Journal of Environmental Management 373 (2025) 123546

Contents lists available at ScienceDirect

Journal of Environmental Management

journal homepage: www.elsevier.com/locate/jenvman

Research article

Liming-induced taxonomic homogenization of chironomid assemblages in Scandinavian lakes as unraveled by paleolimnological reconstructions

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ARTICLE INFO

Handling editor: Jason Michael Evans

Keywords:
Acidification
Lake
Liming
Chironomidae
Stable isotopes
Paleolimnology

ABSTRACT

In the 1980s, liming became a large-scale, governmentally supported restoration program implemented by many countries to mitigate the effects of acidification of freshwaters. Despite some 50 years of liming of thousands of lakes and streams, its efficacy remains largely debated. This study is the first of its kind to use paleolimnological reconstructions using both subfossil chironomid assemblages and their carbon stable isotopic composition to compare the ecological trajectories of limed and control (unlimed) lakes over the last 100 years in order to unravel the effects of liming on Scandinavian lakes. Our study revealed strong effects of liming on lake water chemistry and sedimentary characteristics of limed lakes. Overall, higher present-day pH values were observed in lake water of the limed lakes (average pH of 6.7 ± 0.2) than in control lakes (average pH of 5.9 ± 0.5), and the pH variability was much lower among limed lakes. A decrease in the dissimilarity of the chironomid assemblages among limed lakes was also observed as liming progressed, and the degree of dissimilarity after liming was largely lower than pre-acidified levels. This pattern suggests that liming favoured the selection of similar chironomid taxa in limed lakes, thus providing complementary empirical evidences about the effects of liming on aquatic communities through taxonomic homogenization of chironomid assemblages. As the ecological trajectories of limed and control lakes strongly differed, our study also questions the impact of liming on the resilience of Scandinavian lakes and, importantly, their ability to cope with ongoing and future climatic and environmental changes. Finally, isotope-based results indicated that liming masks potential complex effects on carbon flows at the base of the food web by shifting algal carbon isotopic baselines. The use of carbon stable isotope analysis of chironomid head capsules to study the effects of liming on energy flows within lake food webs is, therefore, not suitable.

1. Introduction

Acid rain due to anthropogenic atmospheric emissions triggered the acidification of countless ecosystems during the last century (Mylona, 1996), resulting in rapid biological changes in many aquatic ecosystems (especially in Scandinavia; Skjelkvåle et al., 2005). In the 1980s, the largely successful control of atmospheric emissions resulted in marked reductions in sulfur deposition, reaching pre-acidified levels in the late 1990s and early 2000s (Stoddard et al., 1999; Fölster et al., 2014). These reductions have resulted in substantial chemical recovery of many freshwater ecosystems, mainly characterized by an increase in pH and acid neutralization capacity (Garmo et al., 2014; Fölster et al., 2014). To speed up the recovery process, liming interventions became a large-scale, governmentally supported restoration measure implemented by many countries in the 1980s (Bernes, 1991; Svenson et al., 1995), and in Sweden alone, more than 8000 lakes have been limed since the early 1980s. However, despite liming resulting in improved water quality, its efficacy in mitigating effects on biodiversity and ecosystem functioning remains largely debated (see also Angeler et al., 2017).

Liming has contributed to an increase in the pH and buffer capacity in many acidified waters, potentially resulting in improved water quality for aquatic communities (Bengtsson et al. 1980), but numerous studies have reported contrasting results regarding ecological responses to liming (Hörnström, 2002; Clair and Hindar, 2005). Specifically, some studies focusing on benthic invertebrates in lakes suggested a higher occurrence of acid-sensitive taxa after liming (Hultberg and Andersson, 1982; Eriksson et al., 1983), whereas others reported limed lakes tended to have lower diversity and abundances of invertebrates when compared to reference lakes (Persson and Appelberg, 2001; Appelberg and

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https://doi.org/10.1016/j.jenvman.2024.123546
Received 20 August 2024; Received in revised form 18 November 2024; Accepted 29 November 2024

Svenson, 2001). Repeated liming is also assumed to alter the ecosystems' natural disturbance regime (McKie et al., 2006), potentially leading to a homogenization of community assembly processes (Baho et al., 2014). Furthermore, liming is known to influence the density and activity of microbial communities involved in the recycling of sedimentary organic matter (Bell and Tranvik, 1993; Gahnström, 1995), but its implications for energy flows within lake food webs have been largely overlooked. The lack of long-term data beyond traditional monitoring windows (a few decades at best; see also Norberg et al., 2008), however, complicates identifying the mechanisms underlying lake ecosystem responses to liming.

Analysis of biological remains archived in lake sediments is a powerful approach to circumvent the lack of monitoring data (Walker, 2001) and to 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 lake sediments, are morphologically and chemically well-preserved in sediments. 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 effects of liming on lakes. Novel techniques consisting of analyzing the carbon stable isotopic composition ($\delta^{13}C$) of subfossil chironomids have also been developed to provide quantitative and qualitative measurements of carbon flows in food webs (Frossard et al., 2013; Belle et al. 2017, 2020). Differences in carbon isotopic fractionation by primary producers (aquatic *vs*. terrestrial producers) and bacteria lead to basal food resources that differ in their $\delta^{13}C$ values (Jones et al., 1999; Vuorio et al., 2006), thus allowing us to elucidate the impacts of liming on long-term carbon processing at the base of lake food webs. Hence, combining taxonomic and isotopic approaches using subfossil chironomids will allow us to better unravel the effects of liming on lakes and their communities.

This study aims to quantify the effects of liming on chironomid taxonomic composition and carbon flows at the base of lake food webs using paleolimnological reconstructions. Using temporal changes in taxonomic composition of subfossil chironomid assemblages in limed and control (unlimed) lakes, we tested the hypothesis that liming-induced changes in lake water chemistry resulted in taxonomic shifts in chironomid assemblages. We also analyzed the isotopic composition of chironomid head capsules to quantify the extent to which liming affected carbon flows through lake food webs by driving changes in the microbial communities involved in the recycling of sedimentary organic matter.

