Water Research 294 (2026) 125486

Contents lists available at ScienceDirect

Water Research

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

Interactions between human activities and natural processes shape specific conductance and ion composition of United States lakes

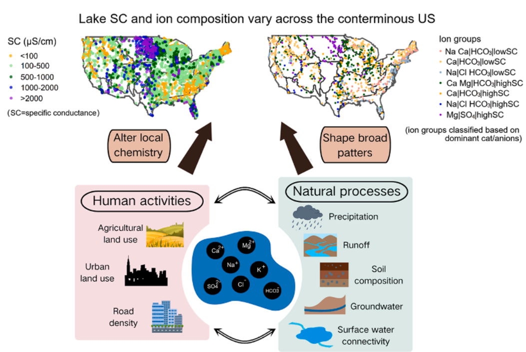
Xinyu Sun [a,b,*], Kendra Spence Cheruvelil [a,c], Patrick J. Hanly [a], Katherine E. Webster [a], Patricia A. Soranno [d]

[a] Department of Fisheries and Wildlife, Michigan State University, East Lansing, Michigan, USA
[b] Research Center for Eco-Environmental Sciences, Chinese Academy of Sciences, Beijing, China
[c] Lyman Briggs College, Michigan State University, East Lansing, Michigan, USA
[d] Department of Integrative Biology, Michigan State University, East Lansing, Michigan, USA

HIGHLIGHTS

- Specific conductance (SC) and ions of lakes vary widely across the conterminous US.
- Drivers of lake chemistry vary by region and interact with each other.
- Natural watershed factors shape broad patterns; human impacts alter local chemistry.
- Chloride concentration is most closely related to road density and urban development.
- Understanding macroscale lake chemistry drivers is vital for mitigating salt impacts.

GRAPHICAL ABSTRACT



ARTICLE INFO

Keywords:
Salinization
Road density
Macroscale variation
Geology
Hydrology
Macrosystem

ABSTRACT

Specific conductance (SC) and major ions are important water quality constituents and key indicators of freshwater salinization. Being relatively conservative and less influenced by biological activity, they integrate hydrologic, climatic, and anthropogenic influences, allowing us to track and understand lake responses to global change. However, the patterns and drivers of macroscale (regional to continental) variation of these water chemistry parameters for populations of lakes are relatively unknown. We examined the spatial variations in SC (N=9,784 lakes) and major anion and cation composition and concentrations (N=1,218 lakes) across the conterminous United States, and quantified their relationships with a wide range of natural and human factors. High SC lakes were mainly located in the Plains, Desert Southwest, and Florida. While calcium and bicarbonate were the dominant ions in 46% of the study lakes, chloride was dominant in 14% of lakes, and magnesium and sulfate were the dominant cation and anion, respectively, in 8% of lakes. Among the multiple natural drivers we tested, the primary controls of SC and ion composition were soil, hydrology, and climate. However, their influences differed substantially across ecoregions and among lakes due to interactive effects among them and with human disturbances. Moreover, chloride exhibited strong anthropogenic signals, with concentrations predominantly related to road density and urban development. Our study builds upon previous local and regional work

* Corresponding author.
E-mail addresses: xysun@rcees.ac.cn, 16xs6@queensu.ca (X. Sun).

https://doi.org/10.1016/j.watres.2026.125486
Received 27 October 2025; Received in revised form 8 January 2026; Accepted 30 January 2026
Available online 31 January 2026

by documenting nationwide variations in ion concentrations and composition. While natural processes shape baseline ionic assemblage, human activities are the primary context modulating these effects and can cause considerable deviations in ion concentrations and composition, contributing to freshwater salinization and impacting ionic interactions and lake biota.

1. Introduction

Specific conductance (SC) is a critical indicator of water quality, widely used to assess risks of freshwater salinization to aquatic organisms, drinking water quality, and industrial and recreational water usability (Hintz & Relyea 2019; Kaushal et al. 2019; Dugan 2024). Changes in SC have been related to negative impacts on lakes in some regions around the world and have been attributed to natural and human disturbances such as climate change, extreme climatic events, road salt application, and agricultural activities (Kaushal et al. 2019; Olson 2019; Schacht et al. 2023). A few studies have documented increases in concentrations of individual ions such as chloride in lakes due to human activities (e.g., Dugan et al. 2017; Solomon et al. 2023). However, we lack a comprehensive understanding of the variation of SC and multiple major ions across lakes at the macroscale (i.e., regional to continental), how ionic composition differs among lakes, and their potential relationships with multi-scaled natural environmental and human drivers.

The impacts of SC on freshwater organisms are related not only to the magnitude of SC, but also to the concentrations and composition of the major anions and cations that contribute to SC (Cañedo-Argüelles et al. 2016). Lab and microcosm experiments have shown that identical SC but different anion composition (e.g., solutions dominated by chloride (Cl^-) vs. sulfate (SO_4^{2-}) ions) can lead to divergent effects on organisms and communities (Nostro et al. 2005; Clements & Kotalik 2016; Van Gray & Ayayee 2024). Multiple ions can also interact synergistically or antagonistically to affect aquatic organisms, leading to unexpected outcomes (Elphick et al. 2011). For example, the toxicity of Cl^- on cladocerans decreased with higher calcium (Ca^{2+}) concentration (Elphick et al. 2011; Rogalski et al. 2024), and the toxicity of potassium ion (K^+) could be alleviated by high sodium ion (Na^+) concentrations (Mount et al. 2016). These findings underscore the necessity of understanding how both SC and the constituent major ions differ among lakes, across different types of lakes, and in diverse ecoclimatic settings to build a more complete understanding of the potential response of ion chemistry and, thus, lake ecosystems to global changes.

Local and regional studies have shown that SC and major ions in lakes are influenced by hydrogeographic factors, although these influences can vary substantially across regions. For example, studies at local and regional scales have identified several key natural drivers including soil and rock weathering, climate, evaporation, topography, and groundwater (Gorham et al. 1983; Gorham 1961; Swanson et al. 1988; La Baugh et al. 2000). Regional studies of lake chains found that landscape position, the location of a lake within hydrologic flowpaths (Kratz et al. 1997), also affects SC and ions in lakes (Soranno et al. 1999). Moreover, lakes in or near coastal areas receive substantial inputs of Na^+ and Cl^- from sea salt-influenced precipitation and saline groundwater intrusion (Eilers et al. 1988; Kiflai et al. 2022; Haque 2023). Underlying these general relationships is substantial regional heterogeneity in the influence of specific natural factors. For example, high surface water connectivity is related to higher or lower SC in different regions. Martin and Soranno (2006) found that lakes connected to other water bodies (i.e., higher connectivity) in Michigan, USA, tended to have higher SC than less connected lakes, whereas La Baugh et al. (2000) observed higher SC in isolated lakes (i.e., without in/outflow) than other lakes in North Dakota, USA. Moreover, groundwater effects on SC vary regionally, being either negative (Redder et al. 2021), negligible, or positive (Hunsaker & Johnson 2017). Such variability and complexity underscore the need for macroscale research to better understand how natural drivers interact with local and regional contexts to influence lake chemistry, which can be further complicated by anthropogenic impacts.

In recent years, an increasing number of studies have shown that human activities can cause long-term changes to SC and ion composition in lakes. For instance, salt inputs from irrigation runoff, residential discharge, winter road salt application, and mining can increase lake SC (Oswald et al. 2019; Dumelle et al. 2024). In particular, agricultural effluents often contain high concentrations of K^+, Mg^{2+}, Cl^-, and SO_4^{2-}; road deicing salts can contribute significant amounts of Na^+, Mg^{2+}, Ca^{2+}, and Cl^-; and industrial runoff can contribute SO_4^{2-} (Meybeck 2003; Dugan et al. 2017; Dugan 2024). However, to fully understand these human impacts, it is necessary to examine them in the context of underlying natural drivers of variation.

A macroscale understanding of the spatial variation of SC and ion composition in lakes and the influences of natural and human factors on them has been elusive for two reasons. First, most previous studies examined how a limited set of natural and human predicting variables affect lake SC and individual ions (e.g., climate and location of lakes in Nebraska, USA, Bennett et al. 2007; DeSellas et al., 2024). Second, most lake studies have focused on one to a few waterbodies or watersheds, while US national-scale studies have to date only been conducted on streams and rivers (e.g., Meybeck 2003; Griffith 2014; Stets et al. 2020). Findings from stream studies are not usually directly applicable to lakes because streams and lakes differ in morphometry and hydrological pathways that determine water residence time, ion retention time, and evaporation, all of which strongly influence water chemistry (Lottig et al. 2011). Macroscale studies that incorporate a wide range of multi-scaled factors are therefore required to understand the spatial variation of lake SC and ion composition and the influences of natural and human factors on them. This knowledge is critical to predict lake responses to future changes as well as to establish reasonable standards and goals for management and restoration.

To our knowledge, this is the first comprehensive analysis of its kind using a broad set of predictors across thousands of lakes and many regions with diverse ecoclimatic and land use settings. We applied a macroscale framework in two ways: (1) examining continental-scale variations in lake SC and ion composition across ecoregions in the conterminous US (CONUS), and (2) incorporating a large number of natural and human drivers operating at both lake and watershed scales into our analysis. We asked two questions: (1) How do lake SC and major ion concentrations and composition vary across ecoregions in the CONUS? (2) How do key natural and human factors contribute to spatial variation in lake SC and ion composition? Using water chemistry and ecological context data for 9,784 (SC) and 1,218 (major ions; a sub-dataset of the SC dataset) lakes across the broad ranges of climate, hydrology, and land use of the CONUS, we demonstrate substantial spatial variation in major ion chemistry and the related natural and human controls.

