Title: Natural and human drivers of specific conductance and major ion composition in United States lakes

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Author contribution statement: Xinyu Sun and Kendra Spence Cheruvelil conceived the project. Xinyu Sun, Kendra S. Cheruvelil, 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 ion composition are important for understanding and predicting lake water quality and ecosystem responses to global changes and human disturbances. However, little is known about SC and ionic composition for populations of lakes at the continental scale, nor their relationships with natural and human factors operating at multiple spatial scales. We examined the spatial patterns in SC (N=9,784 lakes) and major anion and cation concentrations (N=1,218 lakes) across the conterminous United States, and quantified their relationships with a wide range of multi-scaled natural and human factors. We found substantial spatial variation in ion composition and that lakes with similar SC values can have very different ion composition. Most lakes had relatively low SC (median=206µS/cm), with high-SC lakes mainly located in the Plains, Desert Southwest, and Florida. Calcium and bicarbonate were the most common ions in 61% of the study lakes, with the remaining lakes dominated by the cations magnesium or sodium and the anions sulfate or chloride. Lake SC was associated with natural factors including elevation, watershed soils, and hydrology and was influenced by watershed land uses. Ion composition was associated with similar natural factors along with surface connectivity and precipitation, but also strongly affected by road density and urban development. Our results suggest that while geological, hydrological, and climate processes control the ion inputs from natural sources, human disturbances can cause SC and major ions to deviate from their background levels.

Keywords: Salinity; Conductivity; Salts; Major ions; Geology; Hydrology; Road density; Macroscale

Introduction

Specific conductance (SC) is a critical indicator of lake water quality due to its profound effects on aquatic organisms, drinking water quality, and industrial and recreational water use (Kaushal et al. 2018; Hintz & Relyea 2019; Dugan 2024). SC, which is often used as a proxy for salinity (Calver et al. 2009), has been fluctuating greatly in freshwater ecosystems in some regions of the world with resultant negative impacts; these fluctuations 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 changes in concentrations of individual ions such as chloride in lakes due to human activities (e.g., Dugan et al. 2017; Kaushal et al. 2018). However, we lack a macroscale understanding of the variation of SC across broad ranges of lakes, how ionic composition broadly differs among lakes, and the potential influences of multi-scaled natural environmental and human activities.

Studies focusing solely on SC are necessary but not sufficient to build this understanding because the impacts of salts on freshwater communities are related to major ion concentrations and compositions as well as SC (Cañedo-Argüelles et al. 2016). Lab and microcosm experiments have shown that water with the same SC but different ion compositions (e.g., solutions or media 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 to affect aquatic organisms, leading to unexpected outcomes (Elphick et al. 2011). For example, the toxicity of Cl^- on cladocerans was greater in softer water than in hard water (Elphick et al. 2011; Rogalski et al. 2024), and the toxicities of potassium ion (K^+) could be alleviated by high sodium ion (Na^+) concentrations (Mount et al. 2016). These findings underscore the necessity of understanding major ion concentrations and composition in lakes for a better assessment and prediction of ions and SC effects on freshwater ecosystems.

Variation in the SC and major ions of surface waters has been related to both natural and human factors. For example, SC in streams across the conterminous United States (CONUS) ranged from extremely low (<2 μS/cm) to saline (>10,000 μS/cm), depending on the dominant hydrologic and geologic sources and/or natural ecological context setting (e.g., evaporation; magnesium (Mg^{2+}), calcium (Ca^{2+}), and SO_4^{2-} ions from weathering of rocks; and Na^+ and Cl^- ions from saline groundwater) (Gibbs 1970; Griffith 2014; Olson & Cormier 2019). Studies of lakes in south-central North Dakota revealed that within-region SC and major ion concentrations were related to lake elevation, soils, and groundwater (Swanson et al. 1988). La Baugh et al. (2000) found that SC in lakes and wetlands in central North America varied with evaporation, precipitation, and groundwater fluxes. Landscape position, the location of a lake within hydrologic flowpaths (Kratz et al. 1997), has also been found to affect SC and ions in lakes. Regional studies of lake chains, one measure of landscape position, found that lakes connected to other water bodies (having higher surface connectivity) had higher SC than less connected lakes (Martin & Soranno 2006; Soranno et al. 1999). In addition, lakes without an outflow can be sinks of ions for catchments in some evaporative regions resulting in elevated SC (Saleem et al. 2015; Ding et al. 2024). Moreover, lakes in or near coastal areas can receive substantial amounts of salt inputs from sea-salt influenced precipitation and saline groundwater intrusion (Kiflai et al. 2022; Haque 2023). Human activities and urban development can sometimes cause long-term or permanent changes to SC and ion composition. For instance, salt inputs from irrigation runoff, residential discharge, winter road salt application, wastewater effluents, and mining can increase SC (Oswald et al. 2019; Stets et al. 2020; 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).

