

Title: Interactions Between Human Activities and Natural Processes Shape Specific Conductance and Ion Composition of United States Lakes

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Author contribution statement: Xinyu Sun and Kendra Spence Cheruvellil conceived the project. Xinyu Sun, Kendra Spence Cheruvellil, Patrick J. Hanly, Katherine E. Webster, and Patricia A. Soranno designed the analyses and interpreted the results. Xinyu Sun gathered and processed data. Xinyu Sun and Patrick J. Hanly performed analyses and made figures, tables, and supplements. Xinyu Sun wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

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 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.

Keywords: Salinization; Road density; Macroscale variation; Geology; Hydrology; Macrosystem

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; land use/cover around lakes in Ontario, Canada, 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 and natural and human controls on major ion chemistry.

2. Material and methods

2.1 Data collection

We used data from the LAGOS-US research platform (Cheruvilil et al. 2021) that includes lake, natural environmental, and human activity data for 479,950 lakes ≥ 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 (Cheruvilil 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 ecoregions 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 $\mu\text{S}/\text{cm}$ (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 + $15 \times \text{interquartile range} = 4,983 \mu\text{S}/\text{cm}$; 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 $\mu\text{S}/\text{cm}$ SC (mean $\pm$ standard deviation (SD) = $343 \pm 511 \mu\text{S}/\text{cm}$, median = 206 $\mu\text{S}/\text{cm}$). 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 ($\geq 85\%$ 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 ($\mu\text{eq/L}$; Table S2). In this study, we used bicarbonate (HCO_3^-) (in $\mu\text{eq/L}$) 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 $\text{pH} > 8.3$, 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 $\mu\text{eq/L}$) 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.

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 (Figure 1). Most lakes with relatively high SC (SC higher than 90% of all lakes; $SC \geq 696 \mu\text{S/cm}$) were located in the Southeast, central US (e.g., Prairie Peninsula, Northern Plains, Central Plains, and Southern Plains), and Desert Southwest NEON ecoregions (Figure 1c). Of these, 202 lakes, mostly located in the Northern Plains, had SC higher than 2,000 $\mu\text{S/cm}$. Lakes with relatively low SC (SC lower than 10% of all lakes; $SC \leq 34 \mu\text{S/cm}$) 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 $\mu\text{S/cm}$), followed by those in the Northern Plains (897

$\mu\text{S}/\text{cm}$), and the Central Plains (894 $\mu\text{S}/\text{cm}$). The Pacific Northwest had the lowest mean SC (72 $\mu\text{S}/\text{cm}$), followed by the Northeast (139 $\mu\text{S}/\text{cm}$) and Mid-Atlantic (146 $\mu\text{S}/\text{cm}$) ecoregions. Most of the lakes with multiple sampling dates within a year had low intra-year temporal variation in SC (CV: mean $\pm$ SD=10% $\pm$ 13%, median=6%), and those with high CV (greater than 100%) were predominantly found in the Northeast, Southeast, and Great Lakes ecoregions (Figure S5).

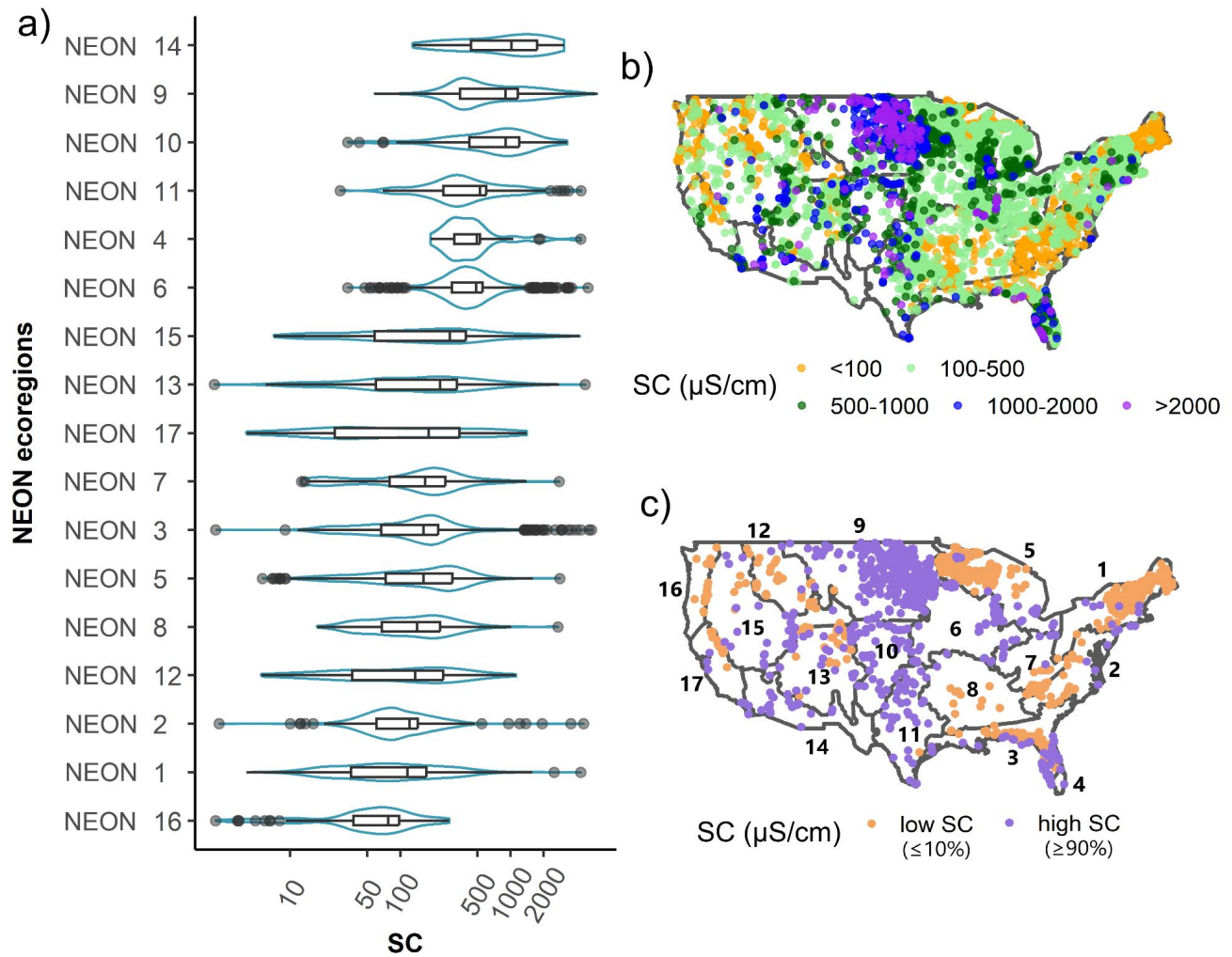


Figure 1. Specific conductance (SC; $\mu\text{S/cm}$) by NEON ecoregion for the full dataset (N=9,784).

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).

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 (Figure 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. 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 (Figure 2b-i; $p < 0.001$). Specifically, Ca^{2+} and K^{+} had the strongest associations with SC, followed by HCO_3^{-} , Cl^{-} , Na^{+} , Mg^{2+} , and SO_4^{2-} .

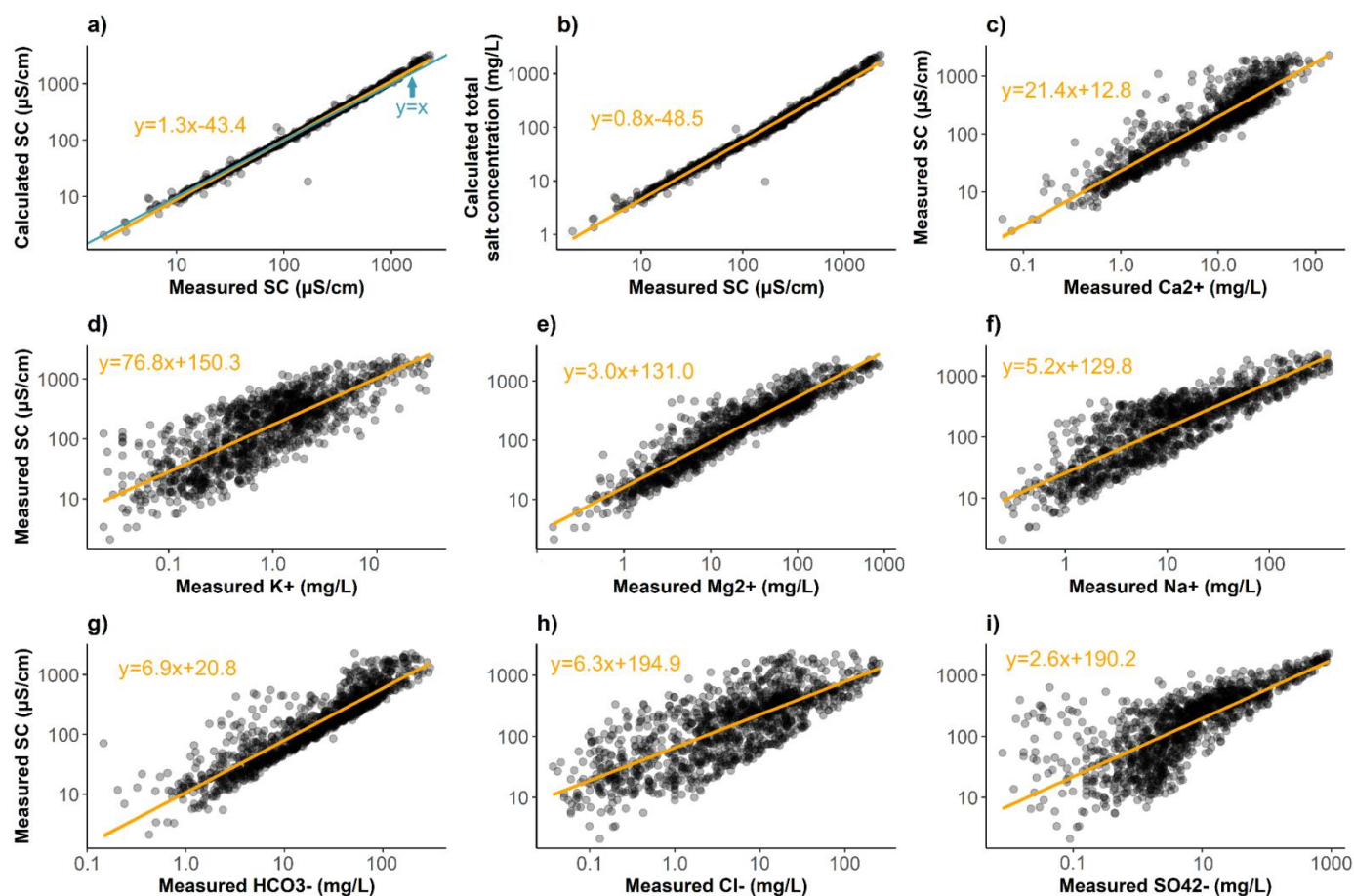


Figure 2. Relationships between measured SC and calculated SC (a), calculated total salt concentration (b), and the concentration of each ion (c-i) in 1,218 lakes across the CONUS. Each dot represents a lake, and the orange prediction lines were fitted with a linear model with the equation above each line. In plot (a), the blue line is $y=x$. The orange shadow area indicates one standard deviation.

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 S6 and 7). 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 S6a). 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 S6b).

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 (Figure 3a). There was a subsequent steep decline in SC for lakes located above 120 m; thereafter, SC gradually declined and eventually became stable as lake elevation increased. The percentage of clay in the soil was negatively associated with SC until 2% clay content, then SC remained low and started to increase when clay content exceeded 12% (Figure 3b). 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 (Figure 3c). Lake SC was negatively associated with annual runoff and became stable at a low SC level when runoff exceeded about 20 inches/year (Figure 3d). Finally, we observed that most high SC lakes had low watershed forest land cover (which also represents areas with high human disturbance), whereas SC was lowest in lakes with watersheds with moderate forest cover. Lake SC increased after forest cover reached about 80% (Figure 3e).