2. Material and methods

2.1. Study sites and recent environmental changes

Eight small (area range 30–300 ha) and deep (maximum water depth range 16.5–32 m) lakes with relatively small catchments (ranging 2.3–38.1 km^2) located in Sweden were studied (Table 1 and Fig. 1). The lakes lie on the Fennoscandian shield, a bedrock predominated by highly siliceous granite and gneiss, making the water weakly conductive, slightly acidic, and poorly capable of acid neutralization. Liming started in the early 1980s for Lake Lagmanshagasjön, Lake Majsjön, Lake Södra Färgen, and Lake Tryssjön to mitigate the effects of acidification(see Table 1 for exact years; https://kalkdatabasen.lansstyrelsen.se), whereas the other four lakes were not limed (control sites).

Modelled SO_4^{2}- deposition data for the period 1880–2020, available

Fig. 1. Map showing the location of the study sites. Dark blue symbols refer to the limed lakes, and orange symbols represent control lakes.

Table 1

Physical and chemical characteristics of the 8 studied lakes. Abbreviations for variables include: Limed ~ start year of liming (NO, not limed); CA – Catchment area (km^2); Depth – maximum lake depth (m); Area – lake area (km^2); Abs420 – absorbance at 420 nm; Chl – total chlorophyll 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); NO2+NO3 – sum of nitrite and nitrate ions (μg/L N), NH_4N – ammonium (μg/L N), Secchi – water transparency as Secchi disk depth (m), O2 – oxygen concentration (mg/L). Major ion concentrations (Ca$^{2+,}$ Mg^{2+}) are expressed in mg/L. Surface water data from summers of years 2015–2020, except for O2 which is from bottom water measurements from https://miljodata.slu.se/mvm/.

Lake	Limed	CA	Depth	Area	Abs420	Ca	Chl	Cond25	Mg	NH4N	NO2NO3	pH	TOC	Tot_P	Tot_N	Secchi	O2
Holmeshultasjön	NO	5.8	16.5	0.6	0.1	4.8	4.0	6.4	1.8	13.5	91.6	6.9	10.1	7.0	254.0	3.3	1.3
Lagmanshagasjön	1986	38.1	17.0	3.0	0.4	6.3	3.7	6.4	1.2	33.0	188.0	6.9	19.7	7.0	433.0	1.5	3.7
Majsjön	1980	19.8	23.5	3.0	0.2	4.4	4.1	5.7	0.9	13.3	160.8	6.7	9.9	7.0	410.0	2.5	6.4
Södra Färgen	1983	25.6	17.3	2.8	0.2	5.5	4.4	7.3	1.2	28.3	137.7	6.9	9.4	4.0	570.0	2.7	NA
Torrgårdsvatten	NO	14.8	29.2	0.5	0.0	0.7	0.9	4.8	0.7	38.7	139.3	5.5	1.8	4.5	271.0	2.4	5.5
Tryssjön	1981	12.2	19.6	0.3	0.3	2.7	1.2	3.3	0.4	23.2	16.3	6.4	13.7	8.7	412.0	11.1	8.7
Övre Skärsjön	NO	8.8	32.0	1.7	0.2	1.2	2.4	2.2	0.7	22.0	65.6	5.8	10.2	6.6	321.0	2.1	8.0
Örvattnet	NO	2.3	32.0	0.8	0.0	0.7	2.0	1.7	0.3	27.9	64.7	5.5	4.6	5.6	250.0	4.2	9.6

from the European Monitoring and Evaluation Program (EMEP), were extracted using lake coordinates. Late summer water chemistry data from the lakes was retrieved from the Swedish data host for freshwater monitoring (https://miljodata.slu.se/mvm/) from 2015 to 2020, calcium, magnesium, total organic carbon, total chlorophyll-*a*, nutrient and bottom water oxygen concentrations, and light absorbance at 420 nm, water conductivity, pH and Secchi depth (Table 1). Furthermore, long-term mean annual temperature data from the SMHI database (https://www.smhi.se) was used as a measure of climate change during the study period.

2.2. Sediment coring and dating techniques

In June–July 2020, sediment cores were retrieved from the deepest point of the lakes using a gravity corer (9 cm in diameter: UWITEC). At the laboratory, all sediment cores were vertically split into two halves, and one split core of each lake was sliced into 1 cm thick sediment layers stored at +4 °C until further analysis. Sediment cores were dated by ^{210}Pb and ^{137}Cs at Liverpool University's Environmental Radioactivity Laboratory following Appleby et al. (1986) and Appleby and Oldfield (1992). Ages were calculated using the Constant Rate of Supply model (CRS; Appleby and Oldfield, 1978; Appleby, 2002). Chronologies are described in detail in ESM1.

2.3. Sediment analysis

The surface of one half of the split core was covered with Ultralene® foil to avoid desiccation and this core was then transported to the University of Stockholm, Sweden to be scanned every 5 mm using an ITRAX XRF Core Scanner (Cox Analytical Systems). XRF measurements were carried out using a Mo tube, set at 30 kV and 30 mA, for 60 s to detect relative sedimentary calcium concentrations (Ca_{sed}-XRF). Elemental intensities were expressed as counts per unit time per unit area (cps).

The uppermost 1 cm of each sediment core was collected and assumed to represent present-day conditions, and analyzed for organic matter concentration (OM, loss-on-ignition as % of dry mass), carbon and nitrogen concentration, and C/N weight ratios at our Stable Isotope Laboratory (SLU, Umeå, Sweden). Sedimentary pigments were analyzed following the modified method of Thrane et al. (2015) and the sum of carotenoid pigments was calculated (TC; Belle et al., 2022). The organic matter fraction of each sediment sample was also analyzed for carbon stable isotopes ($\delta^{13}C_{OM}$) and used as an estimate of the isotopic baseline for chironomid larvae. Before analysis, sediment samples were dried at 60 °C for 72h, ground, and about 3 mg of dried sediments were transferred to silver capsules, and carbonate removal was done using small additions (50 μL) of HCl 1M. Carbonate-free sediment samples were then placed in tin capsules and analyzed using an Isotope Ratio Mass Spectrometer interfaced with an Elemental Analyzer (EA-IRMS) at our Stable Isotope Laboratory (SLU, Umeå, Sweden). Results were expressed as the delta notation with Vienna Pee Dee Belemnite and atmospheric nitrogen as standards: $\delta^{13}C$ (‰) = [(Rsample/Rstandard) − 1] x 1000; where R = $^{13}C/^{12}C$. Sample measurement replications from internal standards (wheat and mays flour) produced analytical errors (1σ) of ±0.15 ‰ for both $\delta^{13}C$ and $\delta^{15}N$ values (n = 30).