2. Material and methods

2.1. Data collection

We used data from the LAGOS-US research platform (Cheruvelil et al. 2021) that includes lake, natural environmental, and human activity data for 479,950 lakes $\geq$ 1 ha surface area across CONUS. We obtained measured epilimnion SC, individual ion concentrations for the cations Ca^{2+}, K^+, Mg^{2+}, and Na^+ and the anions Cl^- and SO_4^{2-}, and alkalinity (as $CaCO_3$) from the LAGOS-US LIMNO module (Shuvo et al. 2023). This module includes lake surface water quality data from the US Water Quality Portal (WQP; 2021); the 2007, 2012, and 2017 US National Lakes Assessment Surveys (NLA; US Environmental Protection Agency (EPA) 2010, 2016, 2022); and the US National Ecological Observatory Network facility (NEON; Keller et al. 2008). We used lake locational, morphometric, and surface water connectivity data from the LAGOS-US LOCUS module (Cheruvelil et al. 2021; Smith et al. 2021). For factors describing the natural context (e.g., soil texture and climate features) and human activities (e.g., road density and land use) that affect lakes, we used data from the LAGOS-US GEO module (Smith et al. 2022). For the natural lake or reservoir designation, we used data from the LAGOS-US RESERVOIR module (Polus et al. 2022; Rodriguez et al. 2023). Additionally, we acquired evapotranspiration and snowpack water equivalent storage data from Blodgett (2023) and livestock manure application data from US EPA EnviroAtlas (2015). We used NEON ecoregions, which are classified based primarily on climate (213, 800-770,995 km^2; Hargrove & Hoffman 1999), as a spatial delineation to account for large-scale geographical variation in the analyses (Soranno et al. 2025). We removed highly correlated variables, resulting in 46 multi-scaled natural and human factors, and these factors were assigned to one of 10 categories: climate, hydrology, lake and watershed (morphometry), lithology, location, soil, surface connectivity, terrain, human activities, and land use/land cover (LU/LC) (see Table S1 for a list of factors and groups).

2.2. Data processing

We used 2000-2021 epilimnetic measurements of lake SC, major ion concentrations, and alkalinity. Because we had much more SC than ion data, we created two datasets for further analyses: a full dataset with only SC data and a sub-dataset with SC, alkalinity, and complete major ion data. We applied water quality QA/QC procedures from LAGOS-NE LIMNO (v. 1.087.3; Soranno et al. 2019) to these datasets. Specifically, we removed lakes with long-term average SC lower than 2 μS/cm (i.e., values that could indicate potential measurement errors; 197 (2%) lakes removed) and higher than the upper threshold for outliers (i.e., 75th percentile + 15*interquartile range = 4,983 μS/cm; 87 (1%) lakes removed), resulting in 11,616 lakes with SC data (Figure S1). Next, we further extracted the SC data collected between April and October (90% of data) during the most recent sampling year for each lake (median year = 2015; Figure S2a), computed the mean SC of each lake, and merged those data with multi-scaled natural and human factors, yielding 9,784 lakes with complete data (i.e., the full dataset with no missing values for any factor) that are representative of CONUS lakes (Figure S3). SC in these lakes range from 2 to 6,125 μS/cm SC (mean±standard deviation (SD) = 343±511 μS/cm, median = 206 μS/cm). For the 4,581 lakes with more than one SC sample in the latest sampling year from April to October, we calculated the coefficient of variation (CV) to represent intra-year temporal variation in SC. These lakes were often sampled from June to September (72% of the samples) with a sampling frequency range of 2-7 times.

For the sub-dataset of lakes with values for all variables (SC, ions, and alkalinity), we extracted April to October data (≥85% of data) and used the most recent concurrent (i.e., taken the same day) samples available (one water sample per lake for 1,498 lakes; median year = 2016). Next, to investigate ion composition in lakes, we converted ion concentrations and alkalinity reported in mg/L units in LIMNO-US to microequivalents per liter (μeq/L; Table S2). In this study, we used bicarbonate (HCO_3^-) (in μeq/L) to represent all carbonate forms of alkalinity, including $CO_3{}^{2-}$, which dominates in high pH waters. This decision may underestimate carbonate concentrations in waters with pH > 8.3, where a larger proportion of alkalinity is present as CO_3^{2-} (Andersen 2002). Major ion data came from 1,218 lakes (Figure S2), of which about 85% were sampled by the National Lakes Assessments.

2.3. Data analyses

Data analyses were conducted in R (v4.3.3; R Core Team, 2024). To identify spatial patterns of SC using the full dataset, we plotted the mean and CV of SC over the 17 NEON ecoregions for CONUS. To identify the spatial distribution of lakes with relatively low and high SC, we selected lakes with SC lower than 10% and higher than 90% of all lakes and mapped them with the NEON ecoregions. Next, using the ion sub-dataset, we derived calculated SC and total ion concentration (in mg/L) for lakes with complete major ion data. The calculated SC was computed by multiplying the equivalent concentration (in μeq/L) of each ion by its corresponding equivalent conductivity (Table S2) and summing up the results. The total ion concentration was calculated by summing up the concentration (in mg/L) of each ion. We then applied linear models to examine the correlations between measured SC and calculated SC, total ion concentration, and major ion concentrations.

We used Boruta feature selection ('Boruta' package, v8.0.0, Kursa & Rudnicki 2022) and random forest (RF, 'randomForest' package, v4.7-1.1, Breiman et al. 2022) to examine which and how multi-scaled natural and human factors affect SC in lakes. For these factors, a natural log transformation was applied to highly skewed non-percent data, and a generalized logit transformation was applied to all percent data (Table S1). Two Boruta feature selections with a maximum of 1,000 runs were performed using SC values as the response variable and either natural or human factors as predictors. We ranked natural and human factors separately based on Boruta importance scores (Table S3), then took the first half (i.e., the top half of factors based on importance) from each and input them into an RF model with 5-fold repeated cross-validation to examine the important natural and human factors that affect lake SC.

The effects of the important factors were assessed through partial dependence plots (PDPs; 'pdp' package, v0.8.1, Greenwell 2022). We identified important factors for PDPs using both the percentage increase in mean squared error (% increase MSE) and the increase in node purity. The % increase MSE represents the increase in MSE when a factor is excluded, and the node purity indicates the before-after change in the residual sum of squares at a splitting node (Breiman et al. 2022).

To study the spatial patterns of major ion composition and concentrations, we first applied hierarchical clustering on the log10-transformed equivalent concentrations of all seven major ions using the ion sub-dataset (1,218 lakes) (Ward's method; Härdle & Simar 2019). We did not include SC in this clustering approach since we wanted to identify similarities and variance in ion composition (e.g., relative percentages of major anions and cations) and ionic strength. The hierarchical clustering identified 11 clusters of lakes (Figure S4) that diverged in both dissolved ion composition and concentration. Then, to interpret the ecological significance of the clusters, we manually combined the clusters into seven ecologically-distinct groups based on two characteristics not included in the clustering analysis – those with similar dominant ions and average SC (i.e., whether the average SC is lower or higher than the median SC across all the 1,218 lakes) (Figure S4). We named these seven ion groups based on their dominant cation and anion and used them as the response variable in later analyses. To remove overall ionic strength as an influence on cluster structure, we conducted a complementary clustering analysis using only ion composition. Specifically, we converted ion concentrations to relative ion proportions (i.e., each ion expressed as a fraction of total cations or anions in each lake) and applied hierarchical clustering on proportion values. This approach emphasizes variation in ion composition independent of total ionic strength.

Next, to study how natural and human factors affect major ion composition and concentrations, we ran a Boruta feature selection using all natural and human factors as predictors and removed the unimportant factors identified by Boruta. We then applied a natural log transformation to highly skewed non-percent natural and human factors data (Table S1), and centered and scaled (into z-scores) all continuous factors before running a multinomial GLMNET model with LASSO regularization (alpha=1) ('glmnet' package, v4.1-8, Friedman et al. 2023). We calculated the relative importance of each factor for predicting ion cluster membership by summing the absolute value of the factor's multinomial coefficient across all clusters. The top six factors were then selected for visualization, and we applied Wilcoxon tests to examine differences in the median values of the top six factors between each ion group and the entire set of 1,218 lakes in the ion sub-dataset.

3. Results

3.1. SC in lakes across the CONUS

SC varied within and among ecoregions for the 9,784 lakes (Fig. 1). Most lakes with relatively high SC (SC higher than 90% of all lakes; SC $\geq$ 696 μS/cm) were located in the Southeast, central US (e.g., Prairie Peninsula, Northern Plains, Central Plains, and Southern Plains), and Desert Southwest NEON ecoregions (Fig. 1c). Of these, 202 lakes, mostly located in the Northern Plains, had SC higher than 2,000 μS/cm. Lakes with relatively low SC (SC lower than 10% of all lakes; SC $\leq$ 34 μS/cm) were mostly found in the Northeast, Mid-Atlantic, Southeast, and Great Lakes ecoregions. Among the 17 NEON ecoregions, the Desert Southwest lakes had the highest average SC (1,154 μS/cm), followed by those in the Northern Plains (897 μS/cm), and the Central Plains (894 μS/cm). The Pacific Northwest had the lowest mean SC (72 μS/cm), followed by the Northeast (139 μS/cm) and Mid-Atlantic (146 μS/cm) ecoregions. Most of the lakes with multiple sampling dates within a year had low intra-year temporal variation in SC (CV: mean±SD=10%±13%, median=6%), and those with high CV (greater than 100%) were predominantly found in the Northeast, Southeast, and Great Lakes ecoregions (Figure S5).

Measured and calculated SC were strongly positively correlated for the 1,218 lakes in the ion sub-dataset that had complete SC and major ion data (Fig. 2a; $p<0.001$). The average deviation of calculated to measured SC was low (7%), suggesting that the cations and anions included in our ion sub-dataset were the dominant components of dissolved ions in lake water (Figure S6). There were also positive correlations between measured SC and the calculated total salt concentration and the concentration of each major ion, with the strength of the relationship (i.e., the slope) varying among ions (Fig. 2b-i; $p<0.001$). Differences in slopes among ions reflect their contrasting contributions to total ionic strength. Specifically, Ca^{2+} and K^{+} had the strongest associations with SC, followed by HCO_3^-, Cl^-, Na^+, Mg^{2+}, and SO_4^{2-}.

3.2. Natural and human factors related to lake SC across the CONUS

Lake SC was related to both natural and human factors (RF out-of-bag variance explained=59%; N=9,784; Figures S7&8). Based on the % increase in MSE of the RF model, lake elevation was the most important factor, followed by the percentage of clay in the soil and the percentage of watershed forest land cover (Figure S7a). Using the increase in node purity (Gini coefficient), groundwater recharge was the most important factor, followed by mean annual runoff and percent clay in the soil (Figure S7b).