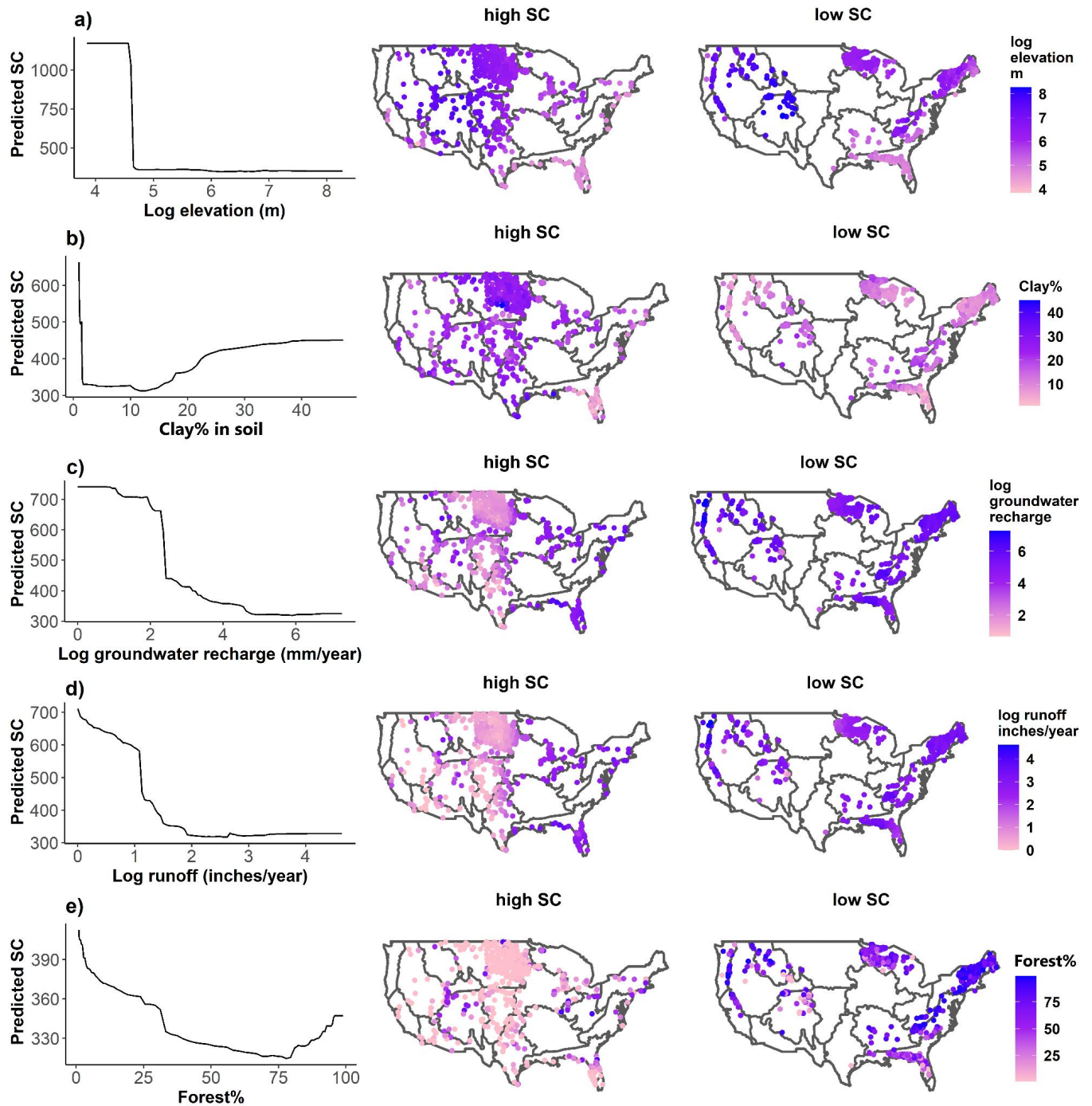


Figure 3. Partial dependence plots (left) showing the average marginal relationships between predicted SC ($\mu\text{S/cm}$) and elevation (a), % clay (b), groundwater recharge (c), runoff (d), and % forest (e). The maps in the middle and right columns show the values of the factor for low SC (SC lower 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.

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 (Figure 4; Table 1; Figure S8). About 46% of the lakes were dominated by Ca^{2+} and HCO_3^- , and 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). About 23% of lakes were co-dominated by the cations Ca^{2+} and Mg^{2+} , 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.

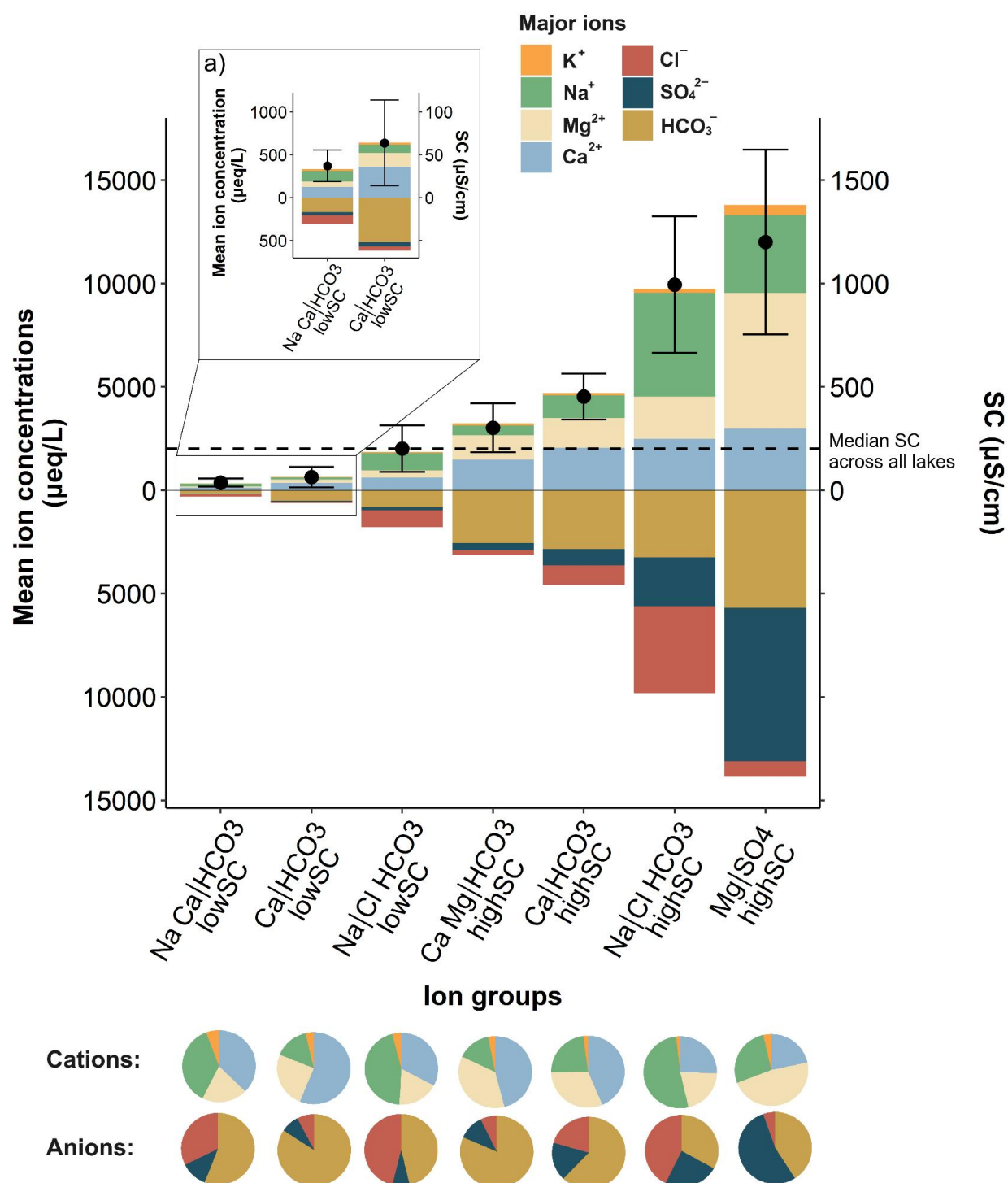


Figure 4. For each ion group (represented by the notation major cation(s) | major anion(s) | relative SC), the mean equivalent concentrations ($\mu\text{eq/L}$) of major ions, mean SC ($\mu\text{S/cm}$), and proportions of cations and anions. Stacked bars represent ion concentrations with cations above

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 $\mu\text{S}/\text{cm}$). 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 $\pm$ SD ($\mu\text{S}/\text{cm}$)
Na Ca HCO ₃ lowSC	Ca ²⁺ , Na ⁺	HCO ₃ ⁻	9%	37 $\pm$ 19
Ca HCO ₃ lowSC	Ca ²⁺	HCO ₃ ⁻	33%	64 $\pm$ 50
Na Cl HCO ₃ lowSC	Na ⁺	Cl ⁻ , HCO ₃ ⁻	11%	202 $\pm$ 112
Ca Mg HCO ₃ highSC	Ca ²⁺ , Mg ²⁺	HCO ₃ ⁻	23%	302 $\pm$ 118
Ca HCO ₃ highSC	Ca ²⁺	HCO ₃ ⁻	13%	453 $\pm$ 111
Na Cl HCO ₃ highSC	Na ⁺	Cl ⁻ , HCO ₃ ⁻	3%	995 $\pm$ 330
Mg SO ₄ highSC	Mg ²⁺	SO ₄ ²⁻	8%	1201 $\pm$ 448

The number of ion groups and the most common groups varied spatially, both within and among the 17 NEON ecoregions of CONUS (Figure 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 (Figure 5).

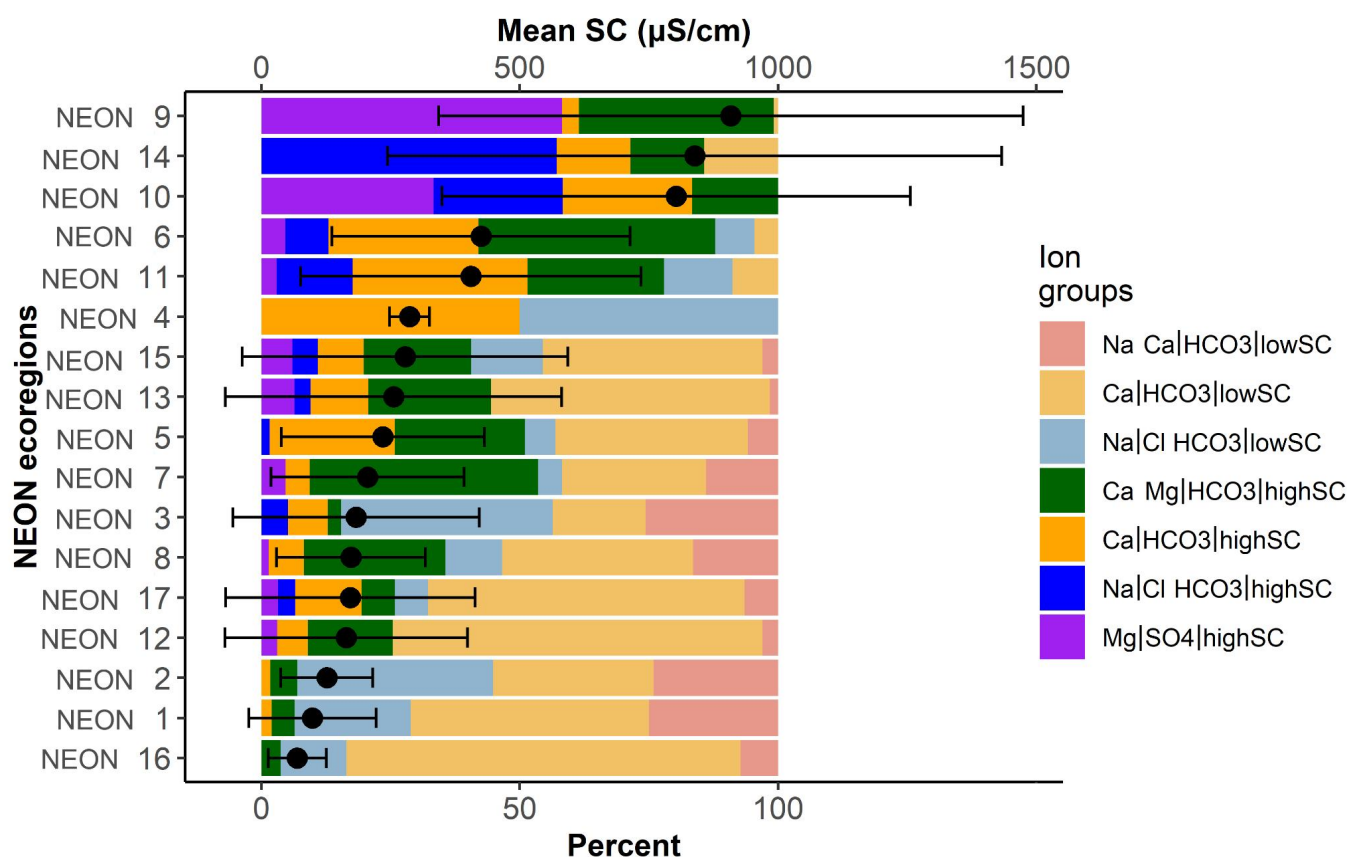


Figure 5. Percent of ion groups in each NEON ecoregion (bottom, x axis) where each color indicates an ion group shown in the legend. In each ion group name, the '|' symbol separates different characteristics of the group, specifically, (co)dominant cation(s), (co)dominant anion(s), and whether the group 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 Figure 1.

Multiple human and natural factors were associated with the spatial variations and variances in ion group assignments and lake ion composition (Figure 6; Figure S9; 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 some, but not all, 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.