2.4. Chitinous remains analysis

Between 8 and 20 sediment samples per core were analyzed for chironomid head capsules. Chironomid head capsules were hand-sorted from each sample of wet sediment (*ca.* 15g wet weight) following Walker (2001) and mounted between microscope slides. Chironomid assemblage composition was identified under a microscope using Brooks et al. (2007) and Rieradevall and 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.

Carbon stable isotope analyses were also performed on chironomid head capsules belonging to the 4th instar (following recommandations from Frossard et al., 2013) of morphotypes *Sergentia coracina*-type and *Chironomus anthracinus*-type. These morphotypes typically inhabit the profundal zones of lakes, and they belong to the functional feeding group of the deposit feeders (Berg, 1995). *Sergentia coracina*-type and *Chironomus anthracinus*-type form an important link between basal resources and higher trophic levels in the food webs, thus being highly suited to unravel the effects of liming on the recycling of sedimentary organic matter and associated microbial communities (see also Gahnström, 1995). These taxa are also usually found in high abundances in Swedish lakes, allowing us to obtain sufficient material for stable isotope analysis. For the extraction of chitinous remains, sediment samples were deflocculated in NaOH (10%) solution, pre-treated using washing with HCl (10%) solution, and sieved through a 100-μm mesh. Head capsules were sorted under a dissection microscope until a minimal mass of approximately 30 μg was obtained. Carbon stable isotopic composition of chitinous remains ($\delta^{13}C_{HC}$) was analyzed using an Isotope Ratio Mass Spectrometer interfaced with an Elemental Analyser (EA-IRMS) at our Stable Isotope Laboratory (SLU, Umeå, Sweden), and results were expressed as the delta notation (see above). Sample measurement replications from internal standards (wheat and mays flour) produced analytical errors (1σ) of ±0.15 ‰ for $\delta^{13}C$ values (n = 14). The potential shift in the isotopic baseline was calculated as the difference between the carbon stable isotopic composition of chironomid remains and organic matter (i.e., $\delta^{13}C_{HC}$-adj = $\delta^{13}C_{HC}$ - $\delta^{13}C_{OM}$). $\delta^{13}C_{HC}$-adj has also been used as an indicator of the selective feeding behaviour of chironomid larvae in previous studies (Belle et al., 2017).

2.5. Data analysis

Principal component (PC) analyses were applied to the present-day water chemistry and sedimentological datasets, respectively, to capture the main differences in lake water and sediment composition between lake groups (limed *vs.* control lakes). Permutational multivariate analysis of variance (PERMANOVA) was used to test whether there was a significant difference in water chemistry and sediment composition between lake groups (using the *adonis* function for R; Oksanen et al., 2015). Non-metric multidimensional scaling (NMDS) based on a Bray-Curtis dissimilarity matrix was performed to explore the similarity of trends in assemblage structure over the study period across lake groups (limed *vs.* control lakes). To quantitatively measure temporal changes in within-group dissimilarity, we used samples representing the pre-acidification, acidification, and post-acidification periods (at *ca.* 1900, 1970, and 2020 AD, respectively) and calculated areas of the convex hull encompassing all the observations for each lake group (limed *vs.* control lakes). A decrease in the convex hull area indicates that samples are closer to each other in the NMDS plot, thus reflecting more similar chironomid taxonomic composition and a decrease in the within-group dissimilarity. To quantify the impacts of liming on carbon processing at the base of the lake food webs, time-series of $\delta^{13}C_{HC}$ and $\delta^{13}C_{HC}$-adj values were divided into two periods: early 1900–1980 and 1980–present-day for the control lakes; for the limed lakes the start of the liming (varying from 1980 to 1986) was chosen as a range limit (see also Table 1). Differences between each period were calculated for each lake (with [average $\delta^{13}C_{HC}$ values after 198x] - [average $\delta^{13}C_{HC}$ values before 198x]=Δ-$\delta^{13}C_{HC}$) and each variable (Δ-$\delta^{13}C_{HC}$ and Δ-$\delta^{13}C_{HC}$-adj). Temporal trends in sedimentary calcium concentrations (Ca_{sed}-XRF) were standardized by calculating z-scores, and boxplots were used to quantify differences between three periods (pre-acidification period: 1900–1940; acidification period: 1940–1980; post-acidification period: 1980–2020) for each lake group (limed *vs.* control lakes), and 1980 was replaced by the starting year of liming, accordingly. All statistical analyses and plots were performed using the R 4.4.0 software (R Core Team, 2024).

3. Results

Principal component analysis on water chemistry data, used to test whether liming influences present-day lake water composition, revealed that the first two PC-axes accounted for 51.3 % and 20.6 % of the total variance (Fig. 2A). PC1 explained variation in lake water calcium concentrations and pH (Fig. 2C), whereas PC2 largely reflected Secchi depth and lake water total phosphorus concentration. Lakes were mainly located along PC1, and PERMANOVA results revealed that the lake water of the limed lakes significantly differed from that of control lakes ($R^2 = 0.61$; *p*-value = 0.04). The first two PC-axes applied to the sedimentological dataset accounted for 42.7 % and 28.5 % of the total variance (Fig. 2B). Overall, lake groups clustered well along both PC1 and PC2, reflecting higher sedimentary calcium concentrations in limed lake sediments and higher $\delta^{13}C_{OM}$ values (Fig. 2D). PERMANOVA results revealed that liming significantly affected sediment composition ($R^2 = 0.46$; *p*-value = 0.04).

Modelled sulfur deposition data for the period 1880–2020, available from the European Monitoring and Evaluation Program (EMEP), showed a sharp increase in deposition from 1940 followed by a peak with high deposition between *ca.* 1960 and mid-1980, and there after deposition has steadily decreased to low levels (Fig. 3A). The onset and maximal imprint of acidification were also characterized by low temporal variability in temperature. However, the post-acidification period was also marked by a period of substantial climate warming starting in the 1980s (Fig. 3A). Results of calcium concentration depth profiles in the sediment cores also showed a clear discrepancy in sedimentary calcium dynamics during the post-1980s period (Fig. 3B). The control lakes underwent a strong decrease in calcium concentrations during the post-acidification period whereas liming induced increasing concentrations largely exceeding historical levels (Fig. 3B).