We visualized the relationships between lake SC and the five most important natural and human factors using partial dependence plots, and mapped these factors for the lakes with relatively high and low SC to aid interpretation. For example, lakes with the highest SC at the lowest elevations were located mostly in the Southeast ecoregion, particularly in Florida (Fig. 3a; Figure S9a). SC declined steeply for lakes above 120

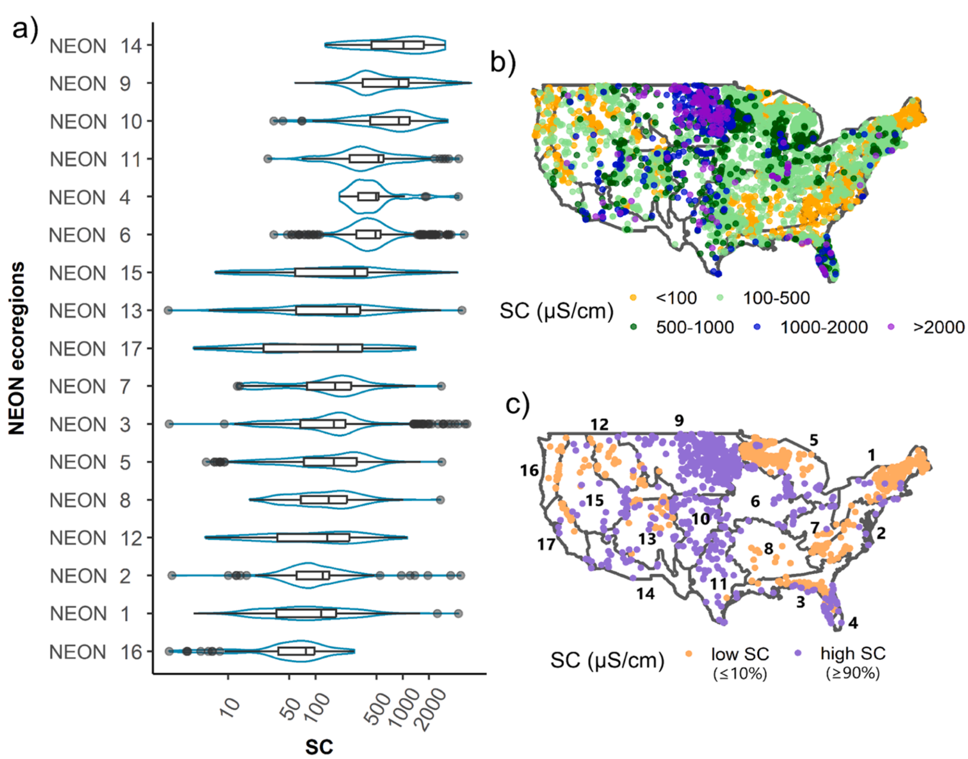


Fig. 1. Specific conductance (SC; μS/cm) by NEON ecoregion for the full dataset (N=9,784). The NEON ecoregions in the violin plots (a) are ordered by average SC; the bold lines in the embedded boxplots indicate the mean and the upper and lower whiskers of the 75th and 25th percentiles. The upper CONUS map (b) shows the mean April-October SC of each study lake. The lower CONUS map (c) shows the location of lakes with low and high SC values (978 lakes with SC lower than the 10% quantile of lakes and 979 lakes with SC higher than the 90% quantile of lakes). NEON ecoregions outlined in black are as follows: 1 = Northeast, 2 = Mid-Atlantic, 3 = Southeast, 4 = Atlantic Neotropical, 5 = Great Lakes, 6 = Prairie Peninsula, 7 = Appalachians & Cumberland Plateau, 8 = Ozarks Complex, 9 = Northern Plains, 10 = Central Plains, 11 = Southern Plains, 12 = Northern Rockies, 13 = Southern Rockies & Colorado Plateau, 14 = Desert Southwest, 15 = Great Basin, 16 = Pacific Northwest, 17 = Pacific Southwest (numbers in plots a and c).

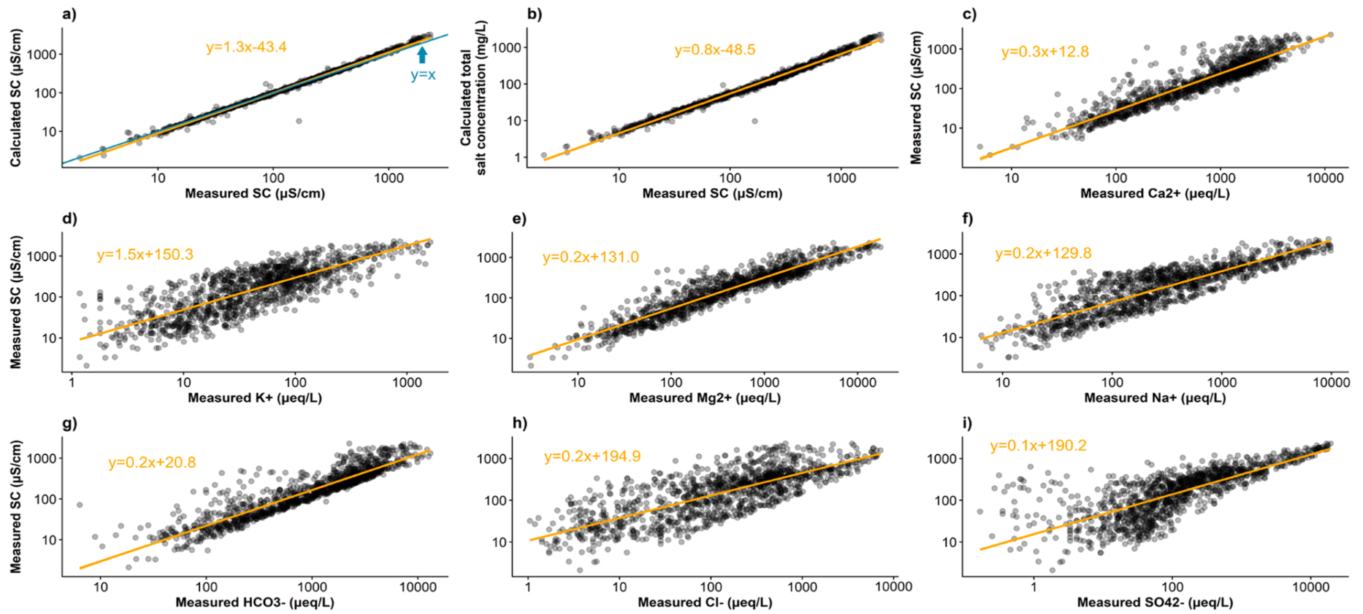


Fig. 2. Relationships between measured SC and calculated SC (a), calculated total salt concentration (b), and the equivalent concentration of each ion (c-i) in 1,218 lakes across the CONUS. Each dot represents a lake, and orange lines represent linear regressions (equation above the line) fitted to untransformed data. The orange shadow area indicates one standard deviation. In plot (a), the blue line is y=x. Both axes are shown on $\log_{10}$ scales for visualization only.

m elevation, then decreased more gradually before stabilizing at higher elevations. Similarly, SC declined rapidly as soil clay content increased from 0% to 2%, which was mainly driven by some lakes in Florida, then leveled off (Fig. 3b; Figure S8b). Then, SC remained low and started to increase when clay content exceeded 12%. Most high SC lakes had low groundwater recharge, indicating dominance by surface water pathways, and a negative association was found between SC and groundwater recharge until about 150 mm/year, at which point SC stabilized at a low level (Fig. 3c; Figure S9c). Lake SC was negatively associated with annual runoff and became stable at a low SC level when runoff exceeded about 20 inches/year (Fig. 3d; Figure S9d). Finally, we observed that most high SC lakes had low watershed forest land cover (which conversely can represent areas with high human disturbance), whereas SC was lowest in lakes with watersheds with moderate forest cover. Lake SC subsequently increased after forest cover reached about 80% (Fig. 3e; Figure S9e).

3.3. *Lake ion composition and associations with natural and human factors across the CONUS*

Our seven ion groups for the 1,218 lake subset exhibited substantial divergence in both ion concentrations and major ion composition (Fig. 4; Table 1; Figure S10). To evaluate whether these groupings were driven primarily by relative ion composition rather than absolute concentrations, we repeated the clustering using ion proportions. This alternative approach also identified seven clusters with broadly similar compositional characteristics (Figure S11). Most lakes were assigned to the same or compositionally similar groups across the two approaches. This consistency supports our decision to focus on the ion group classifications based on concentrations, which allows us to contrast low- and high-ionic strength lakes with comparable ion composition.

We found that 46% of the lakes were dominated by Ca^{2+} and HCO_3^-, and that most of these lakes had SC values lower than the median SC across all 1,218 lakes (i.e., in the Ca|HCO3|lowSC group; Fig. 4;). Lakes co-dominated by the cations Ca^{2+} and Mg^{2+} comprised 23% and had an average SC higher than the median SC across all lakes (i.e., in the Ca Mg|HCO3|highSC group). Na^+, Cl^-, and HCO_3^- were the dominant cation and anions, respectively, in 14% of the lakes, with most lakes having low SC (i.e., in the Na|Cl HCO3|lowSC group). Ca^{2+} and Na^+ were co-dominant in 9% of lakes, all of which had relatively low SC. Finally, 8% of lakes were dominated by Mg^{2+} and SO_4^{2-}, and had the highest average SC among all ion groups.

The diversity of ion groups and the most common groups varied spatially, both within and among the 17 NEON ecoregions of CONUS (Fig. 5). The number of ion groups in each NEON ecoregion ranged from two to seven, with the Great Basin and Pacific Southwest ecoregions both having all seven groups, suggesting high spatial diversity in lake ion chemistry. The Ca|HCO3|lowSC group was the most common in eight ecoregions (Northeast, Great Lakes, Ozarks Complex, Northern Rockies, Southern Rockies & Colorado Plateau, Great Basin, Pacific Northwest, and Pacific Southwest). The Na|Cl HCO3|lowSC group was the most common in the Mid-Atlantic and Southeast NEON ecoregions. Although the Na|Cl HCO3|lowSC group did not dominate the Northeast ecoregion, lakes in this ion group were most commonly located there. The Na|Cl HCO3|highSC group was dominant in the Desert Southwest, and the Ca Mg|HCO3|highSC group was dominant in the Prairie Peninsula and Appalachians & Cumberland Plateau. Finally, the Mg|SO4|highSC group was the most common group in the Northern Plains and Central Plains (Fig. 5).