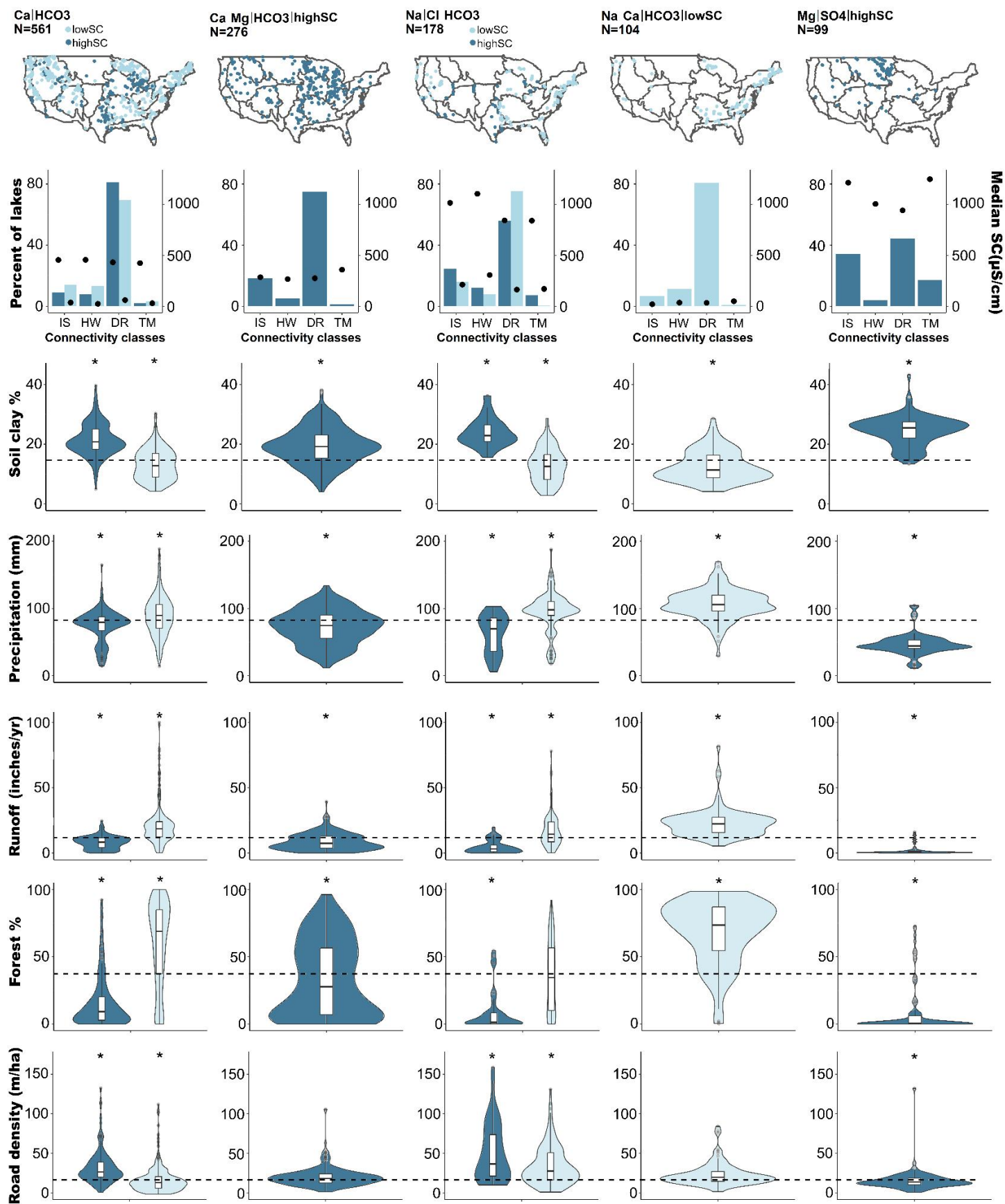


Figure 6. Maps (top), barplots (middle), and violin plots (bottom) of lakes in the seven ion groups based on the dominant cation(s) and anion(s) and SC. Maps show the location of lakes within each ion group, with the text listing the group names and the number of lakes. Barplots show the percentage of 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.

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 ($p < 0.001$). 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 (Figure 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 multiple natural and human factors collectively shape lake SC and ions.

Our study addresses these gaps by analyzing SC and major ions 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 found 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 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 S10) 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. Researchers can also help fill this ion data gap by developing predictive models for ion composition in lakes that can enhance our understanding of major ion levels and their potential impacts on lake ecosystems. By quantifying relationships between major ions and SC, and between major ion composition and key natural and human factors, we provide an important foundation for this work.

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. 2023), 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 Figure 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 S9&11), 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, such as Florida, may experience 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. 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 Mg²⁺ (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 (Figure 6). Moreover, high surface connectivity can either dilute (e.g., in Mg|SO₄|highSC) or enhance (e.g., in Ca|HCO₃|lowSC) (Figure 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 S9), 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 S11), 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.

4.4 Building on macroscale insights to predict and manage lake salinity

Our study used a data-driven approach to capture fine and broad-scale variation among thousands of lakes, providing a foundation for a better understanding of how global changes will affect thousands of heterogeneous systems at macroscales. We have identified three next steps following our results. The first is to quantify the interactive effects of natural and human factors

on lake SC and ion composition to improve predictions of future conditions. In fact, very few studies have looked at the combined effects of such factors on any water quality parameters (e.g., Kernan & Helliwell 2001; Nobre et al. 2020; Lin et al. 2021), and little to no information exists on SC and major ions, despite the likely complex interactive effects. A second is to use this knowledge to identify potential regions under threat from global change stressors. An example of such an approach has been recently conducted for US streams using *a priori* understanding of processes that control salinity in rivers to identify basins in the US to prioritize for monitoring (Conaway et al. 2024). Finally, a third step is to understand and quantify the influence of temporal dynamics on the natural and human factors affecting SC and major ions. Our results provide a foundation for pursuing these critical next steps in understanding, predicting, and managing lake SC and ion dynamics.

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.

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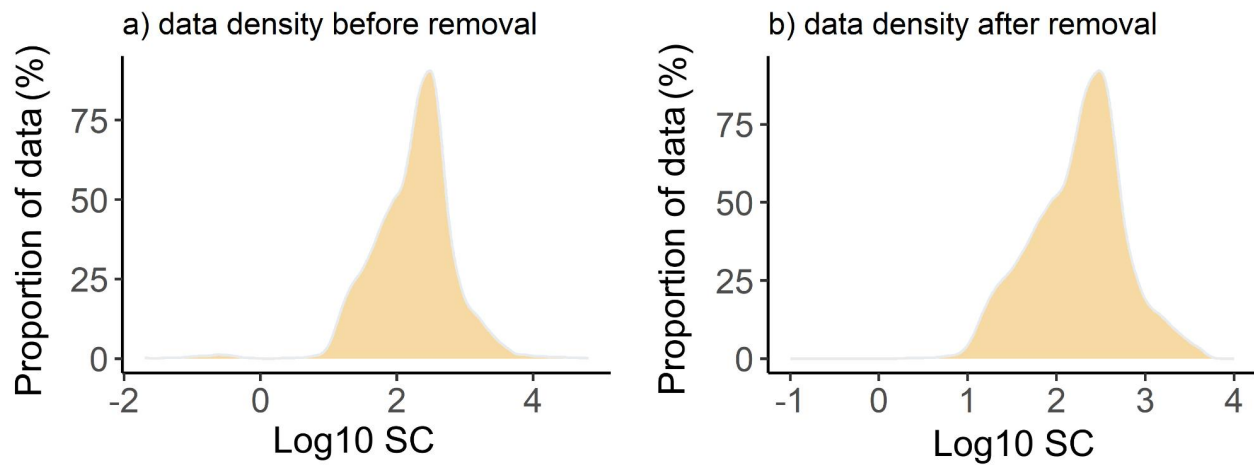


Figure S1. The distribution of log₁₀-transformed specific conductance (SC; $\mu\text{S}/\text{cm}$) data before and after the removal of lakes with extremely low and high SC values.

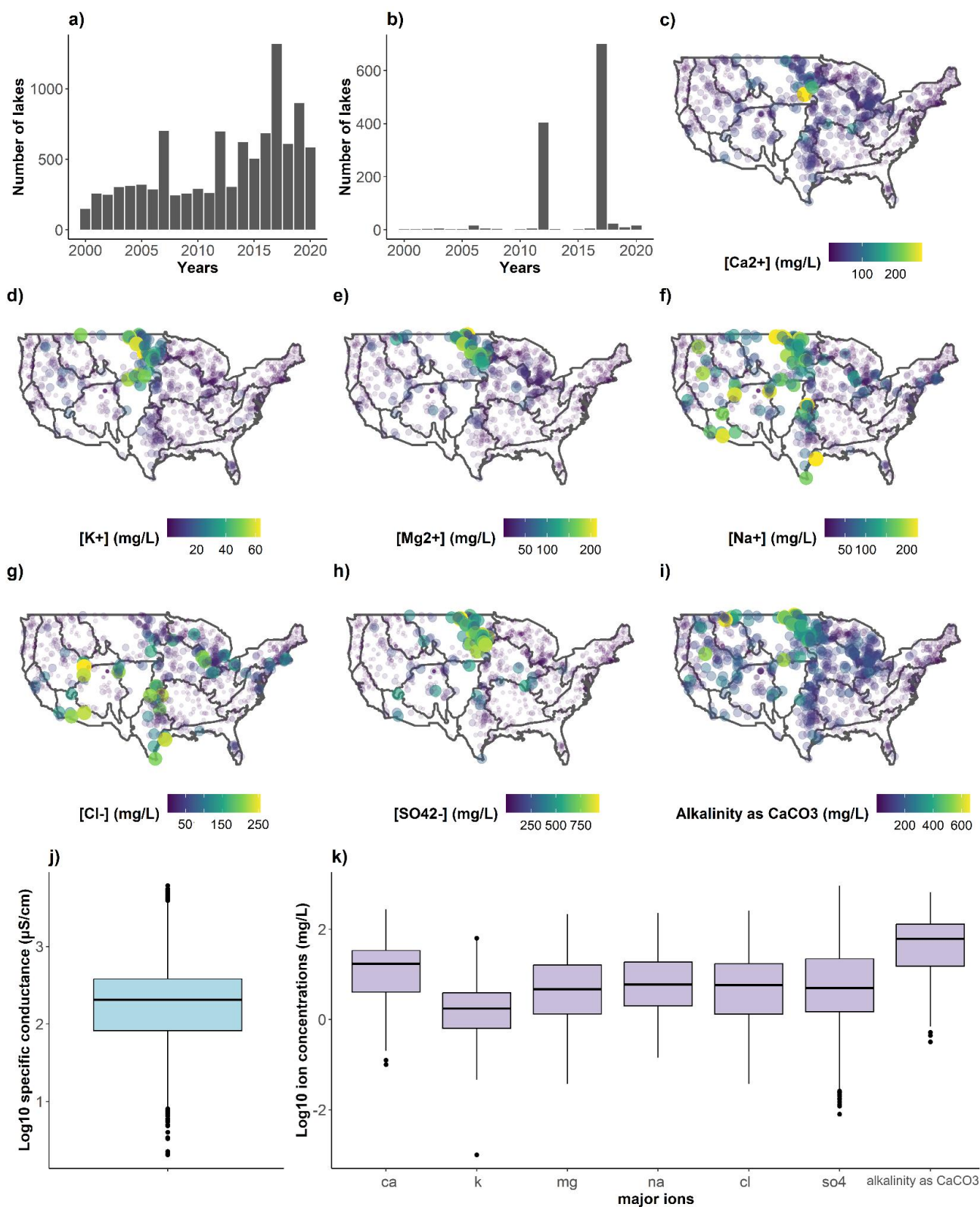


Figure S2. Summary of specific conductance (SC) and major ion data: a) number of lakes sampled in each latest SC sampling year; b) number of lakes sampled in each latest major ion sampling year; c) - i) maps showing major ion concentrations and alkalinity levels as CaCO_3 (mg/L) by NEON region; j) boxplot showing the distribution of $\log_{10}$ -transformed SC data; and k) boxplots showing the distribution of $\log_{10}$ -transformed major ion concentrations. See Figure 1 caption for NEON region names.