A total of 8794 subfossil chironomid head capsules were identified in 116 sediment samples, with sample counts ranging from 26 to 126. Only 3 samples had head capsule counts <50 (with 26, 44, and 49 head capsules identified), and these samples did not belong to the same lake or the same period. The NMDS ordination based on chironomid assemblages showed that each lake has a unique assemblage composition and strong temporal changes in assemblage structure (Fig. 4A; ESM3). Overall, due to the diverse nature of the taxonomic composition of chironomid assemblages in the studied lakes, no specific temporal patterns were identified during the different periods. However, higher relative abundances of *Psectrocladius sordidellus*-type and lower abundances of *Sergentia coracina*-type were generally found in limed lakes during post-acidification, while the abundances of these taxa in control lakes exhibited opposite trends (Fig. 4A, ESM2 and ESM3). NMDS also showed that the oldest samples of each record and present-day samples of each lake record were located in different areas in the ordination plot (Fig. 4A), indicating that present-day chironomid assemblages differed from pre-acidified ones. In both lake groups, the convex hull area at a targeted period was lower during pre-acidified conditions than in the middle of the acidification period (*ca.* 1970; Fig. 4B), revealing a similar response to acidification characterized by increasing within-group taxonomic dissimilarities. However, the dissimilarity of the chironomid assemblage composition in the control lakes has continued to

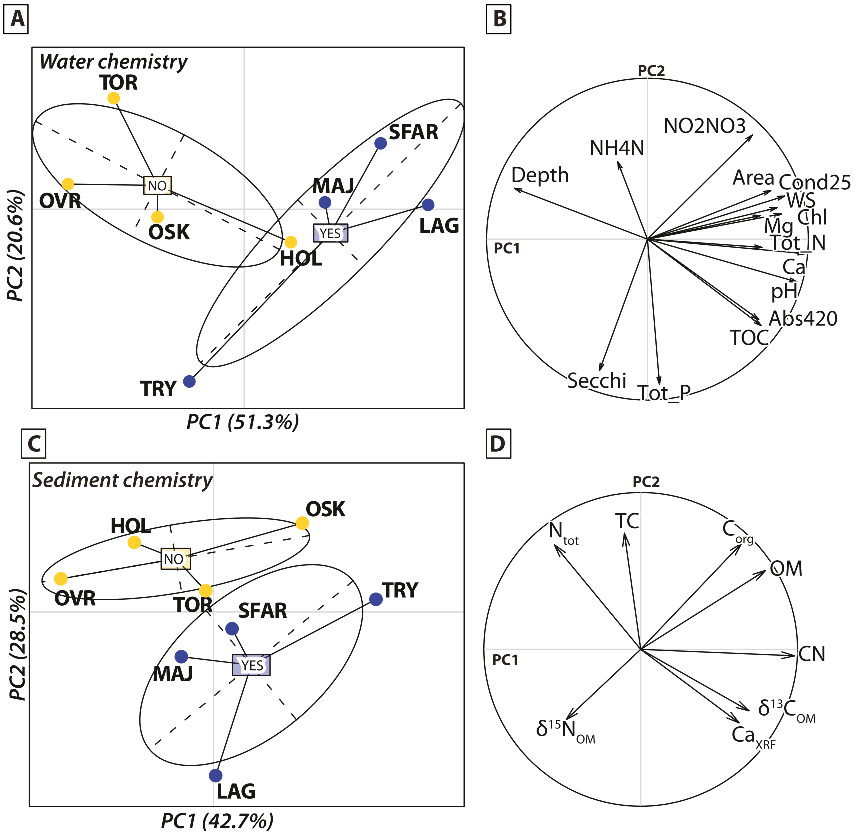

Fig. 2. Factorial maps of principal component analyses (PC1 vs. PC2) performed on present-day standardized lake water chemistry characteristics (**A**), and sediment characteristics (**C**). Ellipses represent management actions (liming = YES in dark blue; no action = NO in orange). Correlation circle representing variable contributions to the first two PC-axes performed on lake water chemistry characteristics (**C**), and sediment characteristics (**D**). Abbreviations in panel **C** are similar to the ones shown in Table 1 and in panel **D** OM refers to organic matter concentration (% of dry weight), N_{tot} to total nitrogen (% of dry weight), C_{org} to total organic carbon (% of dry weight), C/N to atomic ratio of organic carbon to total nitrogen, $\delta^{15}N_{OM}$ to stable nitrogen isotopic composition of sedimentary organic matter (‰), $\delta^{13}C_{OM}$ to stable carbon isotopic composition of sedimentary organic matter (‰), TC to total carotenoids (nmol g^{-1} OM), and Ca_{XRF} to sedimentary calcium concentration.