Previous studies of SC and major ions in freshwater systems generally have only included a limited number of predictors, have not considered a range of human influences, and have predominantly been focused on individual waterbodies or watersheds, with broad-scaled studies on streams and rivers, but not lakes (e.g., Meybeck 2003; Griffith 2014; Stets et al. 2020; but see Dugan 2024). Unfortunately, findings from stream studies are not always 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; Kahlert & Gottschalk 2014). Macroscale studies that incorporate a wide range of multi-scaled (local to regional) factors are therefore required to understand the spatial variation of lake SC and major ions and the influences of natural and human factors on them. This knowledge is critical to establish reasonable standards and goals for management and habitat restoration, as well as to predict lake responses to future changes.

In this study, we investigated two questions about lakes across the broad ranges of climate, hydrology, and land use of the CONUS: 1) What are the macroscale spatial patterns and associations among lake SC and major ion concentrations and composition? and 2) What multi-scaled natural and human factors are most strongly related to them? Using water chemistry and ecological context data from multiple data sources for 9,784 (SC) and 1,218 (major ions) lakes of the CONUS, we answered these questions by documenting spatial variation, and conducting random forest and GLMNET analyses to examine the relationships between natural and human factors and both SC and major ions.

Methodology

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 ≥ 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). The LIMNO 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 (NEON; Keller et al. 2008). In this study, we used epilimnetic SC (i.e., the electrical conductivity of one cubic centimeter of solution at 25°C), a commonly measured constituent of inland waters, as the proxy for salinity (Calver et al. 2009; Cañedo-Argüelles et al. 2016; Dugan 2024). For natural and human factors, we used lake locational, morphometric, and surface water connectivity data from the LAGOS-US LOCUS module (Cheruvelil et al. 2021; Smith et al. 2021); data about the natural context (e.g., soil texture and climate features) and human factors (e.g., road density and land use) from the LAGOS-US GEO module (Smith et al. 2022); and lake reservoir designation (natural lake or reservoir) 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 regions, 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. We removed highly correlated variables, resulting in 46 multi-scaled natural and human factors (see Table S1 for a list of factors).

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 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 so low they could indicate potential measurement errors) and higher than the upper threshold for outliers (i.e., 75th percentile + 15*interquartile range = 4,969 μS/cm), resulting in 11,072 lakes with SC data. 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 S1a), 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 S2). 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 combining SC, ions, and alkalinity data, 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. Major ion data were combined with natural and human factors to generate a 1,218 lakes sub-dataset, of which about 85% were sampled by the National Lakes Assessments (Figure S1).

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 regions 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 regions. Next, using the sub-dataset, we calculated the SC and total ion concentration (in mg/L) for lakes with complete major ion data. We computed SC 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, Cutler & Wiener 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 non-percent data, and a generalized logit transformation was applied to 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, 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 (Cutler & Wiener 2022).

To study the spatial patterns of how multi-scaled natural and human factors affect ion composition using the sub-dataset, we first applied hierarchical clustering on $\log_{10}$-transformed ion equivalent concentrations to identify common patterns among ion concentrations and composition in lakes (Ward's method; Härdle & Simar 2019). We identified 15 clusters (Figure S3) and used those clusters as the response variable in later analyses. Next, we ran a Boruta feature selection using all natural and human factors as predictors and removed the unimportant factors identified by Boruta. We then centered and scaled (into z-scores) all continuous factors before running a multinomial GLMNET model with LASSO regularization ('glmnet' package, v4.1-8, Friedman et al. 2023). Each natural and human factor was 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). 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. Finally, to further characterize the clusters, we grouped clusters based on dominant cations and anions (i.e., dominated by Ca^{2+} and HCO_3^-; Mg^{2+}, Ca^{2+}, and HCO_3^-; Ca^{2+}, Na^+, Cl^-, and HCO_3^-; Mg^{2+} and SO_4^{2-}; or Na^+ and Cl^-) and applied Wilcoxon tests to examine the differences in the top six factors between each cluster group and the group dominated by Ca^{2+} and HCO_3^-, which was the most common ion composition.