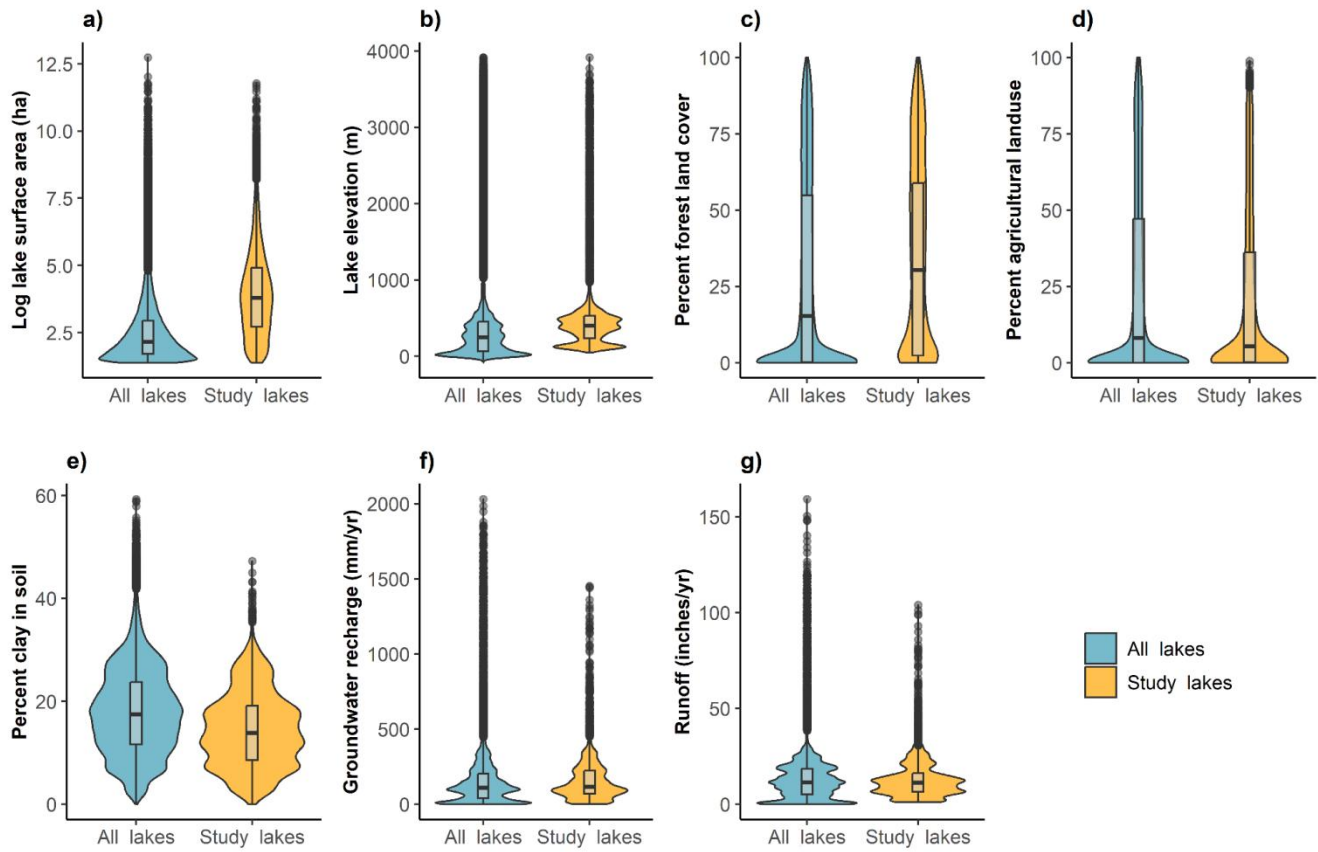
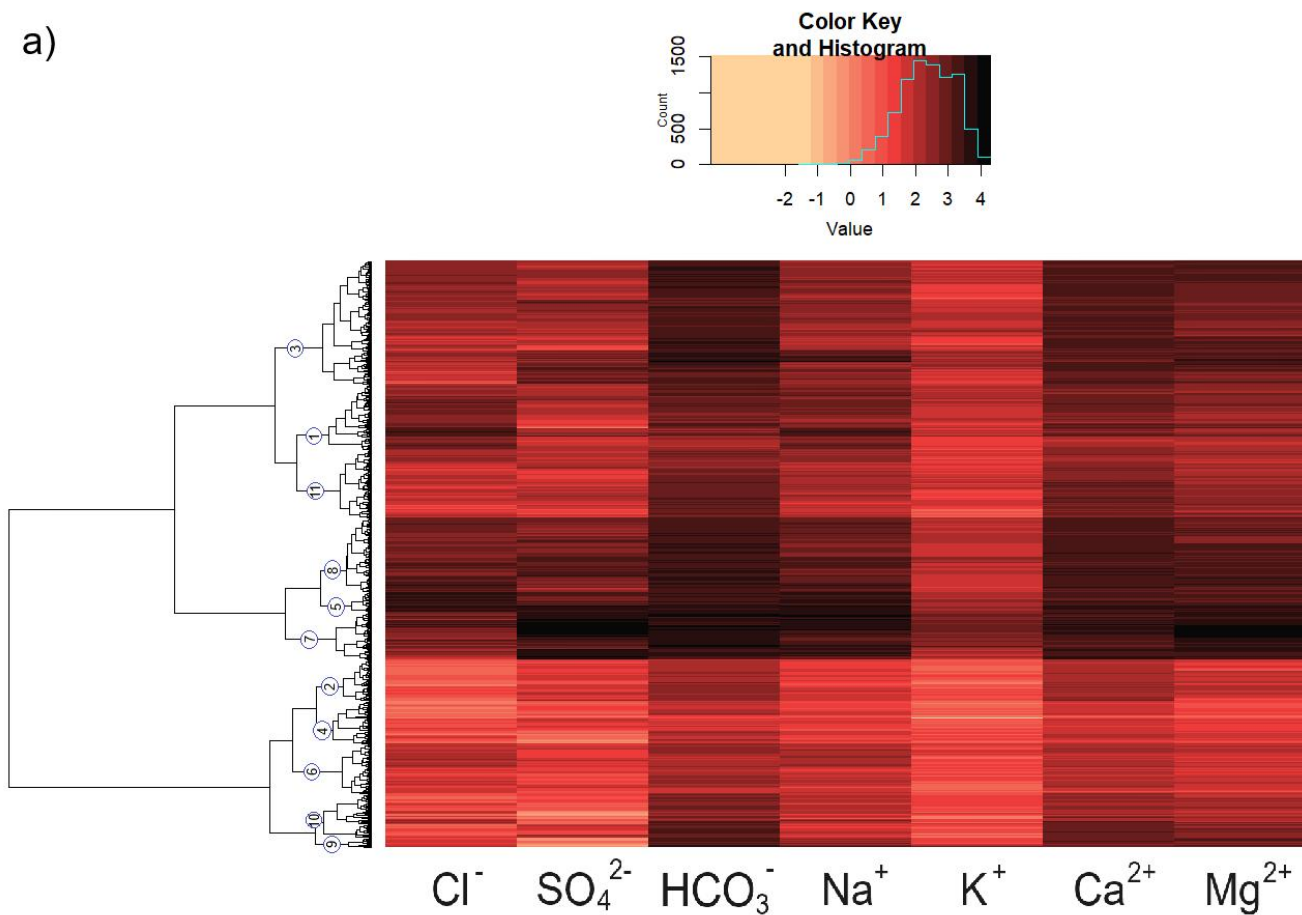
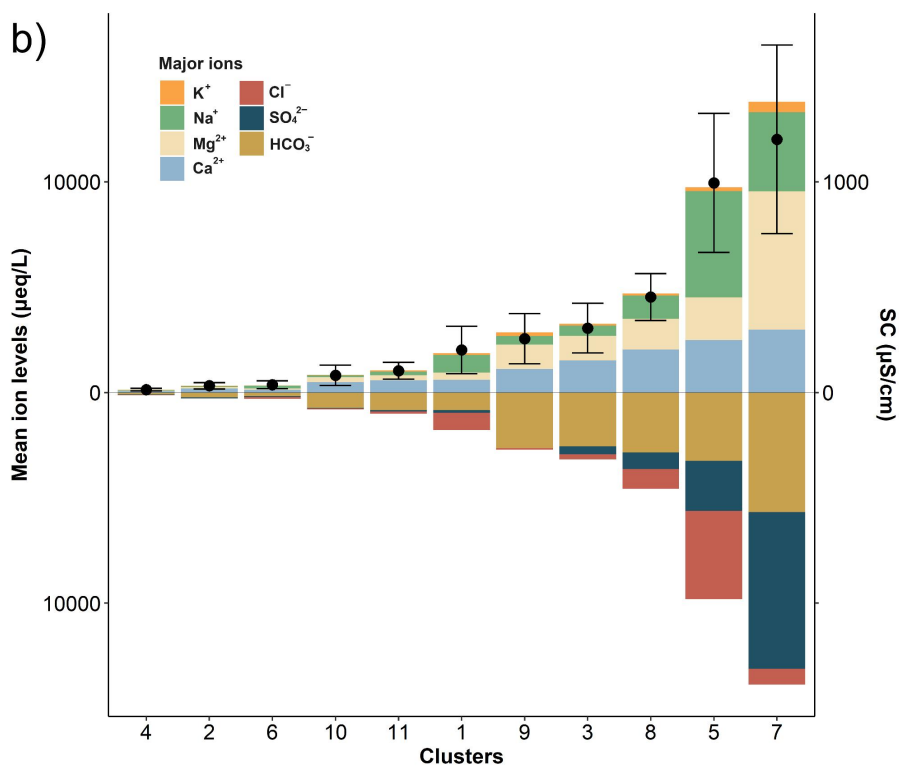


Figure S3. Comparison of all lakes > 4 ha in the U.S. (All lakes, blue) relative to the study lake population (Study lakes, orange). The violin plots show all data for the two groups of lakes, and the boxes within the violin plots are the interquartile ranges with the median. The ‘All lakes’ category was derived from the LAGOS lake population > 4 ha.

a)



b)



Cations:



Anions:



Figure S4. A heatmap showing $\log_{10}$ -transformed major ion equivalent concentrations grouped by 11 clusters (a) and a barplot showing the mean ion equivalent concentrations ($\mu\text{eq/L}$), mean SC ($\mu\text{S/cm}$), and proportions of cations and anions of each cluster (b). In plot a), the dendrogram (output of the hierarchical clustering using Ward's method) is on the left edge of the heatmap, and each row corresponds to a lake. The histogram at the top shows the color key and distribution of data. In plot b), 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. In later analyses, cluster 6 was renamed as Na Ca|HCO₃|lowSC, clusters 4, 2, 10, and 11 were combined into Ca|HCO₃|lowSC, cluster 1 was renamed as Na|Cl HCO₃|lowSC, clusters 3 and 9 were combined into Ca Mg|HCO₃|highSC, cluster 8 was renamed as Ca|HCO₃|highSC, cluster 5 was renamed as Na|Cl HCO₃|highSC, and cluster 7 was renamed as Mg|SO₄|highSC.

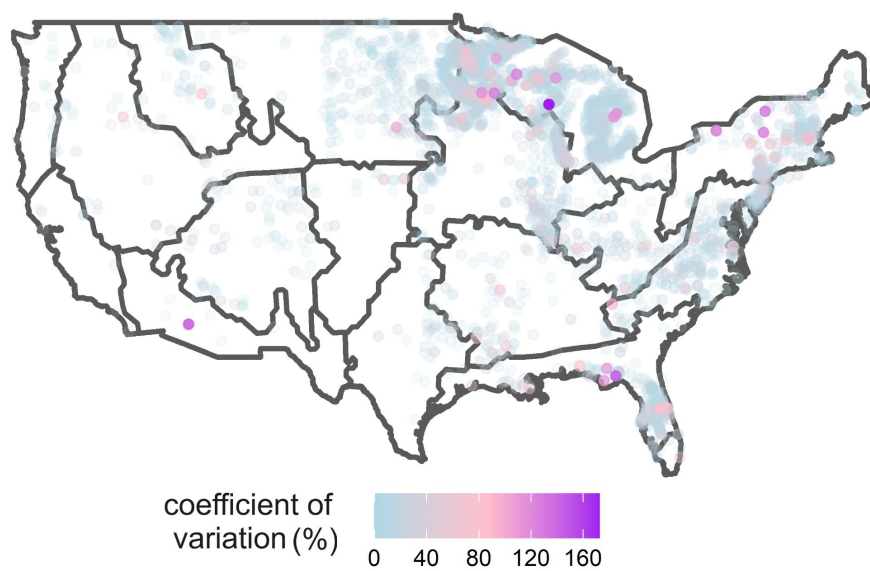


Figure S5. Map showing the intra-year SC coefficient of variation (N=4,581) of each lake by NEON region. Each dot represents a lake. See the Figure 1 caption for NEON region names.