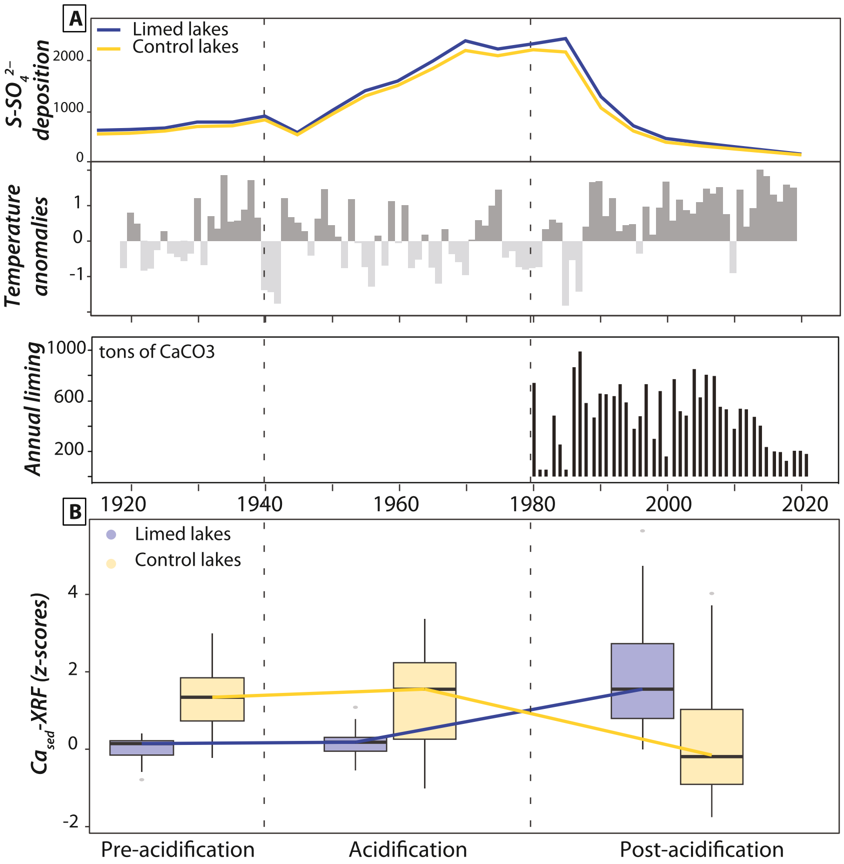

Fig. 3. Panel (**A**) shows average atmospheric sulphate sulfur (S-SO_4^{2-}) deposition time series (1920–2020) for the limed sites (dark blue) and control lakes (orange) from the European Monitoring and Evaluation Program, the evolution of mean annual temperature in Sweden during the period 1920–2020 (Swedish Meteorological and Hydrological Institute; https://smhi.se), and the amount of limestone introduced annually in the studied limed lakes (expressed as tons of $CaCO_3$ per year). (**B**) Boxplots showing the temporal trends in sedimentary calcium concentrations assessed by XRF measurements during the pre-acidification period, the acidification period, and the post-acidification. The post-acidification period (after *ca.* 1980) also corresponds to the liming period for limed lakes. Lakes are grouped according to their liming history: limed lakes in dark blue; and control lakes in orange.

increase during the post-acidification period whereas the limed lakes have become much more similar to each other after liming started (Fig. 4B). The present-day taxonomic dissimilarity observed in the limed lakes largely exceeds pre-acidified levels (green area in Fig. 4A and Fig. 4B).

The $\delta^{13}C_{OM}$ values ranged from −32.2 to −27.7 ‰ (Fig. 5A). The $\delta^{13}C_{OM}$ values were consistently lower after 1980 for control lakes, but the differences were much smaller for limed lakes, and higher $\delta^{13}C_{OM}$ values after liming were even found for one lake. In total, chironomid remains were found in sufficient numbers in 51 samples (Table 2). The $\delta^{13}C_{HC}$ values ranged from −40.8 to −29.3 ‰ (Fig. 5B) and were not associated with changes in morphotypes used for isotopic analysis (Table 2). The $\delta^{13}C_{HC}$-adj values (differences between $\delta^{13}C_{HC}$ and $\delta^{13}C_{OM}$) were always negative (ranging from −11.9 to −0.3 ‰) indicating that $\delta^{13}C_{OM}$ values were consistently higher than those of $\delta^{13}C_{HC}$ (Fig. 5C). The Δ-$\delta^{13}C_{HC}$ values (as Δ-$\delta^{13}C_{HC}$ = [average $\delta^{13}C_{HC}$ values after 198x] - [average $\delta^{13}C_{HC}$ values before 198x]) ranged from −1.9 to 5.3 ‰ (Fig. 6A). Δ-$\delta^{13}C_{HC}$ values were negative for control lakes (indicating more negative $\delta^{13}C_{HC}$ values during the most recent period), whereas positive Δ-$\delta^{13}C_{HC}$ values were found for limed lakes (indicating an increase in $\delta^{13}C_{HC}$ values after liming started; Fig. 6B). The Δ-$\delta^{13}C_{HC}$-adj values, as the differences between average $\delta^{13}C_{HC}$-adj values during [198x-present day] and [1900-198x] periods, ranged from −0.9 to 5.5 ‰ (Fig. 6C), and no specific pattern was found between lake groups (Fig. 6D). Negative Δ-$\delta^{13}C_{HC}$-adj values (such as in Lake Torrgårdsvatten and Lake Tryssjön) indicate that the difference between $\delta^{13}C_{HC}$ and $\delta^{13}C_{OM}$ values increased during the most recent period, whereas positive Δ-$\delta^{13}C_{HC}$-adj values (most lakes) indicate a decrease in the difference between $\delta^{13}C_{HC}$ and $\delta^{13}C_{OM}$ values observed during the 198x-present day period.

4. Discussion

The last 100 years covered by this study was a period of marked taxonomic changes in chironomid assemblages in Scandinavian lakes, likely driven by a complex interaction between climate change, acidification, and liming. However, due to the diversity of chironomid assemblages in the studied lakes, no consistent temporal patterns in taxonomic composition were found, and investigating the degree of similarity among groups of lakes was more appropriate for measuring responses to these pressures. During the acidification period, the patterns in taxonomic composition agreed with similar largescale taxonomic shifts driven by atmospheric depositions in Scandinavia, Eastern Europe, and Northern America (Schindler et al., 1989; Cumming et al., 1992; Moiseenko, 2005; Belle and Johnson, 2024). Specifically, we found increases in within-group chironomid taxonomic dissimilarities during acidification, suggesting that the chironomid taxonomic composition of the lakes followed different trajectories. Although not seen here, a decrease in within-group dissimilarity would have been expected if acidification led to the selection of the same taxa in all chironomid records. Results are, therefore, in line with previous studies reporting that the effects of acidification on aquatic communities may differ depending on key environmental variables, such as in-lake characteristics (Bergström et al., 2005; Bergström and Jansson, 2006; Belle