Multiple human and natural factors were associated with the spatial variations and variances in ion group assignments and lake ion composition (Fig. 6; Figure S12; Table S4). Ion groups showed stronger associations with factors in the categories of soil, terrain, climate, human activities, and LU/LC than in other categories. Ion composition was moderately associated with hydrology, particularly groundwater-related measures, and lake location. Finally, some factors were associated with only subsets of ion groups. For example, surface water connectivity was found to be associated with lake membership in five of the seven ion groups. Below we describe the association between ion groups and the top six natural and human factors (i.e., surface connectivity, percent clay in the soil, precipitation, runoff, percent forest land cover, and road density) from the GLMNET analysis.

The percentage of clay in the soil was significantly higher in lakes with high SC, such as the Ca|HCO3|highSC, Ca Mg|HCO3|highSC, Na|Cl HCO3|highSC, and Mg|SO4|highSC groups, and lower in other ion groups (Wilcoxon, $p<0.001$). The long-term average precipitation, runoff, and percentage forest land cover were all significantly lower in groups with high lake SC, and higher in other ion groups ($p<0.001$).

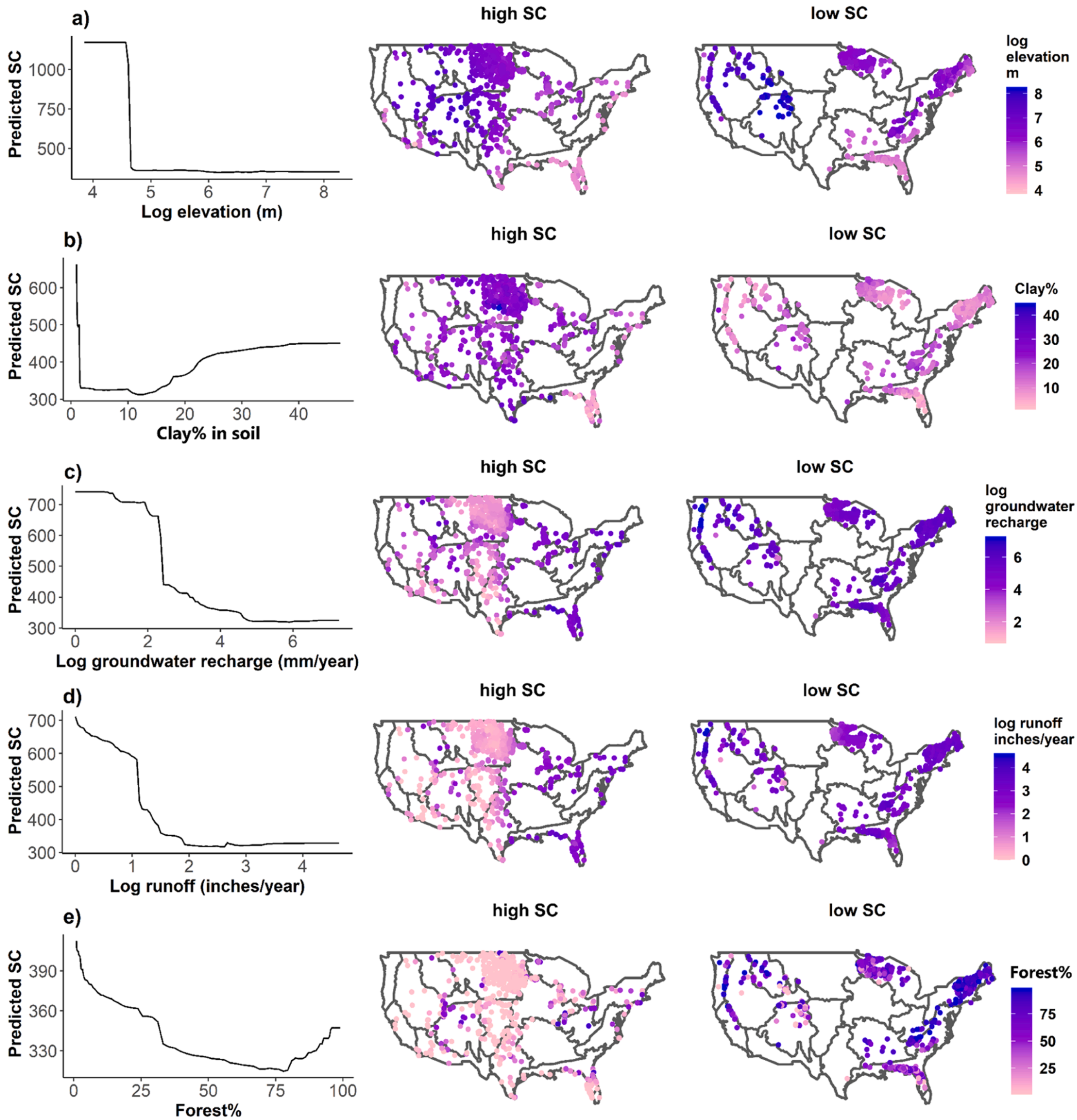


Fig. 3. Partial dependence plots (left) showing the average marginal relationships between predicted SC (μS/cm) and elevation (a), % clay (b), groundwater recharge (c), runoff (d), and % forest (e). The maps in the middle and right columns show the values of the factor for low SC (SC lower than 10% of all lakes; right) and high SC (SC higher than 90% of all lakes; middle) lakes. Note that the maps do not represent modeled contributions; they illustrate how the distributions of each factor differ between lakes with relatively high/low SC values. 'Log' = natural log transformation.

Road density was significantly higher in the Ca|HCO3|highSC, Na|Cl HCO3|highSC, and Na|Cl HCO3|lowSC groups ($p<0.001$). Although the drainage lake was the most common connectivity class for all ion groups, the distribution of other surface water connectivity classes and the association between connectivity class and SC differed by ion group. The Mg|SO4|highSC group had the highest proportion of isolated and terminal lakes among all ion groups (Fig. 6; Table S5). Drainage lakes had slightly higher median SC than other connectivity classes in the Ca|HCO3|lowSC group, while headwater lakes had the highest SC in the Na|Cl HCO3|lowSC and Na|Cl HCO3|highSC groups.

4. Discussion

Despite growing concern about the salinization of inland waters, our understanding of the spatial variation in lake SC and major ion composition and concentrations across diverse ecoregions remains surprisingly limited. Most prior research has been conducted at local or regional scales, often focusing solely on SC, on individual ions like Cl^-, or on specific sources or drivers such as geology and agricultural effluent. However, this narrow focus has left important knowledge gaps, particularly regarding how ion composition varies across scales and how

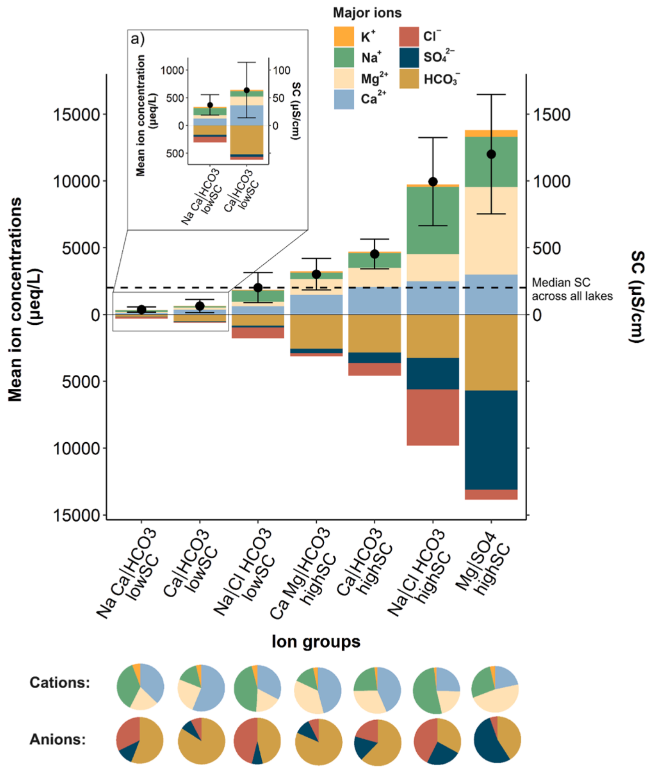


Fig. 4. For each ion group (represented by the notation major cation(s) | major anion(s) | relative SC), the mean equivalent concentrations (μeq/L) of major ions, mean SC (μS/cm), and proportions of cations and anions. Stacked bars represent ion concentrations with cations above and anions below the zero line, respectively, with corresponding values shown on the left y-axis; black dots represent mean ion group SC and correspond to the right y-axis; error bars represent one standard deviation in each direction; and pie charts at the bottom represent the proportions of each cation and anion within a group. The dashed line indicates the median SC across all 1,218 lakes (188 μS/cm). To aid in visualization, subplot (a) shows ion concentrations and SC in the Na Ca|HCO3|lowSC and Ca|HCO3|lowSC.

Table 1
Summary of each ion group's dominant cation(s) and anion(s), percentage of study lakes within each group, and average SC of each group. Groups are listed in ascending order by average SC.

Ion group name	Dominant cation(s)	Dominant anion(s)	Percentage of study lakes	Average SC ±SD (μS/cm)
Na Ca|HCO3|lowSC	Ca^{2+}, Na^{+}	HCO_3^-	9%	37±19
Ca|HCO3|lowSC	Ca^{2+}	HCO_3^-	33%	64±50
Na|Cl HCO3|lowSC	Na^{+}	Cl^-, HCO_3^-	11%	202±112
Ca Mg|HCO3|highSC	Ca^{2+}, Mg^{2+}	HCO_3^-	23%	302±118
Ca|HCO3|highSC	Ca^{2+}	HCO_3^-	13%	453±111
Na|Cl HCO3|highSC	Na^{+}	Cl^-, HCO_3^-	3%	995±330
Mg|SO4|highSC	Mg^{2+}	SO_4^{2-}	8%	1201±448

multiple natural and human factors collectively shape lake SC and major ion concentrations.