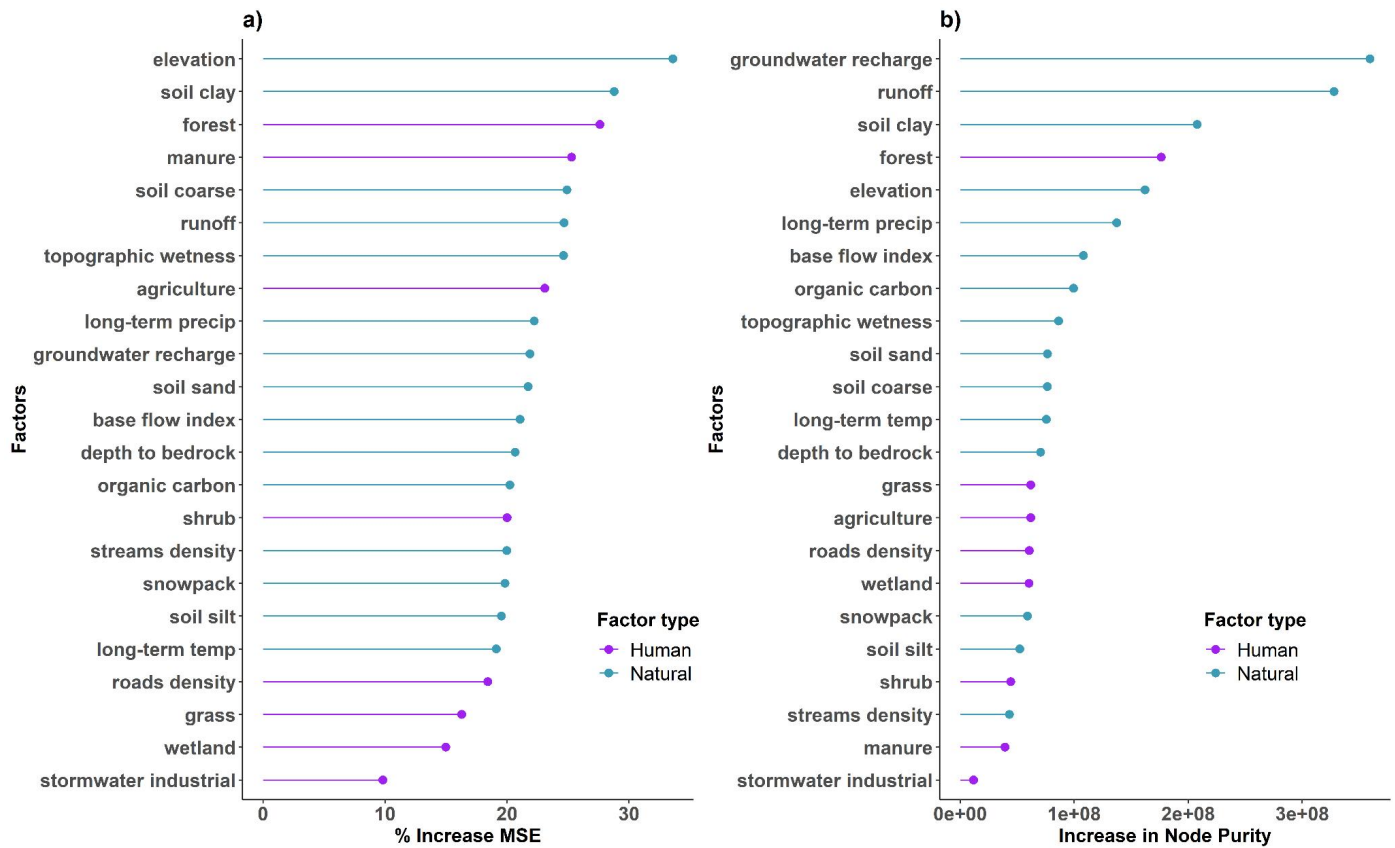
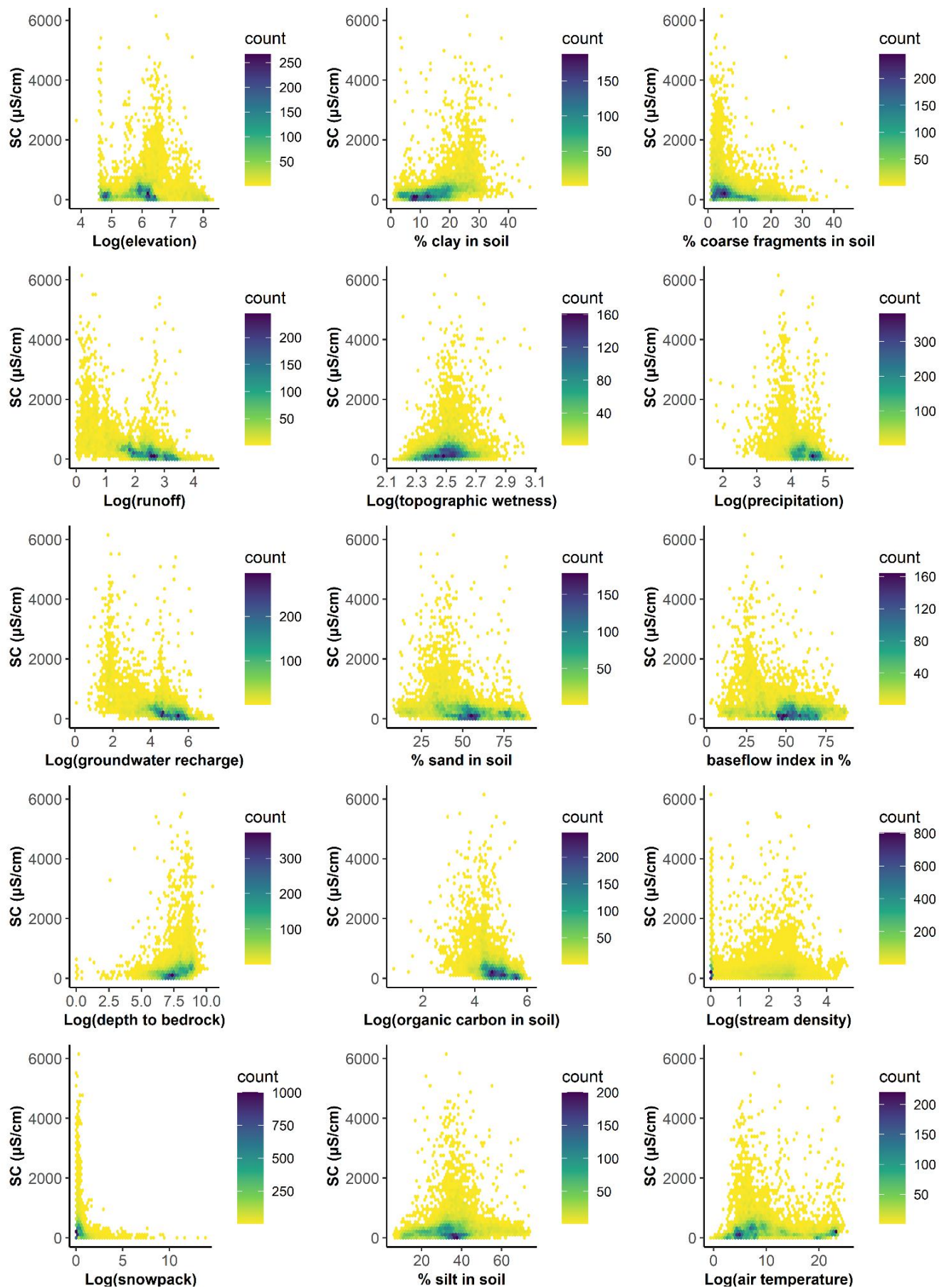


Figure S6. Results from random forest regression model (N=9,784) of natural and human factors and their relationships to lake SC: a) importance scores of important natural and human factors based on the percentage increase in mean squared error (MSE); b) importance scores of important natural and human factors based on the increase in node purity (from Gini Index).



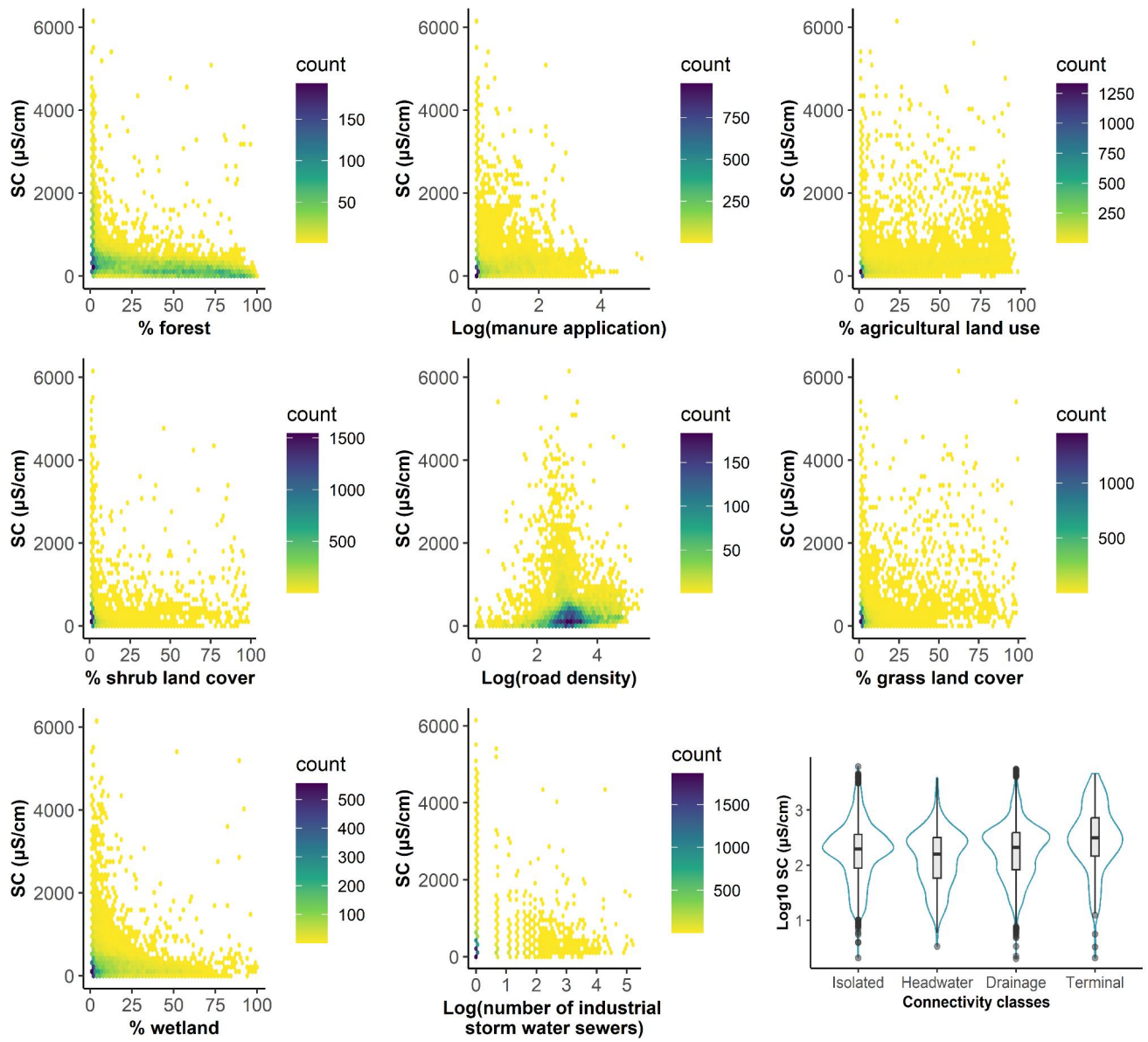


Figure S7. 2-D density plots showing the relationships between lake SC and all the variables included in the random forest and surface water connectivity. The color indicates the number of lakes.

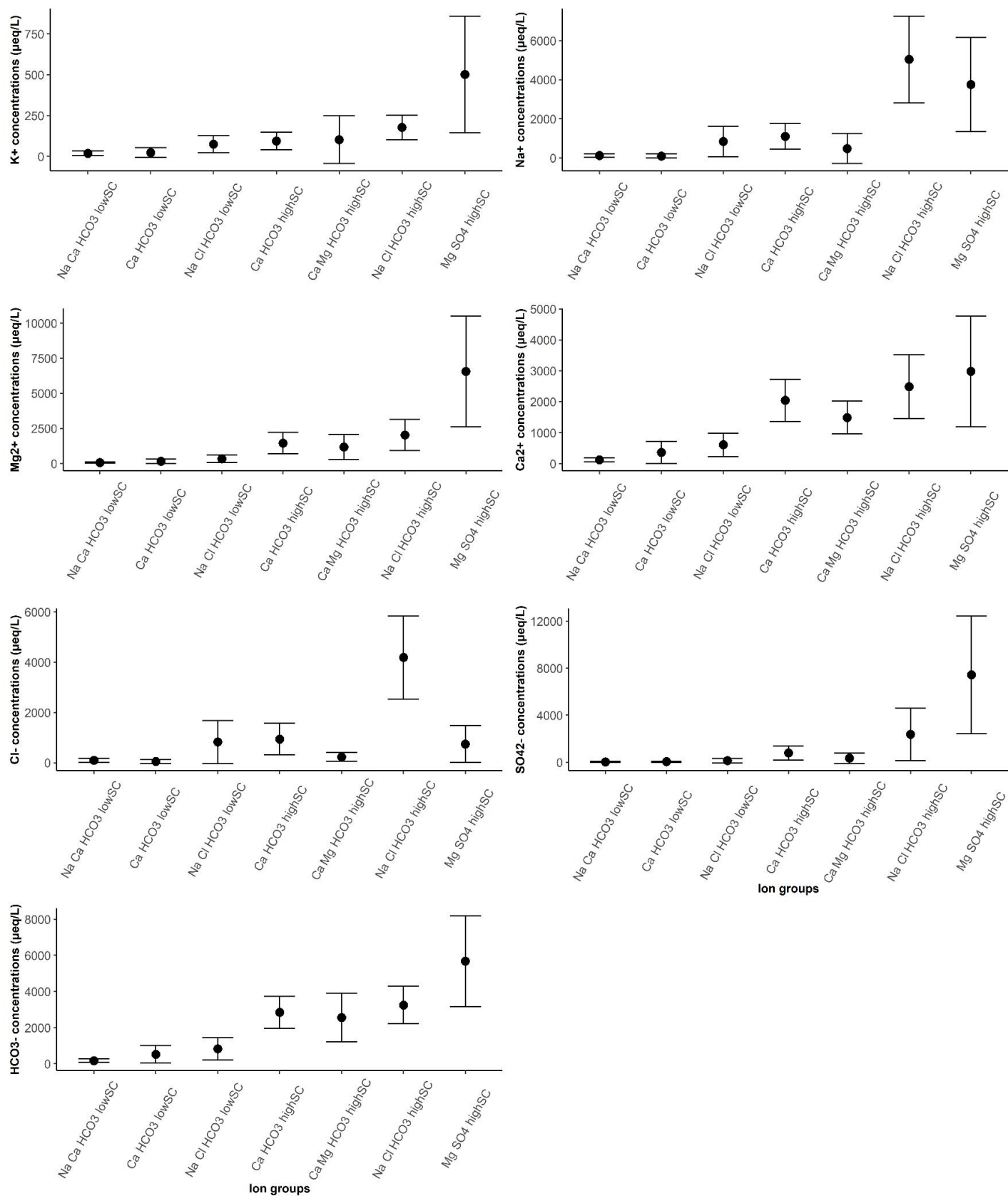


Figure S8. The concentration (in $\mu\text{eq/L}$) of each major ion by ion groups.