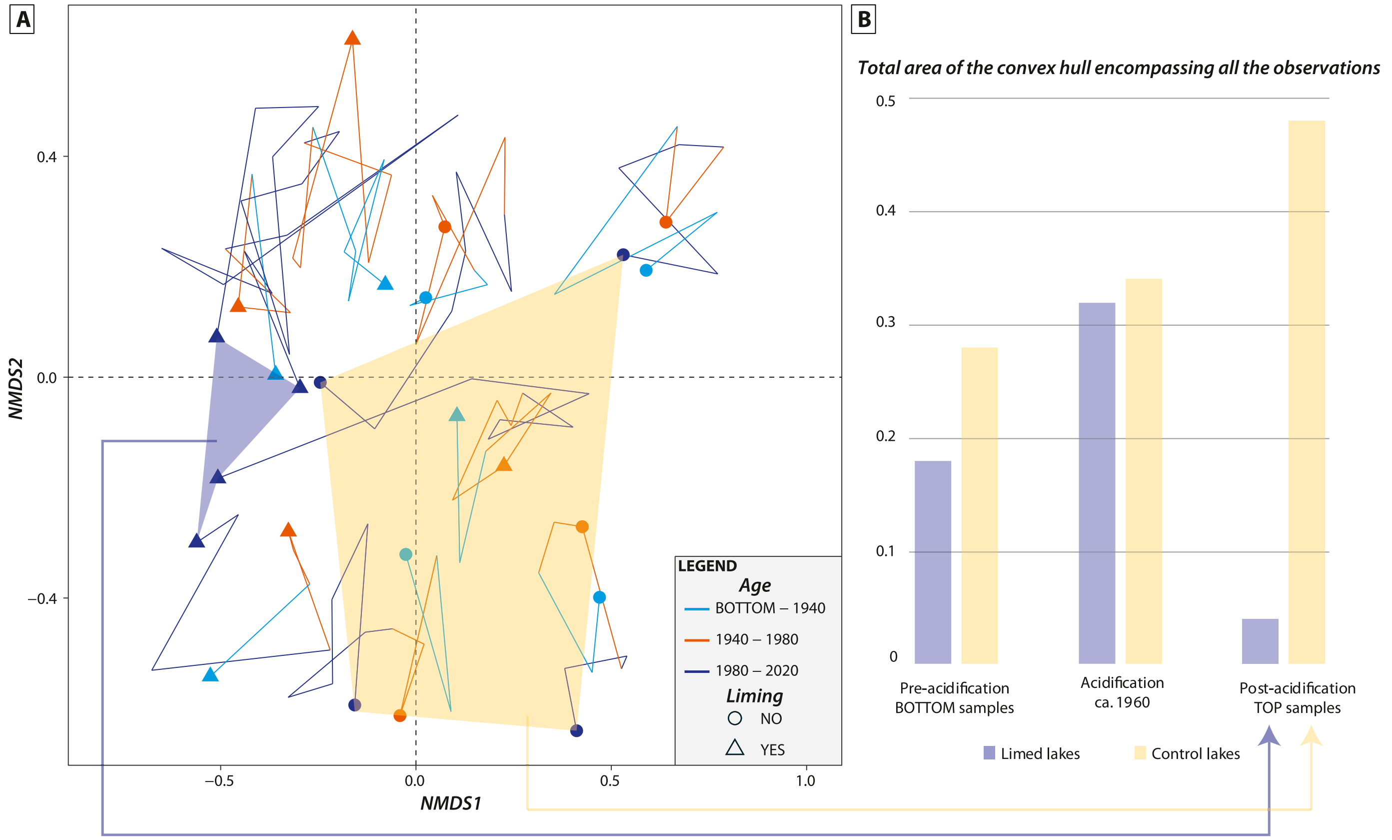

Fig. 4. **(A)** Non-metric multidimensional scaling (NMDS) ordination showing temporal trends of chironomid assemblages in limed (represented by triangles) and control lakes (circles) over the last 100 years. Line colours refer to the pre-acidification (blue), acidification (orange), and post-acidification periods (purple). **(B)** Barplots showing the convex hull area encompassing all the observations calculated with samples from three sediment layers: pre-acidification samples, samples around *ca.* 1970, and present-day samples to quantitatively measure temporal changes in within-group dissimilarity during the pre-acidification, acidification, and post-acidification periods, respectively. Limed lakes are represented by dark blue bars and control lakes by orange bars. Examples of the convex hull area encompassing all present-day samples for the limed (dark blue shading) and control (orange shading) lakes are also given.

and Johnson, 2024).

During the post-acidification period, temporal trends in chironomid taxonomic composition revealed that all individual lakes and lake groups failed to reach pre-acidified conditions, suggesting that chemical recovery from acidification likely played a limited role in driving taxonomic changes in the studied lakes. These findings are, therefore, well in line with numerous studies showing a lack of biological recovery to pre-acidified conditions for control lakes, when pre-acidified conditions were established using spatial analogue techniques or historical records (Johnson and Angeler, 2010; Angeler and Goedkoop, 2010; Diamond et al., 2022; Belle and Johnson, 2024). Results therefore suggest that the taxonomic patterns observed during the post-acidification period are likely driven by additional key drivers of changes in chironomid assemblages, such as increasing temperature starting in the mid-1970s. In contrast, a drastic decrease in the dissimilarity of the chironomid assemblages among limed lakes was observed as liming progressed and was largely below pre-acidified levels. This pattern suggests that liming likely favoured the selection of similar chironomid taxa in limed lakes, thus providing complementary empirical evidences concerning the effects of liming on aquatic communities through taxonomic homogenization of the chironomid assemblages. Our study also revealed strong effects of liming on lake water chemistry and sedimentary characteristics of limed lakes, supporting previous findings showing changes in water quality after liming (Bengtsson et al., 1980). Among others, higher pH values were observed in the limed lakes (average pH of 6.7 ± 0.2) than in control lakes (average pH of 5.9 ± 0.5), and the pH variability among lakes was also much lower in limed lakes. As water acidity can be a key driver of changes in chironomid assemblages (see also Verbruggen et al., 2011), we could hypothesize that liming-induced changes in lake water acidity toward circumneutral conditions and the lower variability in pH and other environmental variables shown in limed lakes led to the observed taxonomic homogenization of the chironomid assemblages. This finding also indicates that the effects of liming on chironomid assemblages suppress temperature effects, as limed lakes and control (unlimed) lakes followed different ecological trajectories during the post-acidification period. Overall, these findings are in line with previous findings indicating the negative effects of liming on aquatic communities such as lower food web complexity in limed lakes relative to the other lake types (Angeler and Goedkoop, 2010) and lower diversity of benthic invertebrates (Appelberg and Svenson, 2001). Furthermore, taxonomic homogenization can theoretically reduce the long-term resilience of ecosystems, as increased compositional similarity among lakes reduces differences in ecosystem dynamics (Wang and Loreau, 2016). For example, ecosystems with similar species compositions are more likely to respond similarly to environmental changes. Our study, therefore,raises questions about the influence of liming on the resilience of Scandinavian lakes at larger spatial scales, and their abilities to cope with ongoing and future climatic and environmental changes.