Our study addresses these gaps by analyzing SC and major ions

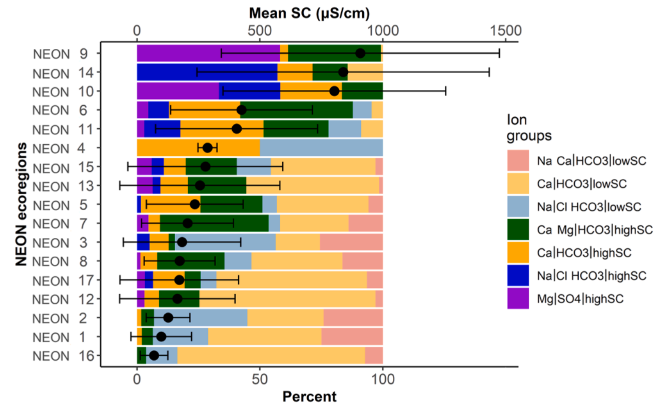


Fig. 5. Percent of ion groups in each NEON ecoregion (bottom, x axis) where each color indicates an ion group shown in the legend. In each ion group name, the '|' symbol separates different characteristics of the group, specifically, (co) dominant cation(s), (co)dominant anion(s), and whether the group average SC is higher or lower than the median SC across all lakes. The solid black dots and error bars indicate SC mean and SD values for each NEON ecoregion (top x axis). The NEON ecoregions are ordered based on average SC. Location, names, and numbers of NEON ecoregions are shown and described in Fig. 1.

across thousands of lakes in the CONUS. We found substantial spatial variation in SC and major ion concentrations and composition across lakes and ecoregions, reflecting the combined and interacting effects of natural and anthropogenic drivers. While natural factors such as geology, hydrology, and climate emerged as dominant controls at broad scales, human influences introduced significant deviations from these patterns at finer scales, particularly in more developed regions. Importantly, the strength and direction of these influences varied across different landscape contexts, with some ions responding more strongly to certain drivers. Our study extends insights from previous local and regional studies and contributes to a more integrated understanding of lake water chemistry at macroscales, which is critical for predicting and mitigating freshwater salinization impacts.

4.1. Spatial variation in lake SC and major ions across the CONUS

We document spatial patterns for low and high SC lakes that complement and extend previous research. For example, the locations of low SC lakes in the Northeast, Mid-Atlantic, Great Lakes, and Northwest ecoregions corroborate findings from studies of US streams (Griffith 2014; Olson & Cormier 2019). While previous macroscale studies identified relatively high SC in the Plains and Desert Southwest (Griffith 2014; Olson & Cormier 2019; Dumelle et al. 2024), as we did; our analysis detected considerably higher SC levels in these regions than previously documented. We also found high SC in the Southeast, particularly in Florida, which was not reported in previous national-scale stream studies. This difference could be attributed to sample size differences among these studies, as well as to differences in temporal dynamics and water chemistry between lakes and streams in the Southeast. For instance, there were 315 stream sites in Olson & Cormier (2019) compared to 1,561 lakes in the Southeast and Atlantic Neotropical ecoregions in our dataset. Additionally, 26% of Southeast lakes in our dataset were sampled multiple dates, and we found relatively high CVs (Figure S5) among those dates. Previous local-scale studies have attributed high SC in the Southeast to ion inputs from precipitation and seawater intrusion (Kiflai et al. 2022; Haque 2023) as well as to discharges from stormwater pipes and detention ponds (Beckingham et al. 2019). Our results demonstrate that high SC lakes occur in the southeastern US, which has the potential to change SC prediction and management in this ecoregion to reduce stress on freshwater biota.

Management agencies responsible for monitoring US lake water

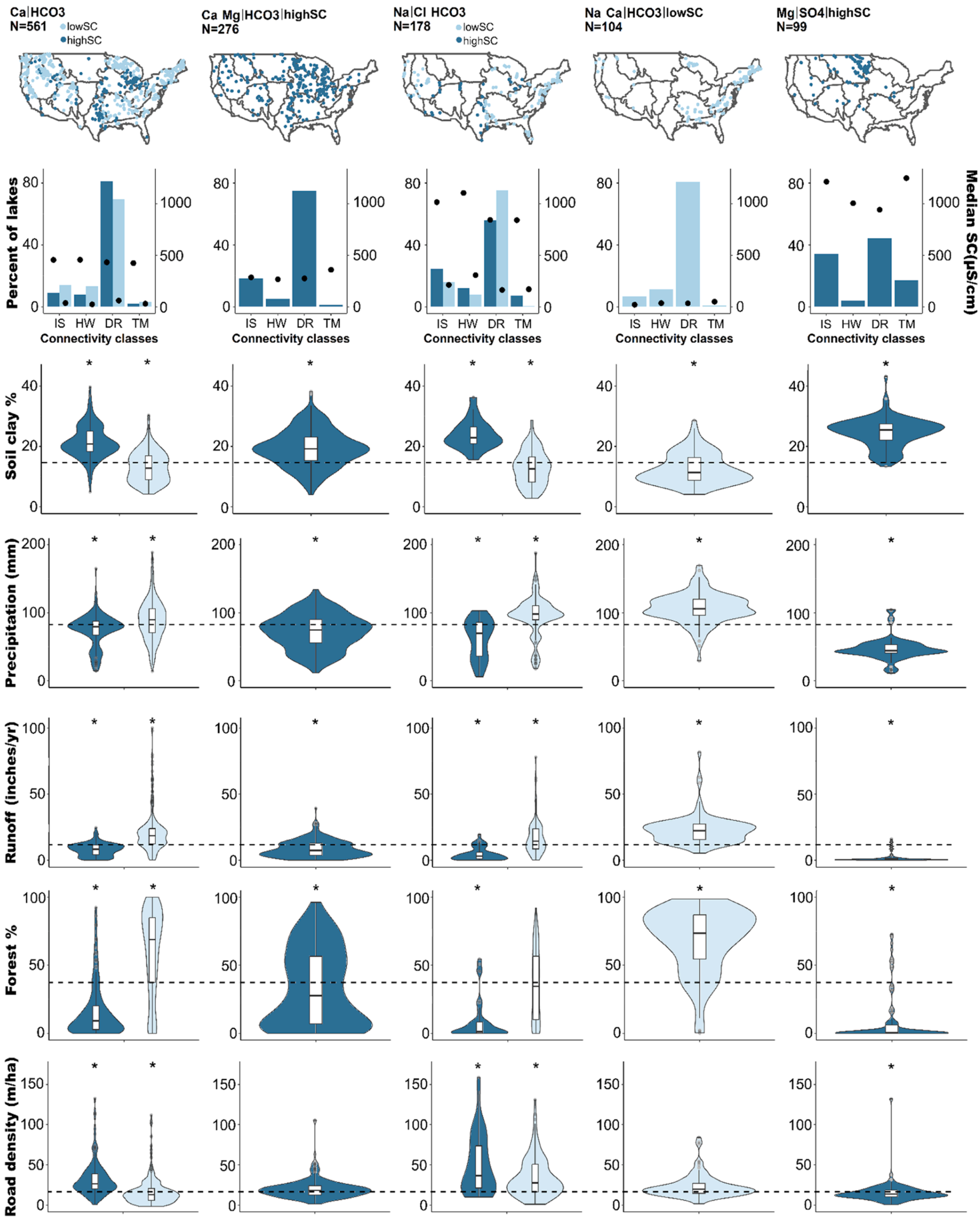


Fig. 6. Maps (top), barplots (middle), and violin plots (bottom) of lakes in the seven ion groups based on the dominant cation(s) and anion(s) and SC. Maps show the location of lakes within each ion group, with the text listing the group names and the number of lakes. Barplots show the percentage of lakes (bars, left axis) and median SC (black dots, right axis) in the four surface connectivity classes (IS=isolated (no surface in/outflow); HW=headwater (only with surface outflow); DR=drainage (with both surface inflow and outflow); TM=terminal (only with surface inflow)). Violin plots show the data distribution for each top natural and human factor by ion group. In the embedded boxplots, the bold line indicates the median and the upper and lower whiskers indicate the 75th and 25th percentiles. The horizontal dashed lines are the median values of the 1,218 lakes (i.e., all-lake-median). The star above the violin plot indicates a significant difference ($p \leq 0.05$) in that factor between the corresponding ion group and the all-lake-median.

quality are more likely to measure SC than major ions due to the high costs associated with measuring ions compared to SC. However, although we observed a strong linear relationship between SC and total salt concentration (calculated by summing up the concentration of each ion), different combinations of ions can make up SC and total salt concentration (Figure S13) and ions differ in their effects on biota. Therefore, it is important to account for the ion composition when managing lake chemistry or when using SC to predict ion concentrations, which means that monitoring agencies should supplement their SC data with ion data, particularly for lakes with high SC (e.g., lakes in the Southeast and Central Plains had limited ion data). Sampling ion data (as done by the US National Lakes Assessment) as well as SC will provide important insights beyond what can be revealed by SC alone.

Our macroscale approach both corroborated fine-scale studies in some cases and revealed novel patterns in ion concentrations and composition within and among regions in others. For example, Ca^{2+}, and sometimes Na^{+}, were the dominant cations in most lakes, as expected based on limnological first principles (Dugan 2024). However, in about 8% of lakes located mostly in the Northern Plains, Mg^{2+} was the dominant cation (a few others were located in the Prairie Peninsula and West regions). In addition, our national-scale study identified 14% of lakes, mostly in the Eastern and Northwestern US, that were co-dominated by the anions Cl^{-} and HCO_3^{-}, which has not been observed in regional-scale research (e.g., Gorham et al. 1983).

Building on previous regional work that demonstrated within-region heterogeneity in ion composition is driven by both natural processes and human activities (Baker et al. 1991; DeSellas et al., 2024), our work provides the first national-scale comparison across diverse US ecoregions. We found substantial within-region variation in ion concentrations and composition, as illustrated in Fig. 5. This variation is intriguing because earlier studies suggested that ion composition is primarily shaped by a consistent set of natural factors (e.g., geology, climate, hydrology), with regional differences reflecting only variation in factor characteristics (Griffith 2014; Olson & Cormier 2019). Our results highlight that it is not sufficient to assume that lakes within a region will have similar lake chemistry but that local drivers contribute to substantial intra-regional variation. This broader perspective underscores the complex interactions of factors operating at multiple spatial scales.