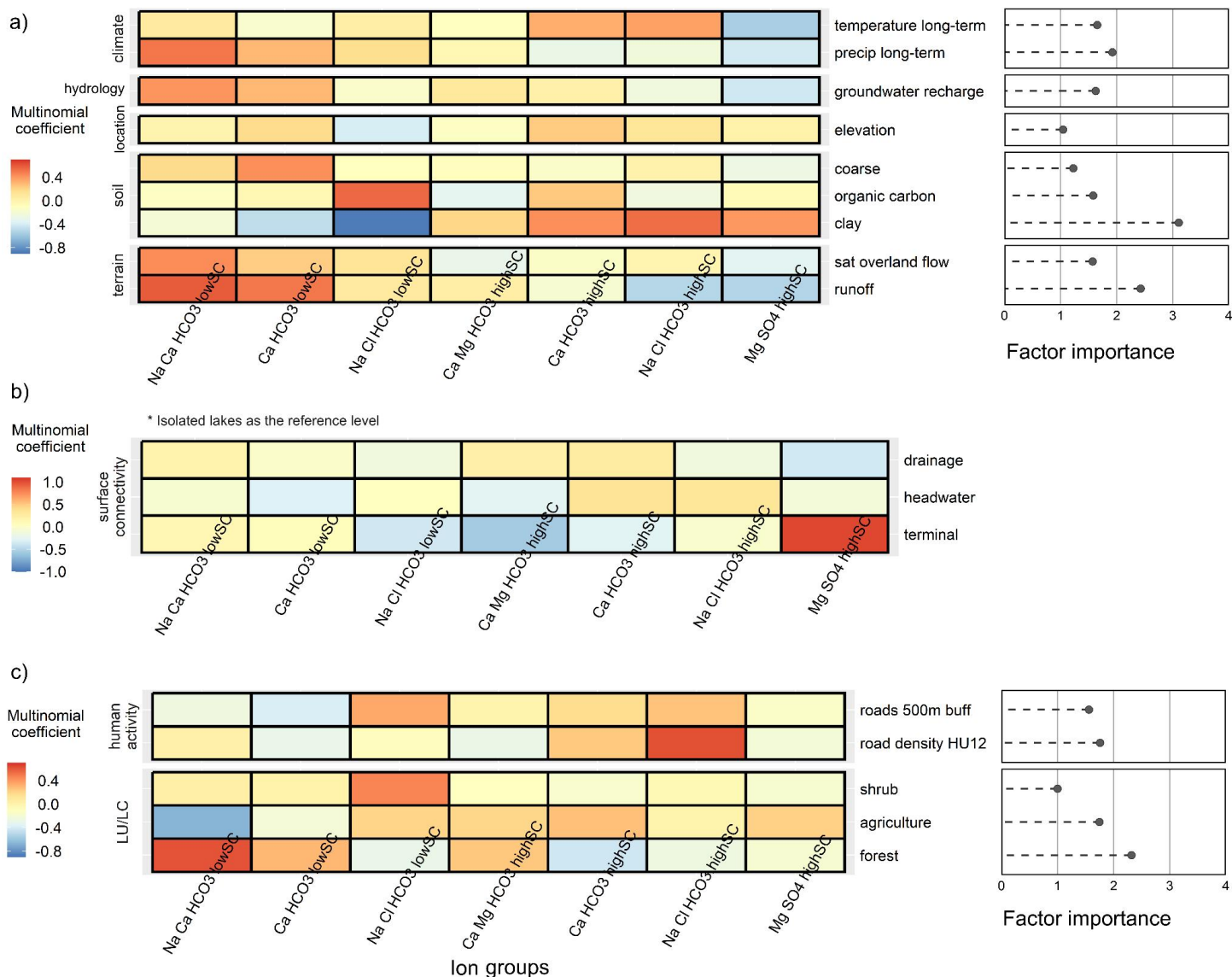


Figure S9. Heatmaps showing multinomial coefficients generated from a single GLMNET model predicting ion group assignment based on each natural (a,b) and human factor (c), with the factor importance plotted on the right (lollipop plots) that was calculated as the absolute sum of the ion group-specific coefficients. Numeric factors in plots a) and c) were centered and scaled. The text on the left of the heatmaps indicates factor categories, and the text on the right indicates factor names. Surface connectivity (plot b) was input as a categorical natural variable in the model; we plotted this factor separately to avoid confusion and did not calculate its importance score. Only factors with importance values ≥ 1 were plotted (10 of 30 inputted natural factors, surface connectivity was counted as one factor, and 5 of 12 inputted human factors). A full table of coefficients can be found in Table S4.

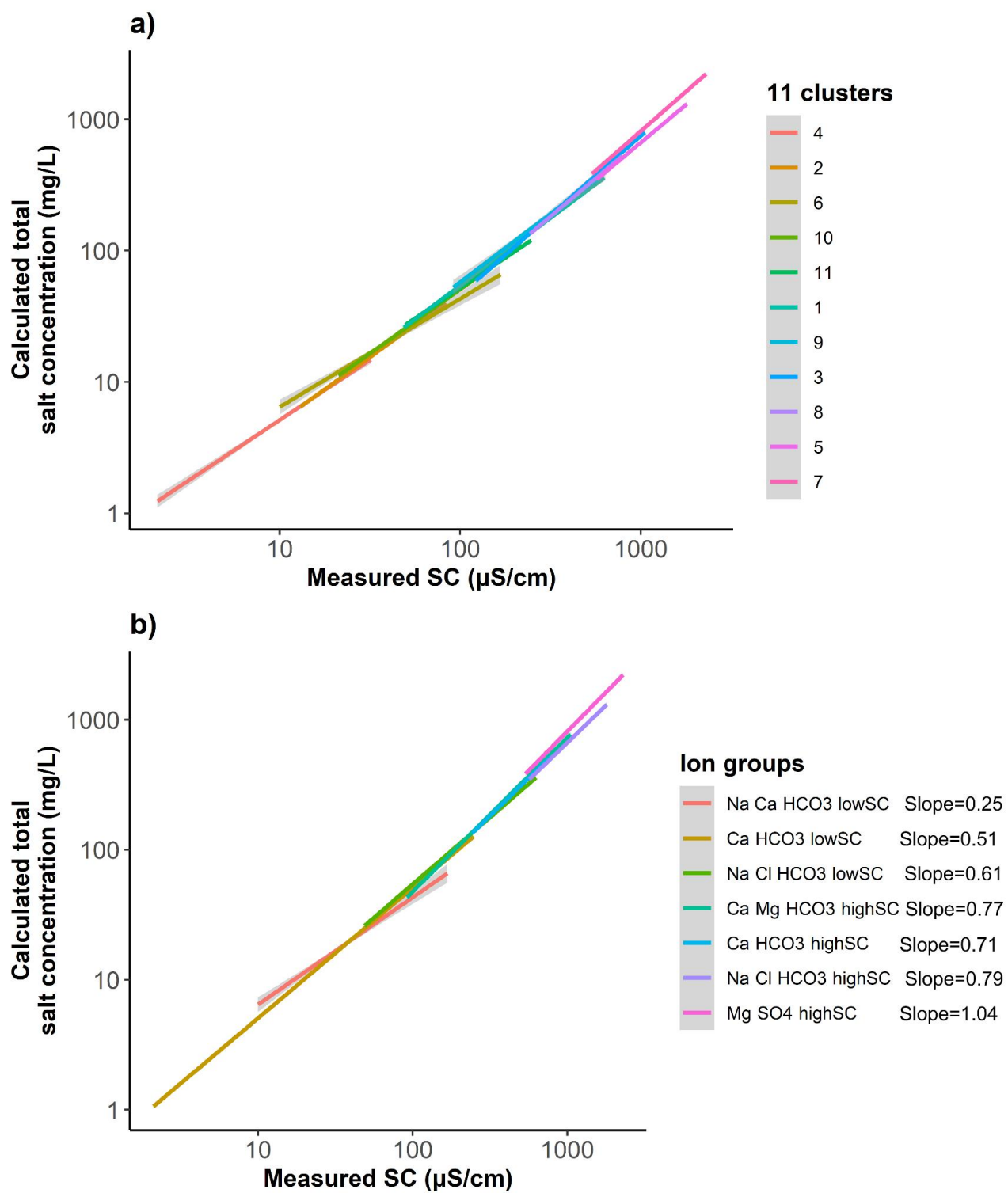
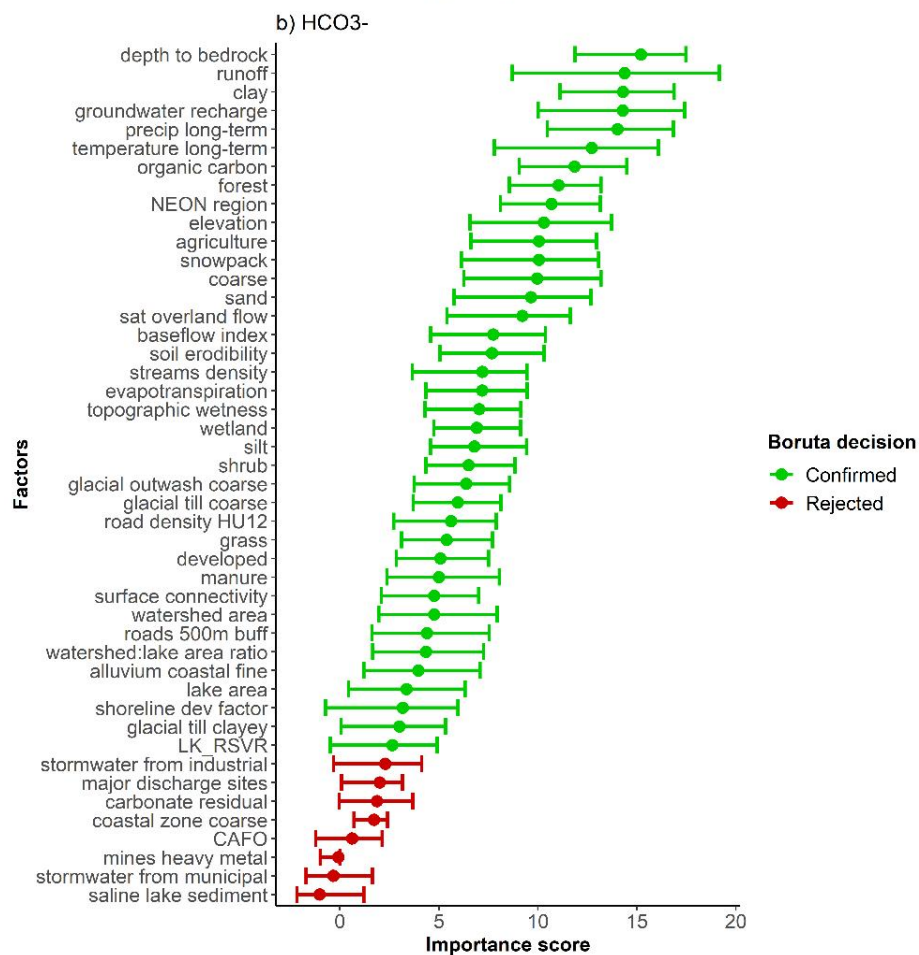
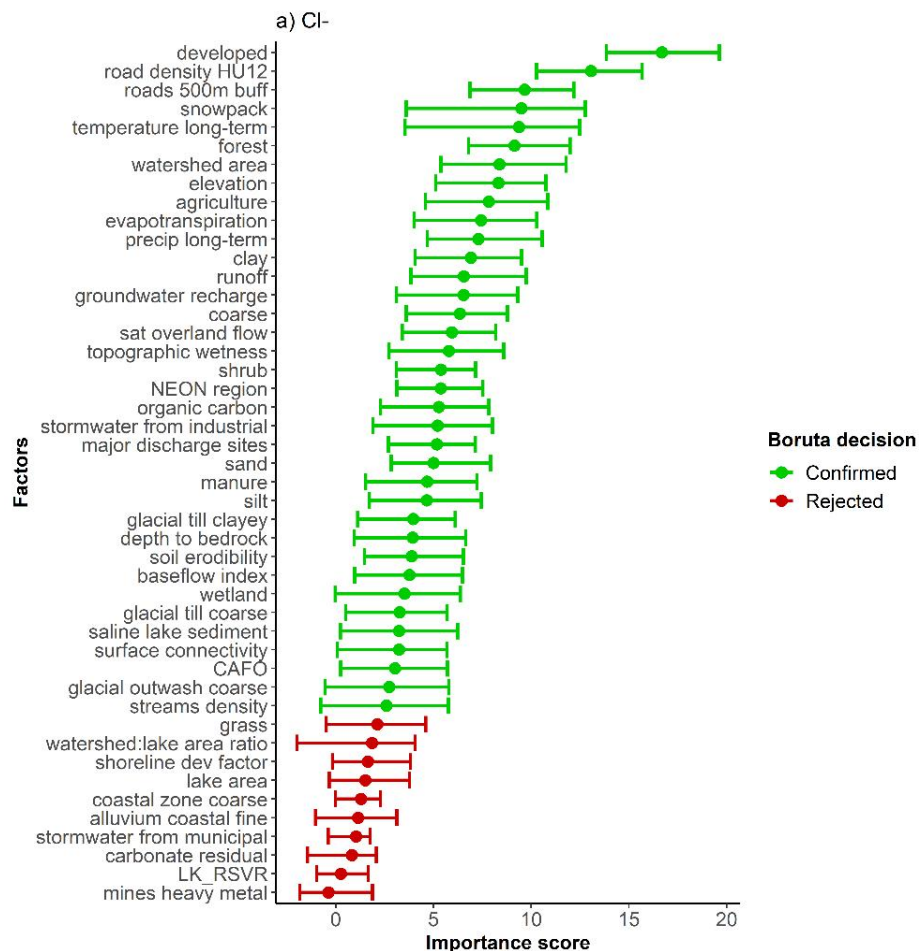