Results

SC in lakes across the CONUS

We found that SC varied within and among regions for the 9,784 lakes in the full dataset, much more so than within years. SC ranged from 2.0 to 6,125 µS/cm SC (mean±standard deviation (SD)=343±511 µS/cm, median=206 µS/cm). Most lakes with relatively high SC (SC higher than 90% of all lakes; SC ≥ 696µS/cm) were located in the Southeast, Prairie Peninsula, Northern Plains, Central Plains, Southern Plains, and Desert Southwest NEON regions (Figure 1). 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 ≤ 34µS/cm) were mostly found in the Northeast, Mid-Atlantic, Southeast, and Great Lakes regions. Among the 17 NEON regions, 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). In contrast, the Pacific Northwest had the lowest mean SC (72 µS/cm), followed by the Northeast (139 µS/cm) and Mid-Atlantic (146 µS/cm) regions. In contrast, 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 regions (Figure S4).

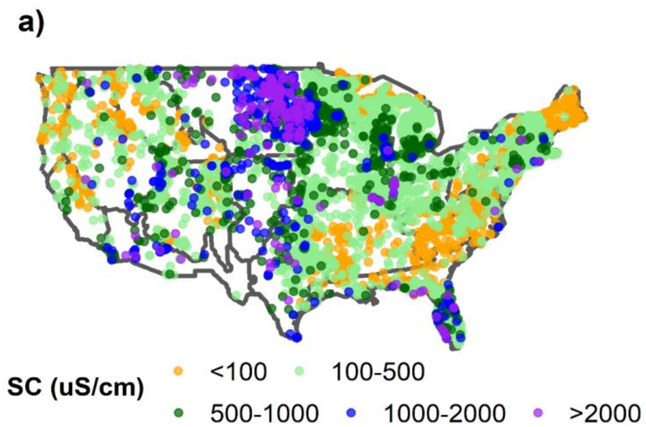


Figure 1. The mean April-October specific conductance (SC) of each study lake (a; N=9,784) and the location of lakes with low and high SC values (b; 978 lakes with SC lower than 10% of lakes and 979 lakes with SC higher than 90% of lakes, respectively). NEON regions outlined in black are as follows: 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 plot b).

Measured and calculated SC were strongly positively correlated for the 1,218 lakes in the sub-dataset with complete SC and major ion data (Figure 2a; $p<0.001$). The average deviation of calculated to measured SC was about 8%, suggesting that our sub-dataset represented a majority of dominant major ions. We found positive correlations between measured SC and the total ion concentration and between measured SC and 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+}, K^{+}, Mg^{2+}, Na^{+}, and HCO_3^{-} had stronger associations with SC compared to those shown for Cl^{-} and SO_4^{2-}.