4.2. Natural and human factors are strongly related to lake SC and major ions

Our findings show how factors interact with each other to play substantially different roles among lakes both across and within ecoregions, and that human disturbances cause some ions in individual lakes to deviate from 'background' levels expected from natural factors. In particular, Cl^{-} was the only anion strongly associated with urban development and road density (Figures S12&14), highlighting its value as a tracer of anthropogenic influences. Therefore, effective strategies designed to manage water quality and lake ecosystems should monitor and target both SC and specific ions, such as Cl^{-}, that reflect local human disturbance.

4.2.1. Individual and interactive effects on SC

Our study supports established expectations that natural features, such as precipitation-driven surface runoff, groundwater flow, and soil composition, influence lake SC. For example, lakes with high clay watersheds had high SC and were located in the Prairie Peninsula, Plains, and Desert Southwest regions. However, most relationships involve some interactions between human and natural drivers, or interactions between local and watershed drivers. For instance, SC was negatively related to lake elevation, which likely reflects a combination of human impacts and natural processes. Specifically, lower-elevation lakes may receive more ions from rock weathering (Müller et al. 1998) and have higher anthropogenic ion inputs, as indicated by higher percentages of developed land use (Table S6). In contrast, some areas like Florida have relatively low soil clay content but still show elevated SC due to seawater intrusion (Eilers et al. 1988; Kiflai et al. 2022). Moreover, we found negative relationships between SC and both groundwater recharge and runoff, which strongly vary at the watershed scale (Lapierre et al., 2018). This result suggests that low SC lakes are more dependent on precipitation and surface water inputs (Webster et al. 2006), as observed in ecoregions like the Northeast, Southeast, and Great Lakes. In contrast, lakes in the Plains, where groundwater is a dominant source and precipitation is limited, exhibited very high SC values, likely due to the dominant role of evapoconcentration (La Baugh et al. 2000; Li et al. 2020). Together, these findings highlight the complex interplay between natural characteristics and human land use in shaping lake SC at the national scale, while also suggesting that even within the same ecoregion, lakes may be influenced by different dominant drivers, as further evidenced by differences in ion composition discussed in subsequent paragraphs.

4.2.2. Individual and interactive effects on ion concentrations and composition

We found that multiple natural features often act collectively on ion composition, resulting in distinct ionic assemblages across lakes. Importantly, analyses based on relative ion composition yielded similar groupings, indicating that the observed patterns were not solely driven by total ion concentrations. For example, the Mg|SO4|highSC group includes lakes with distinct ion signatures that reflect the combined effects of surface connectivity, hydrology, and soil composition. Surface connectivity reflects the relative importance of water and ion inputs from precipitation, surface water, and groundwater sources (Riera et al. 2000; Bennett et al. 2007). Lakes in the Mg|SO4|highSC group, which has distinct ion composition and the highest average SC among all groups, had the highest proportions of terminal and isolated lakes among all groups; and 41% of all terminal lakes and 20% of all isolated lakes were in this group (Table S5). These isolated and terminal lakes can be ion sinks for catchments, particularly in evaporative regions (Saleem et al. 2015; Cotner et al. 2022; Ding et al. 2024). In addition to the influence from hydrology, we also found that lakes in this group are associated with high percentages of clay soils, which could be a major source of cations since clay soils often contain higher amounts of cations such as Mg^{2+} (Ross et al. 2008). These patterns suggest that the Mg|SO4|highSC lakes function as geochemical endpoints within their catchments, where ion accumulation is driven by both hydrologic isolation and underlying soil properties.

We found that the impact of a given natural factor on lake ion composition varies with the local context and interactions with other factors. For example, lakes in Ca|HCO3|lowSC and Ca|HCO3|highSC groups share similar ion composition, but very different concentrations, indicating similar geological settings but differing hydrologic and/or climatic conditions that influence solute accumulation (Fig. 6). Moreover, high surface connectivity can either dilute (e.g., in Mg|SO4|highSC) or enhance (e.g., in Ca|HCO3|lowSC) (Fig. 6) solute concentrations. This result implies that although the water inputs from tributaries can import ions into lakes and increase ionic concentrations, other natural processes may mask this effect by being more influential forces (e.g., evaporation concentrates ions), in which case tributary water inputs could have a dilution effect on ion concentrations.

Our results also showed that both the intensity of human activity and its interaction with local natural context play critical roles in shaping lake ion composition. The most important human-related factor that affected ion composition was road density (Figure S12), which was significantly higher in and positively associated with lake membership in Na|Cl HCO3|highSC and Na|Cl HCO3|lowSC groups. Some lakes in these same groups are located in regions where winter road salt applications would be expected (i.e., northern and higher-elevation areas of the US; Dugan et al. 2017), and had higher concentrations and proportions of Na^{+} and Cl^{-} than other ion groups. This finding is consistent with studies showing that winter road salt enters lakes and accumulates

Cl^- over time (Kaushal et al. 2021; Solomon et al. 2023). Complementing and extending a long-term study that found an increasing trend of Cl^- in 125 of 371 lakes in North America (Dugan et al. 2017), our results emphasize the importance of controlling road salt applications in regions with high impervious surface area and road density near lakes. Interestingly, some lakes in the Na|Cl HCO3|highSC and Na|Cl HCO3|lowSC groups were located in the Southern US, where road salt is less common, suggesting that other sources of Na^+ and Cl^- that are correlated with road density may contribute to this unique ion composition, such as development and impervious surfaces that promote runoff. Furthermore, although these two ion groups had similar human impacts and ion composition, they differed in total salt content, resulting in varied concentrations of multiple ions. This difference was likely driven by their variations in surface connectivity and freshwater input (e.g., from precipitation and surface runoff), indicating that human impacts are modulated by watershed hydrology. Because ions can act interactively to affect toxicity (e.g., Cl^- and Ca^{2+}; Huber et al. 2024; Buren & Arnott 2025), such differences in lake ion characteristics could result in divergent biological responses, thus requiring different management strategies.

4.3. Ionic composition provides insights into the influence of human activities on lakes

Our findings suggested that the composition of individual ions provided additional insight into whether observed patterns largely reflect natural processes or have been significantly influenced by anthropogenic factors. Across all lakes, Cl^- consistently emerged as the only anion whose top three influential factors were all human-related (i.e., developed land use and the two ways of estimating road density; Figure S14), highlighting its role as a strong indicator of anthropogenic impacts. In contrast, HCO_3^- and SO_4^{2-} were more strongly associated with natural processes, reflecting the importance of geological and hydrological controls. This macroscale comparison underscores that ion composition not only reveals whether lake chemistry is dominated by natural processes or human influences, but also provides a practical tool for monitoring and managing freshwater ecosystems by identifying where human activities most strongly alter natural chemical baselines.

5. Conclusions

Specific conductance (SC) and major ion composition and concentrations are widely used indicators of freshwater salinization, yet their patterns and drivers remain poorly understood at continental scales. Our macroscale analysis across a broad range of ecoregions provided sufficient variation in drivers to assess and compare the importance of human versus natural factors. We found substantial variation in ion composition, with 14% of lakes being dominated by Na^+, Cl^-, and HCO_3^-, and 8% of the lakes being dominated by Mg^{2+} and SO_4^{2-}. These results highlight the importance of sampling and considering multiple major ions, in addition to SC, to obtain a comprehensive understanding of lake ion chemistry. We also found that, while some factors, such as soil, hydrology, and climate, act as primary controls, the roles of natural and human factors in shaping SC and ion composition interact with each other in complex ways and differ markedly across ecoregions and lakes. Notably, certain ions showed distinct anthropogenic influences; in particular, higher Cl^- levels were predominantly related to road density and urban development. Our results highlight how human disturbances can directly and indirectly alter ion export to lakes, changing major ion concentrations and composition, which can then affect ionic interactions and lake biota. Predicting future spatial variation in ion chemistry will require considering the trajectories of human disturbances alongside anticipated changes in natural features, highlighting the need for integrated, macroscale approaches to understand, forecast, and manage lake water chemistry under ongoing environmental changes.

CRediT authorship contribution statement

Xinyu Sun: Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Kendra Spence Cheruvelil:** Writing – review & editing, Supervision, Investigation, Funding acquisition, Conceptualization. **Patrick J. Hanly:** Writing – review & editing, Investigation, Funding acquisition, Data curation. **Katherine E. Webster:** Writing – review & editing, Visualization, Methodology, Investigation. **Patricia A. Soranno:** Writing – review & editing, Supervision, Investigation, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgment

This work was supported by the US National Science Foundation (NSF) Macrosystems Biology & NEON-Enabled Science Program (DEB #1638679) and the United States Department of Agriculture (USDA) National Institute of Food and Agriculture, Hatch project 1013544.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.watres.2026.125486.

Data availability

The data, metadata, and codes have been uploaded to Zenodo and are available from: https://doi.org/10.5281/zenodo.15256977.

References

Andersen, C.B., 2002. Understanding carbonate equilibria by measuring alkalinity in experimental and natural systems. J. Geosci. Educ. 50 (4), 389–403. https://doi.org/10.5408/1089-9995-50.4.389.

Baker, L.A., Eilers, J.M., Cook, R.B., Kaufmann, P.R., Herlihy, A.T., 1991. Interregional comparisons of surface water chemistry and biogeochemical processes. Ed.. In: Charles, D.F. (Ed.), Acidic Deposition and Aquatic Ecosystems. Springer, New York, pp. 567–613. https://doi.org/10.1007/978-1-4613-9038-1_23.

Beckingham, B., Callahan, T., Vulava, V., 2019. Stormwater ponds in the southeastern U. S. Coastal plain: hydrogeology, contaminant fate, and the need for a social-ecological framework. Front. Environ. Sci. 7. https://doi.org/10.3389/fenvs.2019.00117.

Bennett, D.M., Fritz, S.C., Holz, J.C., Holz, A.A., Zlotnik, V.A., 2007. Evaluating climatic and non-climatic influences on ion chemistry in natural and man-made lakes of Nebraska, USA. Hydrobiologia 591 (1), 103–115. https://doi.org/10.1007/s10750-007-0798-z.

Blodgett, D.L. (2023). *Twelve-digit hydrologic unit soil moisture, recharge, actual evapotranspiration, and snowpack water equivalent storage from the National Hydrologic Model Infrastructure with the Precipitation-Runoff Modeling System 1980-2016*. https://doi.org/10.5066/P9W148A1.

Breiman, L., Cutler, A., Liaw, A., & Wiener, M. (2022). Random forest: Breiman and cutler's random forests for classification and regression (Version 4.7-1.1). https://cran.r-project.org/web/packages/randomForest/index.html.