Using isotope analyses of subfossil chironomid head capsules, we aimed to uncover temporal changes in organic matter sources fueling chironomid biomass from the pre-acidification times to the present. During the pre-acidification period, results showed that the $\delta^{13}C_{HC}$ values (ranging from −40.8 to −29.3‰) were lower than the $\delta^{13}C_{OM}$ values (ranging from −32.2 to −27.7‰) indicating preferential incorporation of lighter carbon sources from the pool of carbon sources available in the sediment. As aquatic organic matter is known to exhibit

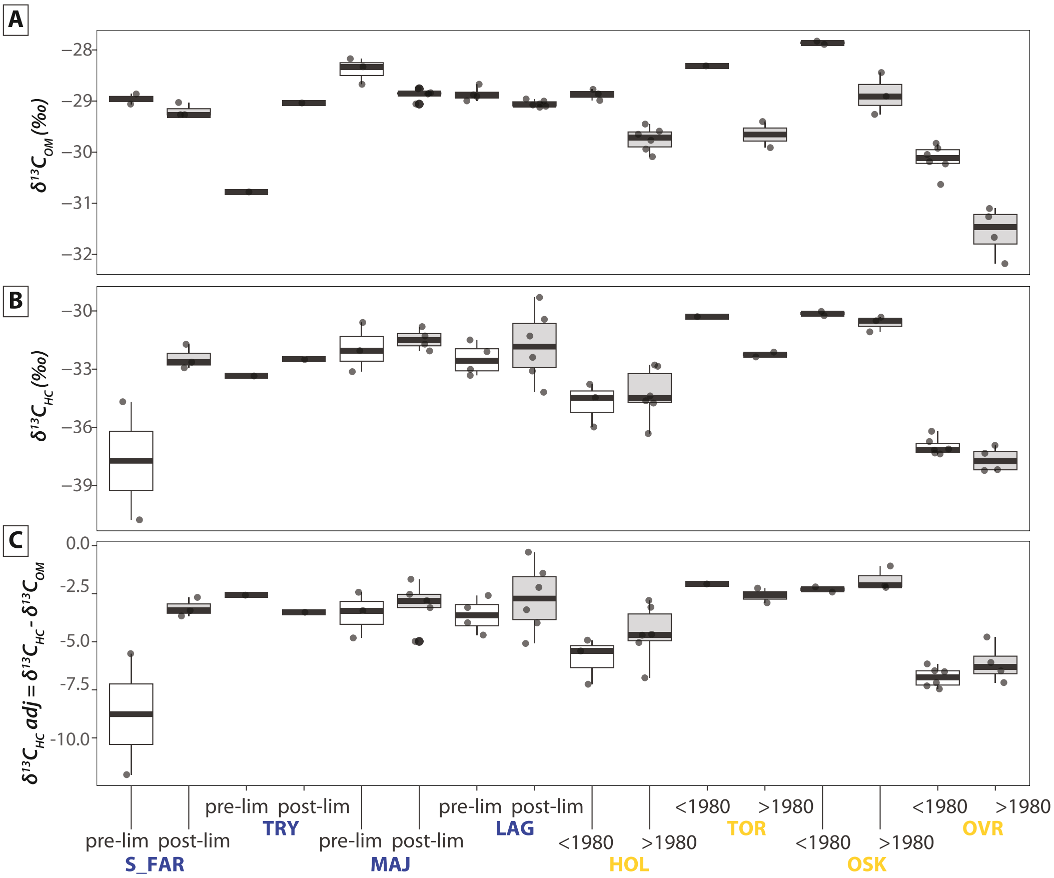

Fig. 5. Boxplots showing (**A**) the carbon stable isotopic composition of organic matter ($\delta^{13}C_{OM}$; ‰), **(B)** the carbon stable isotopic composition of chironomid remains ($\delta^{13}C_{HC}$; ‰), and (**C**) the difference between the carbon stable isotopic composition of chironomid head capsules and organic matter ($\delta^{13}C_{HC}$-adj) before/after 198*x* periods. Years varied depending on when liming strated (see also Table 1), and this date has been fixed to 1980 for the control lakes. Lakes are abbreviated to their first three letters and colorcoded according to their liming history: limed lakes in dark blue; and control lakes in orange.

Table 2
Summary of the number of samples, and morphotypes analyzed for carbon stable isotopic composition of subfossil chironomids. Lakes are grouped according to their liming history: limed lakes in dark blue; and control lakes in orange.

Lake	Period	Morphotype	*n* sample
Holmeshultasjön (HOL)	>1980	*Sergentia coracina*-type	6
Holmeshultasjön (HOL)	<1980	*Sergentia coracina*-type	3
Torrgårdsvatten (TOR)	>1980	*Sergentia coracina*-type	2
Torrgårdsvatten (TOR)	<1980	*Sergentia coracina*-type	2
Övre Skärsjön (OSK)	>1980	*Sergentia coracina*-type	3
Övre Skärsjön (OSK)	<1980	*Sergentia coracina*-type	2
Örvattnet (OVR)	>1980	*Sergentia coracina*-type	1
Örvattnet (OVR)	>1980	*Sergentia coracina*-type	4
Örvattnet (OVR)	<1980	*Chironomus anthracinus*-type	5
Majsjön (MAJ)	>1980	*Sergentia coracina*-type	4
Majsjön (MAJ)	<1980	*Sergentia coracina*-type	4
Lagmanshagasjön (LAG)	>1986	*Chironomus anthracinus*-type	6
Lagmanshagasjön (LAG)	<1986	*Chironomus anthracinus*-type	4
Tryssjön (TRY)	>1981	*Sergentia coracina*-type	1
Tryssjön (TRY)	<1981	*Sergentia coracina*-type	1
Södra Färgen (SFAR)	>1983	*Chironomus anthracinus*-type	4
Södra Färgen (SFAR)	<1983	*Chironomus anthracinus*-type	2