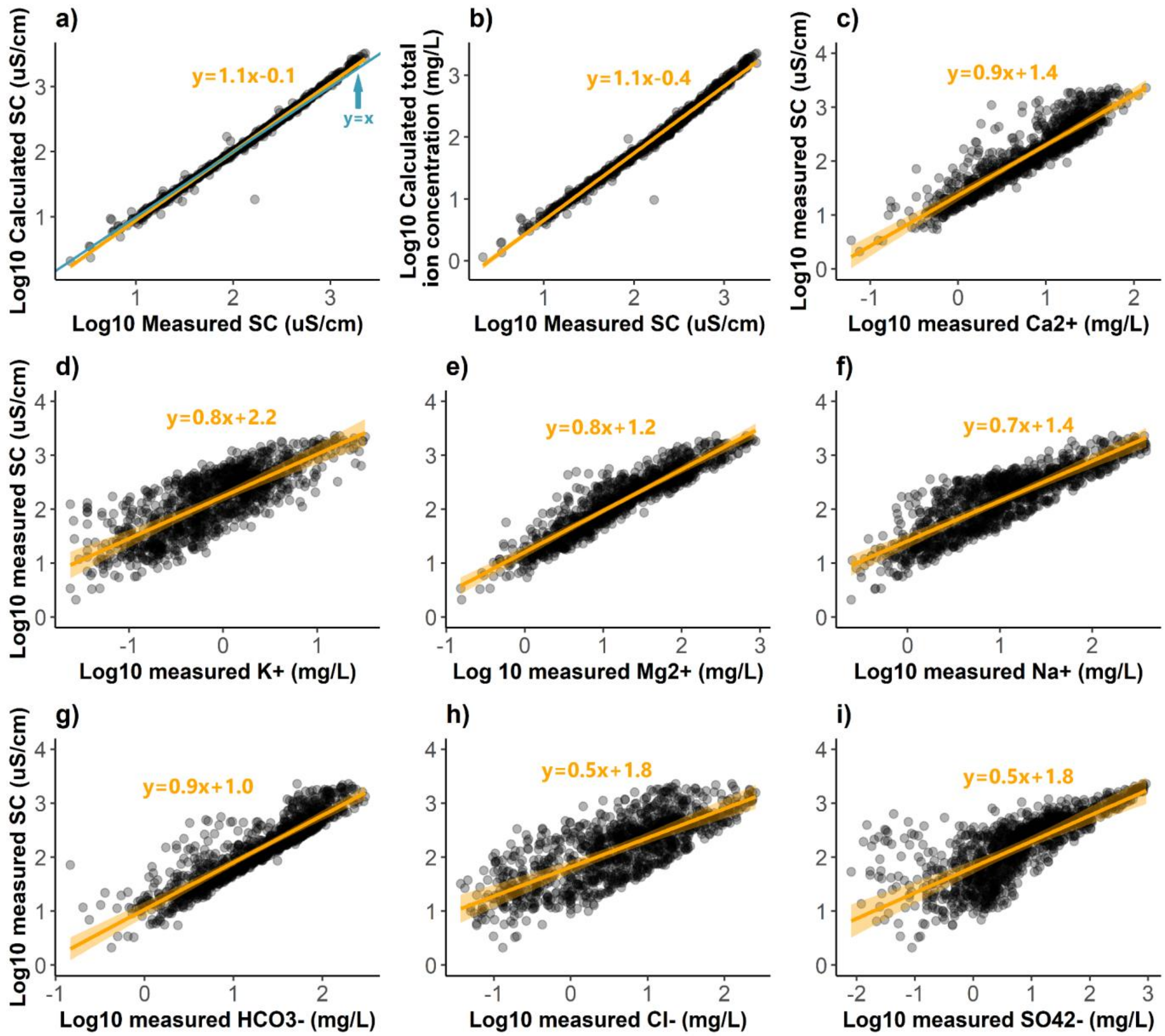


Figure 2. Relationships between log10-transformed measured SC and calculated SC (a), calculated total ion concentration (b), and the concentration of each ion (c-i) in 1,218 lakes across the CONUS. Each dot represents a lake and the orange prediction lines were fitted with a linear model with the equation above each line. In plot (a), the blue line is y=x. The orange shadow area indicates one standard deviation.

Multi-scaled natural and human factors related to SC

Lake SC was related to both natural and human factors (RF out-of-bag variance explained=59%; N=9,784). Lake elevation was the most important factor based on the RF model % increase MSE, followed by the percentage of clay in the soil and the percentage of watershed forest land cover (Figure S5a). Groundwater recharge was the most important factor identified using the increase in node purity (Gini coefficient), followed by mean annual runoff and percent clay in the soil (Figure S5b).

We observed a range of relationships between explanatory factors and lake SC using partial dependence plots (PDPs). Lakes with the highest SC at the lowest elevations were located mostly in the Southeast region. 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 (Figure 3a). The percentage of clay in the soil was negatively associated with SC until 2% clay content, then the 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). Similarly, 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 can represent areas with high human disturbance), whereas SC was lowest in lakes with watersheds with moderate forest cover. Lake SC, however, showed a small increase as forest cover reached about 80% (Figure 3e).

