catchment area and oxygen gradients (open circles vs. squares in Fig. 6).

Discussion

Re-examining the effects of acidification on Scandinavian freshwater lakes using paleolimnological investigations, our study showed a widespread shift in chironomid community composition occurring at *ca*. 1960 concomitant with acidification. Results also showed that taxonomic turn-over was higher in records from nitrogen-limited lakes, likely due to the cumulative effects of acidification and eutrophication driven by atmospheric nitrogen deposition. Despite strong evidence of chemical recovery from acidification, none of the lake records indicated return to pre-acidified community compositions, but instead chironomid communities continued to follow the trajectories triggered by acidification. We hypothesized that when SO_4^{2-} deposition started to decrease after 1980, the influence of pH and/or other acidification-related variables in structuring chironomid community would decrease during the post-acidification period and the relative importance of other rapidly changing drivers, such as brownification-associated and climatic processes, would increase. Results, therefore, suggest the key role of acidification in shaping the response of chironomid communities to future environmental changes. Moreover, our study highlights the urgent need to better unravel the mechanisms underlying impacts and recovery of Scandinavian freshwater lakes under ongoing environmental changes. By allowing to quantify the effectiveness of different management actions taken to counteract acidification and to redefine appropriate restoration targets, future similar paleolimnological studies will also contribute to better manage aquatic ecosystems recovering from acidification worldwide.

Acidification of freshwater lakes in Scandinavia: mechanisms underlying impacts and recovery of chironomid community under accelerating environmental changes

Previous work has shown that chironomid larvae have a wide tolerance to pH (Wiederholm & Eriksson, 1977; Mossberg & Nyberg, 1979; Olander, 2002). However, despite the relatively extensive SO_4^{2-} deposition gradient of our study (from heavily impacted areas in Southern Sweden to moderately impacted areas in North-Eastern Sweden), results revealed long-term taxonomic patterns along the acidification gradient from natural status to more acidic conditions. However, reliable information concerning chironomid affinities to pH are rare and often contradictory, and it is difficult to provide a hierarchical understanding of the drivers (including pH and other environmental variables) regulating chironomid community assembly. For instance, *Microtenpides pedellus* type and *Dicrotendipes nervosus* type, previously depicted as acid-tolerant morphotypes, showed instead a decreasing trend after 1960 in one of the studied sediment records (i.e. Lake Holmeshultasjön). *Sergentia coracina* type, another acid-tolerant morphotype, showed alternatively positive (see also Lake Försjön and Lake Övre Skärsjön) or negative responses (e.g. Lake Torrgårdsvatten) to acidification (Figs. 4 and 5). Discrepancies between expected and observed temporal patterns could be explained by: taxonomic level of identification (e.g. Svitok et al., 2021 reported that *Tanytarsus lugens* type and *Tanytarsus mendax* type had opposite affinities to pH in alpine lakes, but these two morphotypes cannot be distinguished in our study due to the absence of mandibles); species diversity within each morphotype (see also differences in pH affinity within genus *Micropsectra*; Orendt, 1999); and finally a wider tolerance of acidity than previously assumed (Hynynen & Meriläinen, 2005). Furthermore, the 1960 taxonomic shift was, to some extent, characterized by the disappearance of some small-sized taxa with no previously reported sensitivity to pH variation (e.g. *Cricotopus interseptus* type in Lake Bysjön; *Heterotrissocladius marcidus* type in Lake Täftesträsket; *Micropsectra insignilobus* type and *Cladopelma lateralis* in Lake Bysjön; *Heterotrissocladius grimshawi* in Lake Torrgårdsvatten). These findings suggest that tolerance of acidic conditions appears to be partially related to body size (i.e. with tolerance to low pH being potentially lower for smaller species; Weiderholm & Eriksson, 1977).