lower $\delta^{13}C$ values than other basal resources (e.g., terrestrial organic matter, Jones et al., 1999), and the $\delta^{13}C_{HC}$ values matched the range of $\delta^{13}C$ values frequently reported for pelagic algae in Scandinavian lakes (ranging from −38 to −28‰; Vuorio et al., 2006), these findings indicate that chironomid biomass was mainly derived from aquatic organic matter. As liming progressed, its effects on the isotope-based results were characterized by large increases in both $\delta^{13}C_{HC}$ and $\delta^{13}C_{OM}$ values. However, when $\delta^{13}C_{OM}$ values were used to take into account shifting isotopic baselines (Belle et al., 2017), temporal changes in $\delta^{13}C_{HC}$ values did not significantly differ from those of the control lakes. The observed increase in $\delta^{13}C_{HC}$ values as a response to liming was, therefore, likely induced by changes in dissolved inorganic carbon resulting in the production of aquatic organic matter (i.e., algae) with higher $\delta^{13}C$ values. As our study demonstrated that the chironomid biomass in the profundal of the studied lakes was mainly derived from aquatic organic matter, a shift in $\delta^{13}C$ values of this predominant basal resource has likely a larger effect on the chironomid isotopic composition than any other potential responses to liming (e.g., changes in sedimentary microbial composition and activity; Gahnström, 1995). Our isotope-based study indicates that liming masks more potential complex effects on carbon flows at the base of the food web by shifting carbon isotopic baselines. The applied traditional approach to studying the liming effects on energy flows within lake food webs is, therefore, not suitable.

CRediT authorship contribution statement

Simon Belle: Writing – review & editing, Writing – original draft, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Stina Drakare:** Writing – review & editing. **Johnson Richard K.:** Writing – review & editing.

Data statement

Data will be made available upon reasonable request.

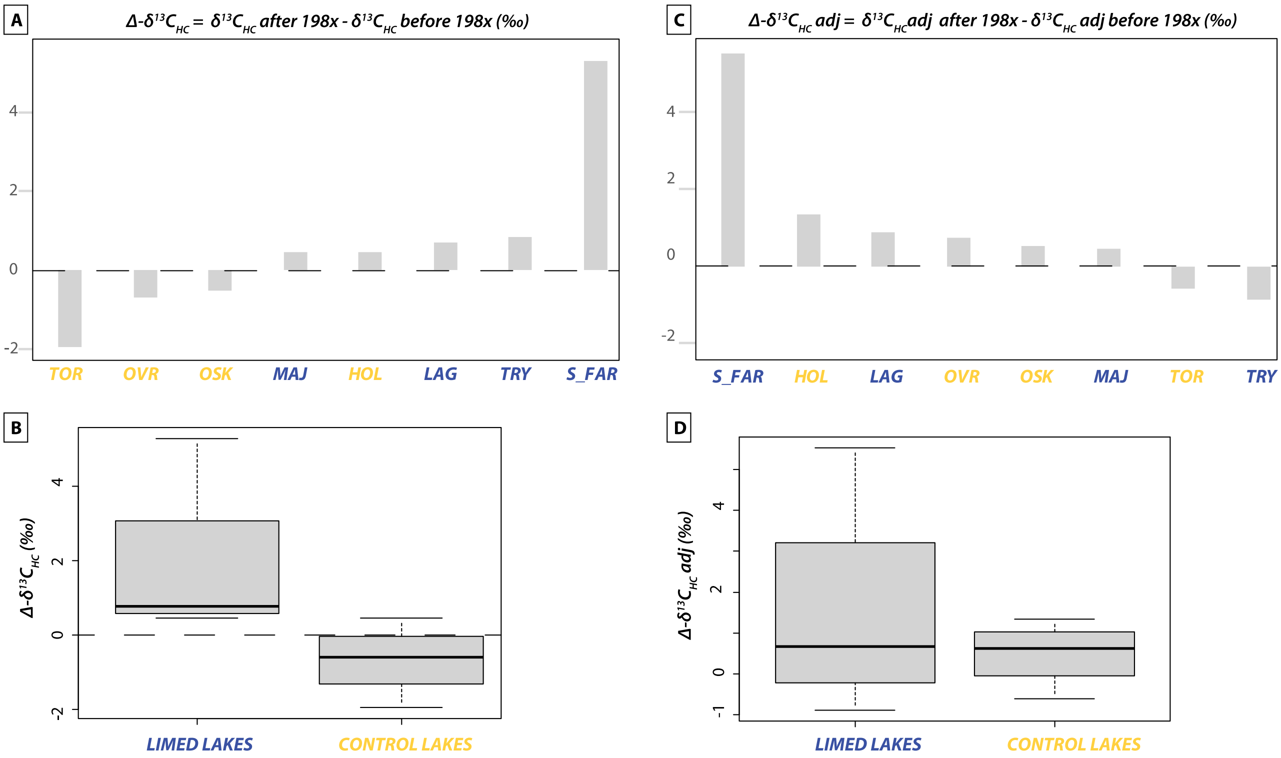

Fig. 6. **(A)** Barplot showing the differences in carbon stable isotopic compositions of chironomid head capsules before/after 198*x* periods (Δ-$\delta^{13}C_{HC}$; ‰), and **(B)** boxplots showing the differences in Δ-$\delta^{13}C_{HC}$ between the two lake groups. **(C)** Barplot showing the differences in carbon stable isotopic compositions of chironomid head capsules and sedimentary organic matter before/after 1980*x* periods (with Δ-$\delta^{13}C_{HC}$-adj; ‰), and **(D)** boxplots showing the differences in Δ-$\delta^{13}C_{HC}$-adj between the two lake groups. Lakes are abbreviated to their first three letters and colorcoded according to their liming history: limed lakes in dark blue; and control lakes in orange. In both panels, years taken as a transition varied depending on the beginning of liming (see also Table 1), and this date has been fixed to 1980 for the control lakes.

Funding

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).

Declaration of competing interest

There is no conflict of interest.

Acknowledgments

We thank Jenny L. Nilsson and Joachim Place for assistance during fieldwork, Malin Kylander and Carina Johansson (University of Stockholm, Sweden) for XRF core scanning, 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. We acknowledge Jenny Ekman and Jonas Lundholm (SLU Umeå, Sweden) for assistance in stable isotope analysis. We also thank David Angeler for comments on earlier versions of this paper. The authors gratefully acknowledge the three anonymous reviewers for their constructive comments on this manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2024.123546.

Data availability

Data will be made available on request.

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