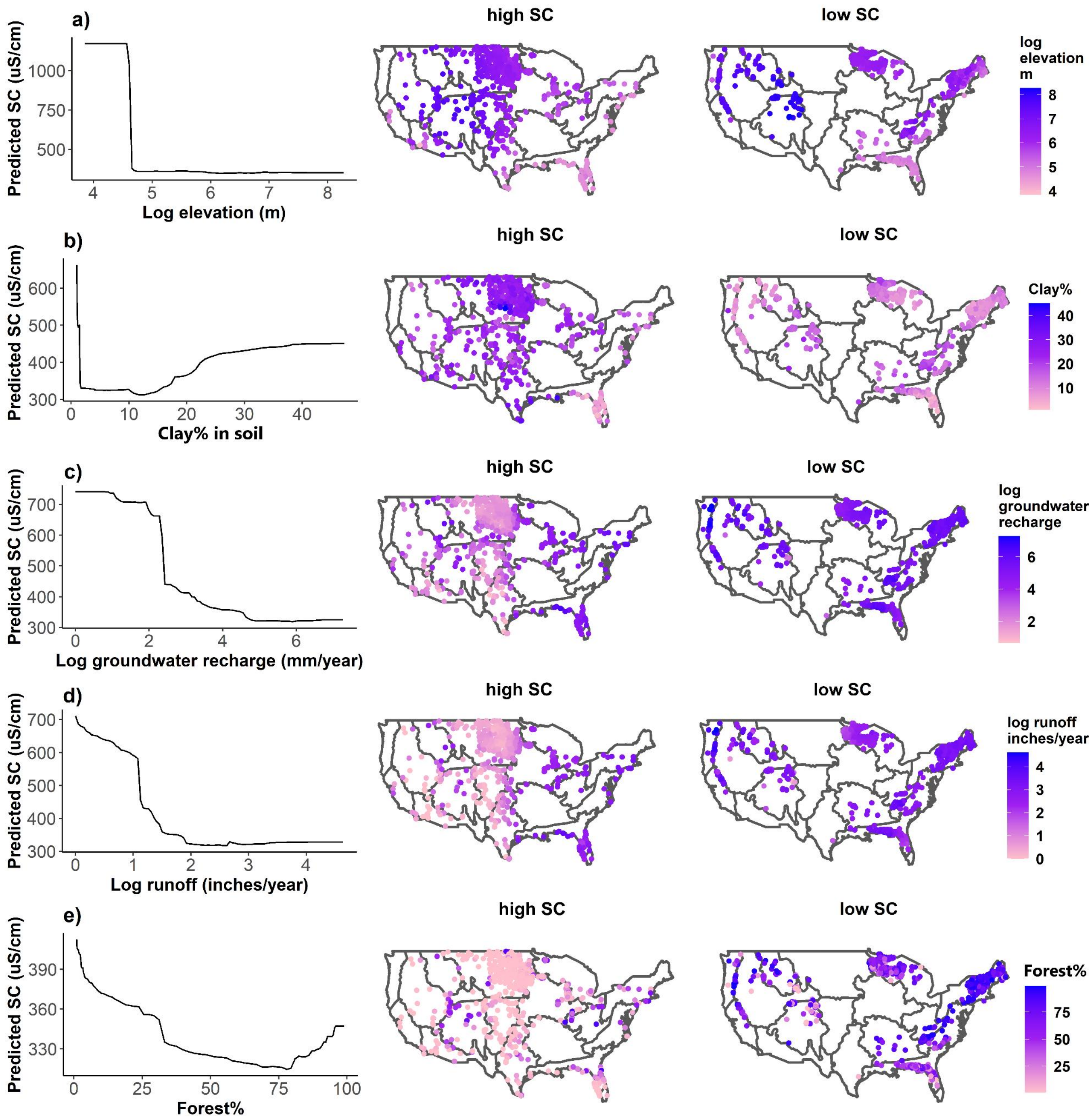


Figure 3. PDPs showing the relationships between predicted SC and the most important natural and human factors (left) and maps showing the values of the important factors of low SC (SC lower than 10% of all lakes; right) and high (SC higher than 90% of all lakes; middle) SC lakes. 'Log' = natural log transformation.

Ion composition in US lakes and associations with multi-scaled natural and human factors

We hierarchically classified the 1,218 lakes in the sub-dataset with both SC and major ion data into 15 well-defined clusters with divergent ion concentrations and ion compositions (Figures 4, Table 1). In most clusters (61% of lakes; clusters 4, 11, 2, 15, 14, 13, 3, and 9, ordered based on low to high mean SC within a cluster), and despite differing SC, Ca^{2+} and HCO_3^- were the most abundant cation and anion, respectively. However, about 8% of lakes were dominated by Mg^{2+} and SO_4^{2-} (cluster 8); Ca^{2+} and Mg^{2+} co-dominated in 8% of lakes (clusters 12 and 5); Na^+ and Cl^- were the most abundant cation and anion, respectively, in 5% of lakes (clusters 6 and 1); and Ca^{2+} and Na^+ had similar proportions among cations in 17% of lakes (clusters 7 and 10). Among all the clusters, cluster 8 had the highest SC, followed by clusters 6 and 9; and cluster 4 had the lowest SC, followed by clusters 11 and 2.