Widespread shifts in chironomid biodiversity observed in all studied lakes at around 1960 corresponded with the maximum fallout of anthropogenic SO_4^{2-} deposition (Fig. 2C) whereas other environmental and climatic variables showed no specific pattern (Fig. 2A and B). Higher taxonomic turn-over was found in records from nitrogen-limited lakes, likely due to the cumulative effects of acidification and eutrophication driven by atmospheric nitrogen deposition. Previous studies showed that nitrogen deposition led to stronger impacts on nitrogen-limited lakes, because increasing availability of nitrogen induced higher development of phytoplankton in such ecosystems (Bergström et al., 2005; Bergström & Jansson, 2006). These patterns also coincided with similar large-scale taxonomic shifts observed around mid-1900 in other biological communities in Scandinavia, Eastern Europe, and Northern America (Schindler et al., 1989; Cumming et al., 1992; Moiseenko, 2005). Considering that acidification played a key role in regulating aquatic community assembly over large spatial scales, selecting species with the highest ability to persist under lower pH conditions, anthropogenic SO_4^{2-} deposition should, therefore, have led to dramatic effects on aquatic biodiversity at the regional scale. However, ecological implications for regional diversity and restoration remain largely unknown, as most ecological and paleolimnological studies fail to think beyond the single-lake paradigm (Heino et al., 2021). Furthermore, chironomids with relatively weak adult flying stages can disperse over a short spatial range (up to 400 m reported in agricultural and open landscapes, Delettre & Morvan, 2000; up to 300 m in alpine catchments, Bitusik et al., 2017a). Whereas an active dispersal capability could allow chironomids to recolonize aquatic ecosystems if their quality improves (Lake et al., 2007), their relatively low dispersal potential could lead to slow biological recovery in lakes surrounded by anthropogenic acidified ecosystems (Bitusik et al., 2017a; b), as the distance to undisturbed ecosystems may be too large. The degree of connectivity between lakes and the distance to non-acidified ecosystems could be significant factors explaining the slow recovery rates of acidified lakes, but their influences remain largely understudied.

Temporal changes in subfossil chironomid communities did not support the hypothesis of a strong natural recovery after SO_4^{2-} deposition peaked. A slight recovery in acid-sensitive chironomid morphotypes was only observed in 4 sites, but these communities failed to reach pre-acidification compositions. These findings, therefore, support the view of a slow biological recovery of chironomid communities from acidification as previously observed in other Swedish lakes (Henrikson et al., 1982; Henrikson & Oscarsson, 1985; Holmgren, 2004; Johnson & Angeler, 2010; Angeler & Johnson, 2012). The post-acidification period (after 1980) was also a period of rapid environmental and climatic changes in Scandinavia and likely induced ecological changes in lakes as illustrated by continuous turn-over in chironomid community composition in most sediment records. As a result, identification of biological recovery from acidification was largely hampered by accelerating environmental and climatic changes. Using similar paleolimnological investigations, Svitok et al. (2021) showed that the modern chironomid community composition of lakes recovering from acidification did not reach pre-acidification composition, thus, supporting the view that ongoing changes became the overwhelming driver of change for chironomid community. Acidity is often of least importance compared to the other drivers usually involved in structuring chironomid community composition (such as temperature and oxygen concentrations, Larocque et al., 2001; Verbruggen et al., 2011), and a substantial increase in pH (as a consequence of decreasing SO_4^{2-} deposition) may lead to reshuffling the hierarchy of environmental variables driving community assembly. In our study, post-1980 taxonomic changes were characterized by higher developments of oxygen-tolerant and warm-water morphotypes, and chironomid taxa typically found in humic waters (e.g. see also patterns in *Chironomus anthracinus* type, *Heterotanytarsus*, *Zalutschia zalutshicola* type). These findings confirmed similar changes in chironomid community composition previously reported in Swedish lakes (Henrikson et al., 1982; Henrikson & Oscarsson, 1985), and it is, thus, reasonable to infer that the studied lakes during the most recent period were characterized by browner and nutrient-rich water, as well as lower levels of oxygenation. Post-1980 taxonomic changes in chironomid community could, therefore, be driven by brownification, as increasing water organic matter concentrations was synchronically reported in monitoring records of northern regions (de Wit et al., 2007) and Swedish lakes (Eklöf et al., 2021). Results could corroborate strong effects of brownification on aquatic communities (see also Creed et al., 2018), and suggest that it became the overwhelming driver of ecological changes during the last three decades. However, as chironomid humic water taxa are also indicators of warm-water environments, it is difficult to separate brownification and temperature effects. Nevertheless, we hypothesized that when SO_4^{2-} deposition started to decrease, the influence of pH in structuring chironomid community became less important, leading to a reshuffle of the hierarchy of environmental variables driving community assembly, giving more importance to the brownification-associated and climatic processes. These findings suggest that we should consider investigating how brownification and climate change interact with biological recovery from acidification, instead of focusing on each environmental issue separately, as acidification is expected to play a key role in shaping the response of chironomid communities to future environmental changes.