Buren, S., Arnott, S.E., 2025. The effect of calcium on acute sodium chloride toxicity in Daphnia species. Environ. Toxicol. Chem. 44 (3), 718–727. https://doi.org/10.1093/etojnl/vgae066.

Cañedo-Argüelles, M., Hawkins, C.P., Kefford, B.J., Schäfer, R.B., Dyack, B.J., Brucet, S., Buchwalter, D., Dunlop, J., Frör, O., Lazorchak, J., Coring, E., Fernandez, H.R., Goodfellow, W., Achem, A.L.G., Hatfield-Dodds, S., Karimov, B.K., Mensah, P., Olson, J.R., Piscart, C., Timpano, A.J., 2016. Saving freshwater from salts. Science 1979 351 (6276), 914–916. https://doi.org/10.1126/science.aad3488.

Cheruvelil, K.S., Soranno, P.A., McCullough, I.M., Webster, K.E., Rodriguez, L.K., Smith, N.J., 2021. LAGOS-US LOCUS v1.0: data module of location, identifiers, and physical characteristics of lakes and their watersheds in the conterminous US. Limnol. Oceanogr. Lett. 6 (5), 270–292. https://doi.org/10.1002/lol2.10203.

Clements, W.H., Kotalik, C., 2016. Effects of major ions on natural benthic communities: an experimental assessment of the US Environmental Protection Agency aquatic life benchmark for conductivity. Freshw. Sci. 35 (1), 126–138. https://doi.org/10.1086/685085.

Cotner, J.B., Anderson, N.J., Osburn, C., 2022. Accumulation of recalcitrant dissolved organic matter in aerobic aquatic systems. Limnol. Oceanogr. Lett. 7 (5), 401–409. https://doi.org/10.1002/lol2.10265.

DeSellas, A.M., Paterson, A.M., Rühland, K.M., Smol, J.P., 2024. Lake water chemistry and its relationship to shoreline residential development and natural landscape features in Algonquin Provincial Park, Ontario, Canada. Can. J. Fish. Aquat. Sci. https://doi.org/10.1139/cjfas-2023-0103 cjfas-2023-0103.

Ding, M., Wang, J., Song, C., Sheng, Y., Shawn Hutchinson, J.M., Langston, A.L., Marston, L., 2024. A framework of freshwater and saline lake typology classification through leveraging hydroclimate, spectral, and literature evidence. J. Hydrol. 632, 130704. https://doi.org/10.1016/j.jhydrol.2024.130704.

Dugan, H.A., 2024. Chapter 12 - salinity and ionic composition of Inland Waters. Eds.. In: Jones, I.D., Smol, J.P. (Eds.), Wetzel's Limnology, Fourth Edition. Academic Press, pp. 275–299. https://doi.org/10.1016/B978-0-12-822701-5.00012-4.

Dugan, H.A., Bartlett, S.L., Burke, S.M., Doubek, J.P., Krivak-Tetley, F.E., Skaff, N.K., Summers, J.C., Farrell, K.J., McCullough, I.M., Morales-Williams, A.M., Roberts, D. C., Ouyang, Z., Scordo, F., Hanson, P.C., Weathers, K.C., 2017. Salting our freshwater lakes. Proc. Natl. Acad. Sci. 114 (17), 4453–4458. https://doi.org/10.1073/pnas.1620211114.

Dumelle, M., Ver Hoef, J.M., Handler, A., Hill, R.A., Higham, M., Olsen, A.R., 2024. Modeling lake conductivity in the contiguous United States using spatial indexing for big spatial data. Spat. Stat. 59, 100808. https://doi.org/10.1016/j.spasta.2023.100808.

Eilers, J.M., Landers, D.H., Brakke, D.F., 1988. Chemical and physical characteristics of lakes in the southeastern United States. Environ. Sci. Technol. 22 (2), 172–177. https://doi.org/10.1021/es00167a006.

Elphick, J.R.F., Bergh, K.D., Bailey, H.C., 2011. Chronic toxicity of chloride to freshwater species: effects of hardness and implications for water quality guidelines. Environ. Toxicol. Chem. 30 (1), 239–246. https://doi.org/10.1002/etc.365.

EnviroAtlas, 2015. Manure application (kg N/ha/yr) – [ManureMean]. EnviroAtlas. https://catalog.data.gov/dataset/enviroatlas-manure-application-to-agricultural-lands-from-confined-animal-feeding-operatio-2006.

Friedman, J., Hastie, T., Tibshirani, R., Narasimhan, B., Tay, K., Simon, N., Qian, J., & Yang, J. (2023). GLMNET: lasso and elastic-net regularized generalized linear models (Version 4.1-8). https://cran.r-project.org/web/packages/glmnet/index.html.

Gorham, E., Dean, W.E., Sanger, J.E., 1983. The chemical composition of lakes in the north-central United States. Limnol. Oceanogr. 28 (2), 287–301. https://doi.org/10.4319/lo.1983.28.2.0287.

Gorham, E., 1961. Factors influencing supply of major ions to Inland Waters, with special reference to the atmosphere. Geol. Soc. Am. Bull. 72 (6), 795. https://doi.org/10.1130/0016-7606(1961)72[795:FISOMI]2.0.CO;2.

Greenwell, B.M., 2022. *PDP: Partial Dependence Plots* (Version 0.8.1). https://cran.r-project.org/web/packages/pdp/index.html.

Griffith, M.B., 2014. Natural variation and current reference for specific conductivity and major ions in wadeable streams of the conterminous USA. Freshw. Sci. 33 (1), 1–17. https://doi.org/10.1086/674704.

Haque, S.E., 2023. The effects of climate variability on Florida's major water resources. Sustainability 15 (14), 11364. https://doi.org/10.3390/su151411364.

Härdle, W.K., Simar, L., 2019. Applied Multivariate Statistical Analysis. Springer International Publishing. https://doi.org/10.1007/978-3-030-26006-4.

Hargrove, W.W., Hoffman, F.M., 1999. Using multivariate clustering to characterize ecoregion borders. Comput. Sci. Eng. 1 (4), 18–25. https://doi.org/10.1109/5992.774837.

Hintz, W.D., Relyea, R.A., 2019. A review of the species, community, and ecosystem impacts of road salt salinisation in fresh waters. Freshw. Biol. 64 (6), 1081–1097. https://doi.org/10.1111/fwb.13286.

Huber, E.D., Hintz, L.L., Wilmoth, B., McKenna, J.R., Hintz, W.D., 2024. Coping with stress: salt type, concentration, and exposure history limit life history tradeoffs in response to road salt salinization. Sci. Total Environ. 949, 174998. https://doi.org/10.1016/j.scitotenv.2024.174998.

Hunsaker, C.T., Johnson, D.W., 2017. Concentration-discharge relationships in headwater streams of the Sierra Nevada, California. Water. Resour. Res. 53 (9), 7869–7884. https://doi.org/10.1002/2016WR019693.

Kaushal, S.S., Likens, G.E., Pace, M.L., Haq, S., Wood, K.L., Galella, J.G., Morel, C., Doody, T.R., Wessel, B., Kortelainen, P., Räike, A., Skinner, V., Utz, R., Jaworski, N., 2019. Novel 'chemical cocktails' in inland waters are a consequence of the freshwater salinization syndrome. Philos. Trans. R. Soc. B: Biol. Sci. 374 (1764), 20180017. https://doi.org/10.1098/rstb.2018.0017.

Kaushal, S.S., Likens, G.E., Pace, M.L., Reimer, J.E., Maas, C.M., Galella, J.G., Utz, R.M., Duan, S., Kryger, J.R., Yaculak, A.M., Boger, W.L., Bailey, N.W., Haq, S., Wood, K.L., Wessel, B.M., Park, C.E., Collison, D.C., Aisin, B.Y., aaqob, I., Gedeon, T.M., Woglo, S.A., 2021. Freshwater salinization syndrome: from emerging global problem to managing risks. Biogeochemistry. 154 (2), 255–292. https://doi.org/10.1007/s10533-021-00784-w.

Keller, M., Schimel, D.S., Hargrove, W.W., Hoffman, F.M., 2008. A continental strategy for the National Ecological Observatory Network. Front. Ecol. Environ. 6 (5), 282–284. https://doi.org/10.1890/1540-9295(2008)6[282:ACSFTN]2.0.CO;2.

Kiflai, M.E., Whitman, D., Price, R.M., Frankovich, T.A., Madden, C.J., 2022. Geophysical characterization in the shallow water estuarine lakes of the southern Everglades, Florida. Appl. Sci. 12 (3), 1154. https://doi.org/10.3390/app12031154.

Kratz, T., Webster, K., Bowser, C., Maguson, J., Benson, B., 1997. The influence of landscape position on lakes in northern Wisconsin. Freshw. Biol. 37 (1), 209–217. https://doi.org/10.1046/j.1365-2427.1997.00149.x.

Kursa, M.B., Rudnicki, W.R., 2022. *Boruta: Wrapper Algorithm for All Relevant Feature Selection* (Version 8.0.0). https://cran.r-project.org/web/packages/Boruta/index.html.

La Baugh, J.W., Winter, T.C., Rosenberry, D.O, 2000. Comparison of the variability in fluxes of ground water and solutes in lakes and wetlands in central North America. SIL Proc., 1922-2010 27 (1), 420–426. https://doi.org/10.1080/03680770.1998.11901266.

Lapierre, J., Collins, S.M., Seekell, D.A., Spence Cheruvelil, K., Tan, P., Skaff, N.K., Taranu, Z.E., Fergus, C.E., Soranno, P.A., 2018. Similarity in spatial structure constrains ecosystem relationships: Building a macroscale understanding of lakes. Glob. Ecol. Bio. 27 (10), 1251–1263. https://doi.org/10.1111/geb.12781.

Li, C., Gao, X., Li, S., Bundschuh, J., 2020. A review of the distribution, sources, genesis, and environmental concerns of salinity in groundwater. Environ. Sci. Pollut. Res. 27 (33), 41157–41174. https://doi.org/10.1007/s11356-020-10354-6.

Lottig, N.R., Stanley, E.H., Hanson, P.C., Kratz, T.K., 2011. Comparison of regional stream and lake chemistry: differences, similarities, and potential drivers. Limnol. Oceanogr. 56 (5), 1551–1562. https://doi.org/10.4319/lo.2011.56.5.1551.