Figure S10. Relationships between measured SC and calculated total ion concentration by clusters (a; 11 clusters; ordered based on SC, from the lowest to the highest) and ion groups (b; 7 groups based on dominant cations and anions). The prediction lines were fitted with linear models.



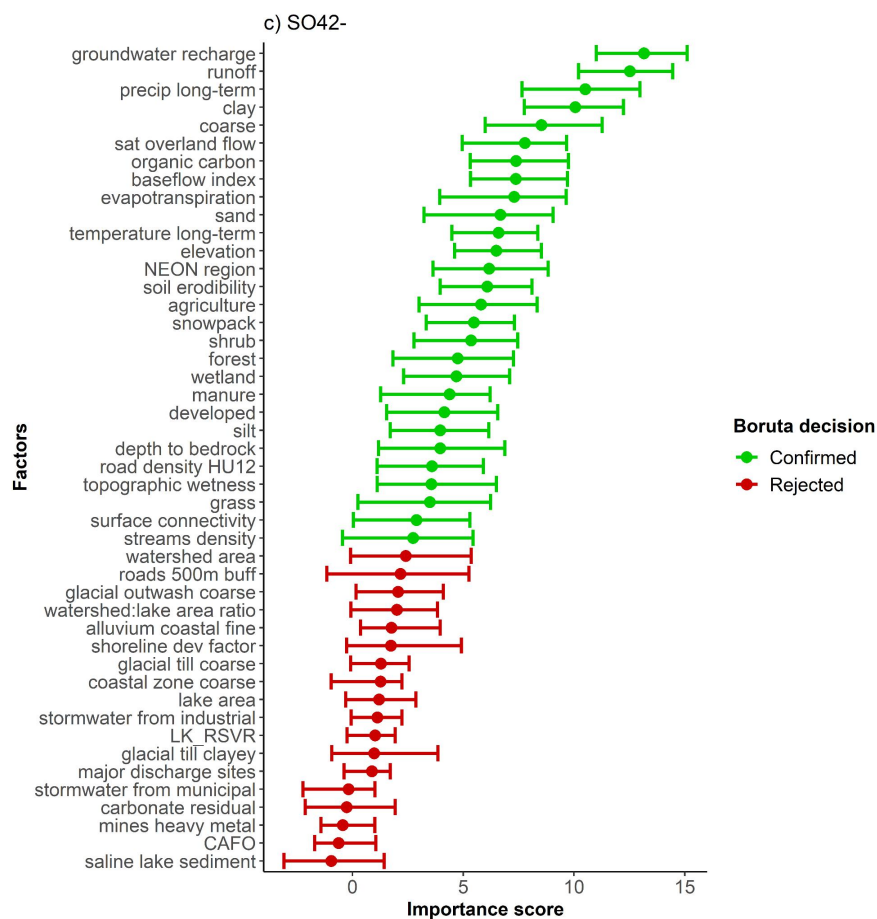


Figure S11. Importance scores from Boruta feature selection for the three anions: Cl⁻ (a), HCO₃⁻ (b), and SO₄²⁻ (c). Green dots and bars indicate that the factors were identified as ‘important’ by Boruta and red dots and bars indicate that Boruta rejected the factors. Dots are the mean Boruta importance values and bars are the minimum and maximum Boruta importance values. Boruta feature selection identifies relevant predictors by comparing the importance of the test feature with the importance of permuted copies of the data known as shadow features (Kursa et al. 2010).

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Supplementary Tables

Paper title: Interactions Between Human Activities and Natural Processes Shape Specific Conductance and Ion Composition of United States Lakes

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Table S1. Table of natural and human factors with variable sources, spatial scale, group, explanation, and data transformation information.

Factor name in the figure	Factor original name	Spatial scale of measurement	Group	Natural Human	Data source	Explanation	Transformation in RF (GLMNET: numeric data were natural log transformed, but percent data remain unchanged)
connectivity	lake_connectivity_class	lake	surface connectivity	N	LAGOS-US LOCUS	Hydrologic connectivity class of the focal lake	NA
elevation	lake_elevation_m	lake	location	N	LAGOS-US LOCUS	Mean elevation in the zone	natural log
reservoir	lake_rsvr_class	lake	lake and watershed	N	LAGOS-US RESERVOIR	The classification of a lake into either natural lake or reservoir	NA
shoreline dev factor	lake_shorelinedevfactor	lake	lake and watershed	N	LAGOS-US LOCUS	A measure of the deviation of lake shape from 1, which is a perfect circle, calculated from the lake water area and perimeter	natural log
lake area	lake_waterarea_ha	lake	lake and watershed	N	LAGOS-US LOCUS	The water area of the lake contained within the outer shoreline	natural log
manure	ManureMean	HU12	human activity	H	EnviroAtlas	Manure application (kg N/ha/yr)	natural log
evapotranspiration	NA, calculated	HU12	climate	N	Blodgett 2023	Long-term average evapotranspiration data by HU12 region	NA
snowpack	NA, calculated	HU12	climate	N	Blodgett 2024	Long-term average snowpack water equivalent storage data by HU12 region	NA
NEON region	neon_zoneid	NEON region	location	N	LAGOS-US LOCUS	National Ecological Observatory Network (NEON) region id	NA
precip long-term	NA, calculated	HU12	climate	N	LAGOS-US GEO	Long-term average precipitation data (5 years before sampling year)	NA
roads 500m buff	road.500buff	500m buffer	human	H	LAGOS-US	Road density in 500 m buffer around	natural log

			activity		GEO	the shoreline of a LAGOS-US lake polygon	
temperature long-term	NA, calculated	HU12	climate	N	LAGOS-US GEO	Long-term average air temperature data (5 years before sampling year)	NA
baseflow index	value.baseflowindex_pct	HU12	hydrology	N	LAGOS-US GEO	Mean within the zone of the percentage of streamflow that can be attributed to groundwater discharge into streams, calculated as baseflow divided by total flow using data from 1951-1980	logit, generalized (-0.01 to 1.01)
groundwater recharge	value.groundwaterrecharge_mmperyr	HU12	hydrology	N	LAGOS-US GEO	Mean within the zone of annual groundwater recharge calculated as baseflow multiplied by mean annual runoff using data from 1951-1980	natural log
alluvium coastal fine	value.lith_alluviumcoastalfine_pct	HU12	lithology	N	LAGOS-US GEO	Percent of zone with lithology classified as alluvium and fine textured coastal zone sediment	logit, generalized (-0.01 to 1.01)
carbonate residual	value.lith_carbonateresid_pct	HU12	lithology	N	LAGOS-US GEO	Percent of zone with lithology classified as carbonate residual material	logit, generalized (-0.01 to 1.01)
coastal zone coarse	value.lith_coastalzonecoarse_pct	HU12	lithology	N	LAGOS-US GEO	Percent of zone with lithology classified as coastal zone sediment, coarse textured	logit, generalized (-0.01 to 1.01)
glacial outwash coarse	value.lith_glacialoutwashcoarse_pct	HU12	lithology	N	LAGOS-US GEO	Percent of zone with lithology classified as glacial outwash and glacial lake sediment, coarse textured	logit, generalized (-0.01 to 1.01)
glacial till clayey	value.lith_glacialtillclayey_pct	HU12	lithology	N	LAGOS-US GEO	Percent of zone with lithology classified as glacial till, clayey	logit, generalized (-0.01 to 1.01)
glacial till coarse	value.lith_glacialtillcoarse_pct	HU12	lithology	N	LAGOS-US GEO	Percent of zone with lithology classified as glacial till, coarse textured	logit, generalized (-0.01 to 1.01)
saline lake sediment	value.lith_salinelake_pct	HU12	lithology	N	LAGOS-US GEO	Percent of zone with lithology classified as saline lake sediment	logit, generalized (-0.01 to 1.01)
mines heavy metal	value.mines_heavy_metal_n	HU12	human activity	H	LAGOS-US GEO	Count of heavy metal mines active in 2003 within the zone	natural log
CAFO	value.npdес_саfo_n	HU12	human activity	H	LAGOS-US GEO	Count of concentrated animal feed operations within the zone	natural log
major discharge sites	value.npdес_majordischarge_n	HU12	human activity	H	LAGOS-US GEO	Count of facilities with major discharges within the zone	natural log

stormwater from industrial	value.npdes_stormwaterindustrial_n	HU12	human activity	H	LAGOS-US GEO	Count of industrial storm water sewers within the zone	natural log
stormwater from municipal	value.npdes_stormwatermunicipal_n	HU12	human activity	H	LAGOS-US GEO	Count of Phase I MS4: Municipal separate storm sewer systems within the zone	natural log
road density HU12	value.roads_mperha	HU12	human activity	H	LAGOS-US GEO	Road density within each HU12 region	natural log
runoff	value.runoff_inperyr	HU12	terrain	N	LAGOS-US GEO	Mean within the zone of annual runoff; data from 1951 to 1980	natural log
sat overland flow	value.satoverlandflow_pct	HU12	terrain	N	LAGOS-US GEO	Mean within the zone of the average percentage of saturation overland flow in total streamflow using data from 1951-1980	logit, generalized (-0.01 to 1.01)
clay	value.soil_clay_pct	HU12	soil	N	LAGOS-US GEO	Average percentage mass fraction of clay, 0 to 2 micrometers, in the 0 to 5 cm depth soil layer within the zone	logit, generalized (-0.01 to 1.01)
coarse	value.soil_coarse_pct	HU12	soil	N	LAGOS-US GEO	Average percentage by volume of coarse fragments in the 0 to 5 cm soil depth layer within the zone	logit, generalized (-0.01 to 1.01)
depth to bedrock	value.soil_depthtobedrock_cm	HU12	soil	N	LAGOS-US GEO	Average absolute depth to bedrock within the zone	natural log
k factor	value.soil_kffact	HU12	soil	N	LAGOS-US GEO	Average soil erodibility factor, not adjusted for the effect of rock fragments, within the zone	natural log
organic carbon	value.soil_orgcarbon_gperkg	HU12	soil	N	LAGOS-US GEO	Average organic carbon content, fine earth fraction, in the 0 to 5 cm soil layer within the zone	natural log
sand	value.soil_sand_pct	HU12	soil	N	LAGOS-US GEO	Average percentage mass fraction of sand, 50 to 200 micrometers, in the 0 to 5 cm depth soil layer within the zone	logit, generalized (-0.01 to 1.01)
silt	value.soil_silt_pct	HU12	soil	N	LAGOS-US GEO	Average percentage mass fraction of silt, 2 to 50 micrometers, in the 0 to 5 cm depth soil layer within the zone	logit, generalized (-0.01 to 1.01)
streams density	value.streams_all_mperha	HU12	hydrology	N	LAGOS-US GEO	Density of all streams within the zone, calculated as the sum of the stream length divided by the zone area	natural log
topographic wetness	value.topographicwetness	HU12	terrain	N	LAGOS-US	Mean topographic wetness index of	natural log