Our results also show that catchment size could play a key role in mediating the effects of ongoing environmental and climate changes on chironomid communities. Lakes situated in relatively large catchments could be subjected to higher taxonomic turnover during the post-acidification period (after 1980), as a result of higher terrestrial organic carbon export leading to browner water and lower oxygen concentrations (see also Creed et al., 2018). Our data could, therefore, corroborate the influence of catchment properties on water organic carbon concentrations in lakes (Houle et al., 1995, 2020; Sobek et al., 2007), and confirm that ongoing changes are mainly driven by landscape-associated processes. Further investigations are, however, needed to better explore these patterns as many studies have highlighted that lake retention time was a better predictor of water organic carbon concentrations than catchment area.

How to assess biological recovery from acidification and the efficacy of management actions under accelerating environmental changes?

Our study highlights the urgent need to consider the potentially complex interactions between recovery from acidification and ongoing environmental and climatic changes as they may cause hysteresis and recovery trajectories that differ from predictions. Furthermore, unravelling the mechanisms underlying impacts and recovery of Scandinavian freshwater lakes under ongoing environmental changes will help redefine restoration targets, thus, allowing to better quantify the efficacy of the management interventions to mitigate the effects of acidification. Among others, liming, as limestone additions to mitigate acidification (Svenson et al., 1995), became a large-scale and governmentally supported restoration program in the 1980's in many countries (Bernes, 1991). In Sweden, more than 5000 lakes have been limed since 1980, but its efficacy is still largely debated (see also Angeler et al., 2017). Among others, repeated liming of lakes has been regarded as a substantial alteration of natural disturbance regimes (McKie et al., 2006) that could lead to undesired ecological impacts (see also Angeler & Goedkoop, 2010). Furthermore, our study revealed that the influence of pH and/or other acidification-related variables in structuring chironomid communities was only predominant during the maximum fallout of anthropogenic SO_4^{2-} deposition (1960–1980), a period of low environmental and climatic changes. Subsequently, a small increase in pH (driven by decreasing SO_4^{2-} deposition) during a period of rapidly changing environmental and climatic conditions may have reshuffled the hierarchy of environmental variables driving community assembly. In this context, further paleolimnological investigations will probably demonstrate that chironomid community composition in repeatedly limed lakes differed from those of naturally recovering lakes because liming became the overwhelming driver for these managed ecosystems. By quantifying the efficacy of different actions to mitigate acidification, future studies will contribute to better management, as well as possibly redefine restoration targets of aquatic ecosystems recovering from acidification.

Acknowledgements This study is part of the CENTURION (Cumulative effects of climate change and eutrophication on Swedish lakes; Grant Number: NV-802-0047-19) project funded by the Swedish Environmental Protection Agency to Simon Belle (SLU). We thank Jenny L. Nilsson and Joachim Place for assistance during fieldwork, Peter Appleby and Gayane Piliposian (University of Liverpool, UK) for their help during the dating of sediment cores, and Jens Fölster (Swedish University of Agricultural Sciences) for providing SO_4^{2-} deposition data.

Funding Open access funding provided by Swedish University of Agricultural Sciences. Funding was provided by Naturvårdsverket (Grant No. NV-802-0047-19)

Data availability Enquiries about data availability should be directed to the authors.

Declarations

Conflict of interest The authors have not disclosed any competing interests.

Ethical approval There are no ethical issues with the present study. All required sampling licenses will be asked, and special consideration will be given to local communities at each step of the study. All institutions and universities involved in the network are equal opportunity employers with active policies against discrimination based on gender, religion or handicap.

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