Martin, S.L., Soranno, P.A., 2006. Lake landscape position: relationships to hydrologic connectivity and landscape features. Limnol. Oceanogr. 51 (2), 801–814. https://doi.org/10.4319/lo.2006.51.2.0801.

Meybeck, M., 2003. Global analysis of river systems: from Earth system controls to anthropocene syndromes. Philos. Trans. R. Soc. B: Biol. Sci. 358 (1440), 1935–1955. https://doi.org/10.1098/rstb.2003.1379.

Mount, D.R., Erickson, R.J., Highland, T.L., Hockett, J.R., Hoff, D.J., Jenson, C.T., Norberg-King, T.J., Peterson, K.N., Polaske, Z.M., Wisniewski, S., 2016. The acute toxicity of major ion salts to *Ceriodaphnia dubia* : I. influence of background water chemistry. Environ. Toxicol. Chem. 35 (12), 3039–3057. https://doi.org/10.1002/etc.3487.

Müller, B., Lotter, A.F., Sturm, M., Ammann, A., 1998. Influence of catchment quality and altitude on the water and sediment composition of 68 small lakes in Central Europe. Aquat. Sci. 60 (4), 316. https://doi.org/10.1007/s000270050044.

Nostro, P.L., Ninham, B.W., Nostro, A.L., Pesavento, G., Fratoni, L., Baglioni, P., 2005. Specific ion effects on the growth rates of *Staphylococcus aureus* and *Pseudomonas aeruginosa*. Phys. Biol. 2 (1), 1–7. https://doi.org/10.1088/1478-3967/2/1/001.

Olson, J.R., 2019. Predicting combined effects of land use and climate change on river and stream salinity. Philos. Trans. R. Soc. B: Biol. Sci. 374 (1764), 20180005. https://doi.org/10.1098/rstb.2018.0005.

Olson, J.R., Cormier, S.M., 2019. Modeling spatial and temporal variation in natural background specific conductivity. Environ. Sci. Technol. 53 (8), 4316–4325. https://doi.org/10.1021/acs.est.8b06777.

Oswald, C.J., Giberson, G., Nicholls, E., Wellen, C., Oni, S., 2019. Spatial distribution and extent of urban land cover control watershed-scale chloride retention. Sci. Total Environ. 652, 278–288. https://doi.org/10.1016/j.scitotenv.2018.10.242.

Polus, S.M., Hanly, P.J., Rodriguez, L.K., Wang, Q., Díaz Vázquez, J., Webster, K.E., Tan, P.-N., Zhou, J., Danila, L., Soranno, P.A., Cheruvelil, K.S, 2022. LAGOS-US RESERVOIR: data module classifying conterminous U.S. lakes 4 hectares and larger as natural lakes or reservoirs. Environ. Data Initiat. https://doi.org/10.6073/PASTA/F9AA935329A95DFD69BF895015BC5161.

R Core Team, 2024. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Redder, B.W., Kennedy, C.D., Buda, A.R., Folmar, G., Boyer, E.W., 2021. Groundwater contributions of flow and nitrogen in a headwater agricultural watershed. Hydrol. Process. 35 (5), e14179. https://doi.org/10.1002/hyp.14179.

Riera, J.N.L., Magnuson, JN.J., Kratz, T.M.K., Webster, K.E., 2000. A geomorphic template for the analysis of lake districts applied to the Northern Highland Lake District, Wisconsin, U.S.A. Freshw. Biol. 43 (3), 301–318. https://doi.org/10.1046/j.1365-2427.2000.00567.x.

Rodriguez, L.K., Polus, S.M., Matuszak, D.I., Domka, M.R., Hanly, P.J., Wang, Q., Soranno, P.A., Cheruvelil, K.S., 2023. LAGOS-US RESERVOIR : A database classifying conterminous U.S. lakes 4 ha and larger as natural lakes or reservoir lakes. Limnol. Oceanogr. Lett. 8 (2), 267–285. https://doi.org/10.1002/lol2.10299.

Rogalski, M.A., Baker, E.S., Benadon, C.M., Tatgenhorst, C., Nichols, B.R., 2024. Lake water chemistry and local adaptation shape NaCl toxicity in *daphnia ambigua*. Evol. Appl. 17 (3), e13668. https://doi.org/10.1111/eva.13668.

Ross, D.S., Matschonat, G., Skyllberg, U., 2008. Cation exchange in forest soils: the need for a new perspective. Eur. J. Soil. Sci. 59 (6), 1141–1159. https://doi.org/10.1111/j.1365-2389.2008.01069.x.

Saleem, M., Jeelani, G., Shah, R.A., 2015. Hydrogeochemistry of Dal Lake and the potential for present, future management by using facies, ionic ratios, and statistical analysis. Environ. Earth. Sci. 74 (4), 3301–3313. https://doi.org/10.1007/s12665-015-4361-3.

Schacht, J.R.S., MacKeigan, P.W., Taranu, Z.E., Huot, Y., Gregory-Eaves, I., 2023. Agricultural land use and morphometry explain substantial variation in nutrient and ion concentrations in lakes across Canada. Can. J. Fish. Aquat. Sci. 80 (11), 1785–1797. https://doi.org/10.1139/cjfas-2023-0109.

Shuvo, A.K., Lottig, N.R., Webster, K.E., Delany, A., Reinl, K., Gries, C., Smith, N.J., Poisson, A.C., McCullough, I.M., Collins, S.M., King, K.B.S., Phillips, E., Cheruvelil, K.S., Soranno, P.A., 2023. LAGOS-US LIMNO: data module of surface water chemistry from 1975-2021 for lakes in the conterminous U.S. Environ. Data Initiat. https://doi.org/10.6073/PASTA/2C58F5A50AB813919F99CC1F265F271C.

Smith, N.J., Webster, K.E., Rodriguez, L.K., Cheruvelil, K.S., Soranno, P.A., 2021. LAGOS-US LOCUS v1.0: data module of location, identifiers, and physical characteristics of lakes and their watersheds in the conterminous U.S. Environ. Data Initiat. https://doi.org/10.6073/PASTA/E5C2FB8D77467D3F03DE4667AC2173CA.

Smith, N.J., Webster, K.E., Rodriguez, L.K., Cheruvelil, K.S., & Soranno, P.A. (2022). *LAGOS-US GEO v1.0: data module of lake geospatial ecological context at multiple spatial* *and temporal scales in the conterminous U.S.* Environmental Data Initiative. https://doi.org/10.6073/pasta/0e443bd43d7e24c2b6abc7af54ca424a.

Solomon, C.T., Dugan, H.A., Hintz, W.D., Jones, S.E., 2023. Upper limits for road salt pollution in lakes. Limnol. Oceanogr. Lett. 8 (6), 859–866. https://doi.org/10.1002/lol2.10339.

Soranno, P.A., Hanly, P.J., Webster, K.E., Wagner, T., McDonald, A., Shuvo, A., Schliep, E.M., Reinl, K.L., McCullough, I.M., Tan, P.-N., Lottig, N.R., Spence Cheruvelil, K., 2025. Abrupt changes in algal biomass of thousands of US lakes are related to climate and are more likely in low-disturbance watersheds. Proc. Natl. Acad. Sci. 122 (9), e2416172122. https://doi.org/10.1073/pnas.2416172122.

Soranno, P.A., Lottig, N.R., Delany, A.D., Cheruvelil, K.S., 2019. LAGOS-NE-LIMNO v1.087.3: A module for LAGOS-NE, a multi-scaled geospatial and temporal database of lake ecological context and water quality for thousands of U.S. Lakes: 1925-2013. Environ. Data Initiat. https://doi.org/10.6073/PASTA/08C6F9311929F4874B01BCC64EB3B2D7.

Soranno, P.A., Webster, K.E., Riera, J.L., Kratz, T.K., Baron, J.S., Bukaveckas, P.A., Kling, G.W., White, D.S., Caine, N., Lathrop, R.C., Leavitt, P.R., 1999. Spatial variation among lakes within landscapes: ecological organization along Lake chains. Ecosystems. 2 (5), 395–410. https://doi.org/10.1007/s100219900089.

Stets, E.G., Sprague, L.A., Oelsner, G.P., Johnson, H.M., Murphy, J.C., Ryberg, K., Vecchia, A.V., Zuellig, R.E., Falcone, J.A., Riskin, M.L., 2020. Landscape drivers of dynamic change in water quality of U.S. Rivers. Environ. Sci. Technol. 54 (7), 4336–4343. https://doi.org/10.1021/acs.est.9b05344.

Swanson, G.A., Winter, T.C., Adomaitis, V.A., La Baugh, J.W., 1988. Chemical characteristics of Prairie Lakes in South-Central North Dakota: Their Potential for Influencing use by Fish and Wildlife. U.S. Department of the Interior, Fish and Wildlife Service.

U.S. Environmental Protection Agency, 2010. National Aquatic Resource Surveys. National Lakes Assessment 2007. Available from U.S. EPA website. http://www.epa.gov/national-aquatic-resource-surveys/data-national-aquatic-resource-surveys.

U.S. Environmental Protection Agency, 2016. National Aquatic Resource Surveys. National Lakes Assessment 2012. Available from U.S. EPA website: http://www.epa.gov/national-aquatic-resource-surveys/data-national-aquatic-resource-surveys.

U.S. Environmental Protection Agency, 2022. *National Lakes Assessment 2017 Datafiles for Report "National Lakes Assessment 2017: The third collaborative survey of lakes in the United States*. U.S. Environmental Protection Agency. https://doi.org/10.23719/1529585.

Van Gray, J.B., Ayayee, P., 2024. Examining the impacts of salt specificity on freshwater microbial community and functional potential following salinization. Environ. Microbiol. 26 (5), e16628. https://doi.org/10.1111/1462-2920.16628.

Water Quality Portal. (2021). *Washington (DC): National Water Quality Monitoring Council, United States Geological Survey (USGS), Environmental Protection Agency (EPA)*. https://doi.org/10.5066/P9QRKUVJ.

Webster, K.E., Bowser, C.J., Anderson, M.P., Lenters, J.D., 2006. Understanding the lake-groundwater system: just follow the water. Long-term Dynamics of Lakes in the Landscape: Long-term Ecological Research on North Temperate Lakes. Oxford University Press, pp. 19–48.