	etness				GEO	cells within the zone	
watershed area	ws_area_ha	watershed	lake and watershed	N	LAGOS-US LOCUS	Area of zone polygon	natural log
watershed:lake area ratio	ws_lake_arearatio	lake	lake and watershed	N	LAGOS-US LOCUS	Ratio between watershed area and lake water area	natural log
agriculture	NA, combined nlcd_cultcrop82_pct with nlcd_past81_pct	watershed	LU/LC	H	LAGOS-US GEO	Percent of zone classified as cultivated crops or pasture and hay using 2006 data	logit, generalized (-0.01 to 1.01)
grass	nlcd_grass71_pct	watershed	LU/LC	H	LAGOS-US GEO	Percent of zone classified as grassland or herbaceous using 2006 data	logit, generalized (-0.01 to 1.01)
shrub	nlcd_shrub52_pct	watershed	LU/LC	H	LAGOS-US GEO	Percent of zone classified as shrub and scrub using 2006 data	logit, generalized (-0.01 to 1.01)
developed	NA, combined nlcd_devopen21_pct, nlcd_devlow22_pct, nlcd_devmed23_pct, and nlcd_devhi24_pct	watershed	LU/LC	H	LAGOS-US GEO	Percent of zone classified as developed, including open space and low, medium, and high intensity, using 2006 data	logit, generalized (-0.01 to 1.01)
forest	NA, combined nlcd_forcon42_pct, nlcd_fordec41_pct, and nlcd_formix43_pct	watershed	LU/LC	H	LAGOS-US GEO	Percent of zone classified as evergreen forest, deciduous forest, or mixed forest using 2006 data	logit, generalized (-0.01 to 1.01)
wetland	NA, combined nlcd_wetemerg95_pct with nlcd_wetwood90_pct	watershed	LU/LC	H	LAGOS-US GEO	Percent of zone classified as emergent herbaceous or woody wetlands using 2006 data	logit, generalized (-0.01 to 1.01)

Table S2. The conversion factors used to convert major ion concentrations from mg/L to ueq/L and to calculate SC.

Ions	Conversion factor (from mg/L to ueq/L)	Conversion factor for calculating SC using ion equivalent concentrations
Ca	49.9	52.0
Mg	82.29	46.6
Na	43.5	48.9
K	25.58	72.0
Cl	28.21	75.9
SO ₄	20.82	73.9
Alkalinity (as CaCO ₃)	19.98	(as HCO ₃ ⁻) 43

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Table S3. Importance scores and decisions from Boruta feature selection on all natural and human factors.

Natural factors					
variables	meanImp	medianImp	minImp	maxImp	decision
elevation	17.0	17.2	9.7	21.5	Confirmed
runoff	16.1	16.2	11.2	20.1	Confirmed
coarse	15.3	15.4	8.4	20.1	Confirmed
groundwater recharge	14.9	14.9	8.8	19.0	Confirmed
depth to bedrock	14.4	14.5	8.3	18.8	Confirmed
topographic wetness	14.3	14.7	8.1	18.1	Confirmed
clay	14.0	14.0	8.8	19.5	Confirmed
precip long-term	13.0	13.1	7.8	16.5	Confirmed
organic carbon	12.8	12.7	9.1	16.7	Confirmed

baseflow index	12.4	12.5	7.5	15.4	Confirmed
temperature long-term	12.4	12.5	4.0	19.1	Confirmed
sand	12.4	12.8	6.5	17.1	Confirmed
streams density	11.0	11.1	6.2	13.9	Confirmed
silt	10.7	10.9	3.5	14.6	Confirmed
snowpack	10.5	10.5	3.1	17.3	Confirmed
NEON region	10.4	10.6	3.6	14.5	Confirmed
watershed area	10.3	10.4	2.5	14.0	Confirmed
evapotranspiration	9.9	9.9	6.8	12.9	Confirmed
watershed:lake area ratio	8.8	9.3	1.7	12.4	Confirmed
soil erodibility	8.8	8.9	2.9	14.1	Confirmed
sat overland flow	8.7	8.7	5.8	11.5	Confirmed

surface connectivity	7.9	8.0	4.3	10.6	Confirmed
shoreline dev factor	7.8	7.8	4.2	11.4	Confirmed
glacial outwash coarse	7.1	7.2	2.3	10.6	Confirmed
glacial till coarse	6.7	6.8	2.5	9.2	Confirmed
glacial till clayey	6.5	6.6	3.3	8.7	Confirmed
NL_RSVR	4.9	5.0	2.2	7.1	Confirmed
coastal zone coarse	4.3	4.3	1.3	6.9	Confirmed
alluvium coastal fine	4.2	4.1	1.8	7.1	Confirmed
lake area	2.8	2.7	-0.8	6.5	Tentative
carbonate residual	2.7	2.7	-0.4	5.0	Tentative
saline lake sediment	1.0	0.8	-0.6	2.8	Rejected

Human factors					
forest	47.9	48.5	42.4	51.1	Confirmed
manure	32.0	31.7	28.0	34.3	Confirmed
agriculture	30.9	31.5	27.0	32.8	Confirmed
grass	27.9	28.0	23.8	30.6	Confirmed
shrub	22.6	22.4	20.3	25.6	Confirmed
road density HU12	20.8	21.2	16.6	23.3	Confirmed
wetland	18.6	18.9	15.5	19.6	Confirmed
stormwater from industrial	13.7	13.4	12.5	15.6	Confirmed
developed	12.7	12.8	11.4	14.5	Confirmed
roads 500m buff	11.9	12.0	9.6	14.1	Confirmed

major discharge sites	6.3	6.0	4.3	9.6	Confirmed
stormwater from municipal	6.3	6.7	4.0	7.5	Confirmed
CAFO	6.1	5.9	5.1	7.4	Confirmed
metal_mines	0.1	0.1	-1.6	1.4	Rejected

Table S4. Multinomial coefficients from a GLMNET model predicting ion group assignment. The group indicates natural and human factor categories. The N_H indicates whether the factor is a natural (N) or human (H) factor.

Factors	Group	N_H	Ca HCO ₃ highSC	Ca HCO ₃ lowSC	Ca Mg HCO ₃ high hSC	Mg SO ₄ highSC	Na Cl HCO ₃ highS C	Na Cl HCO ₃ lowS C	Na Ca HCO ₃ low SC
clay	soil	N	0.43	-0.48	0.20	0.40	0.53	-0.87	-0.20
terminal	surface connectivity	N	-0.28	0.08	-0.57	1.03	-0.03	-0.37	0.14
runoff	terrain	N	-0.19	0.50	0.05	-0.52	-0.51	0.08	0.59
precip long-term	climate	N	-0.28	0.29	-0.04	-0.41	-0.23	0.16	0.51
temperature long-term	climate	N	0.33	-0.17	-0.10	-0.55	0.37	0.05	0.08
groundwater recharge	hydrology	N	0.02	0.29	0.09	-0.42	-0.24	-0.15	0.41
organic carbon	soil	N	0.24	-0.04	-0.32	-0.06	-0.25	0.55	-0.12
sat overland flow	terrain	N	-0.14	0.23	-0.30	-0.34	-0.01	0.12	0.43

headwater	surface connectivity	N	0.36	-0.30	-0.27	-0.11	0.32	0.05	-0.05
drainage	surface connectivity	N	0.26	-0.02	0.22	-0.37	-0.14	-0.14	0.18
coarse	soil	N	-0.15	0.42	-0.09	-0.27	0.01	-0.10	0.18
elevation	location	N	0.23	0.17	-0.12	0.01	0.11	-0.39	-0.01
glacial till clayey	lithology	N	0.15	-0.04	-0.09	-0.15	0.30	-0.01	-0.16
topographic wetness	terrain	N	0.07	-0.14	-0.12	0.20	0.11	-0.16	0.05
evapotranspiration	climate	N	-0.20	-0.06	0.13	-0.06	-0.09	0.06	0.23
lake area	lake and watershed	N	0.09	-0.15	-0.11	0.06	0.20	-0.15	0.07
depth to bedrock	soil	N	-0.07	-0.16	0.23	0.11	0.07	0.01	-0.19
alluvium coastal fine	lithology	N	-0.05	0.11	-0.26	-0.10	0.20	0.05	0.06
sand	soil	N	-0.12	0.06	-0.13	-0.14	0.00	0.13	0.21
streams density	hydrology	N	0.30	-0.20	0.00	-0.08	0.05	0.04	-0.10

coastal zone coarse	lithology	N	-0.06	-0.26	-0.05	0.00	-0.01	0.37	0.02
baseflow index	hydrology	N	0.11	-0.05	0.16	-0.12	0.00	-0.16	0.05
glacial outwash coarse	lithology	N	0.25	-0.06	0.03	-0.06	-0.05	-0.03	-0.08
shoreline dev factor	lake and watershed	N	0.05	-0.10	-0.07	0.06	0.02	0.13	-0.08
glacial till coarse	lithology	N	-0.05	-0.12	-0.07	0.02	-0.01	0.10	0.12
soil erodibility	soil	N	-0.10	0.02	-0.05	0.00	0.02	0.21	-0.09
silt	soil	N	0.01	0.06	0.06	0.10	0.00	-0.16	-0.07
watershed:lake area ratio	lake and watershed	N	-0.02	-0.08	-0.04	-0.01	0.06	0.15	-0.07
saline lake sediment	lithology	N	-0.07	-0.07	-0.02	-0.01	0.15	0.02	-0.01
carbonate residual	lithology	N	0.03	0.08	0.05	-0.03	-0.07	-0.02	-0.04
watershed area	lake and watershed	N	0.02	-0.09	-0.06	0.02	0.09	0.02	-0.01

NEON region	location	N	-0.03	0.05	0.02	-0.02	-0.01	-0.01	-0.01
snowpack	climate	N	-0.01	0.04	-0.02	-0.01	0.00	-0.02	0.01
forest	LU/LC	H	-0.43	0.30	0.25	-0.19	-0.26	-0.29	0.61
agriculture	LU/LC	H	0.27	-0.21	0.18	0.22	0.00	0.20	-0.66
road density HU12	human activity	H	0.24	-0.29	-0.28	-0.22	0.62	-0.09	0.02
roads 500m buff	human activity	H	0.17	-0.39	0.00	-0.14	0.26	0.35	-0.25
shrub	LU/LC	H	-0.16	0.01	-0.11	-0.18	-0.05	0.46	0.03
stormwater from municipal	human activity	H	-0.11	0.07	0.18	0.07	-0.10	-0.03	-0.09
stormwater from industrial	human activity	H	0.09	0.15	-0.07	-0.03	-0.11	0.05	-0.08
major discharge sites	human activity	H	0.04	-0.10	-0.05	0.01	0.22	-0.04	-0.09
developed	LU/LC	H	0.11	0.00	-0.26	0.00	0.13	0.02	-0.01

grass	LU/LC	H	-0.07	0.08	-0.04	0.01	0.05	-0.07	0.04
wetland	LU/LC	H	0.12	-0.07	0.03	0.02	-0.01	-0.06	-0.03
heavy metal mines	human activity	H	-0.04	-0.01	-0.02	-0.02	0.07	-0.03	0.05
CAFO	human activity	H	0.02	0.01	-0.06	0.02	-0.01	-0.04	0.06
manure	human activity	H	0.04	0.03	0.03	0.01	-0.07	-0.03	-0.01

Table S5. A table showing the number of lakes in each surface connectivity class within each ion group.

	Isolated	Headwater	Drainage	Terminal	Sum
Na Ca HCO ₃ lowSC	7	12	84	1	104
Ca HCO ₃ lowSC	57	54	283	13	407
Na Cl HCO ₃ lowSC	22	11	103	1	137
Ca Mg HCO ₃ highSC	51	14	207	4	276
Ca HCO ₃ highSC	14	12	125	3	154
Na Cl HCO ₃ highSC	10	5	23	3	41
Mg SO ₄ highSC	34	4	44	17	99
Sum	195	112	869	42	1218

Table S6. Results of two-sample t-tests that examined the differences in developed land use and road density between lakes with high and low elevations. Low-elevation lakes had higher developed land use and road density than high-elevation lakes. The breakpoint of the elevation was 120m which was determined based on the partial dependence plot.

	Percentage developed land use	Road density
t-score	35.81	18.46
p-value	<0.001	<0.001