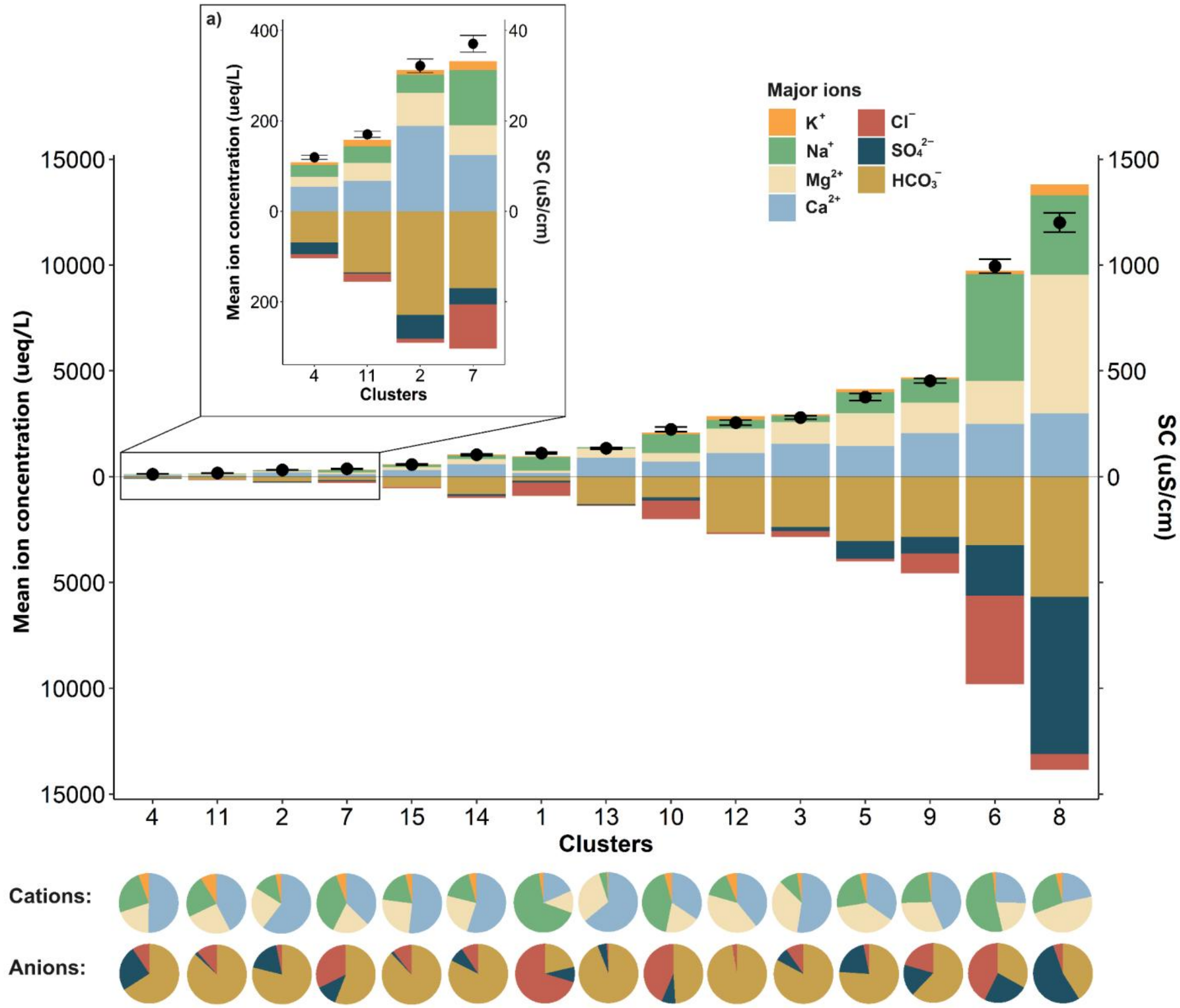
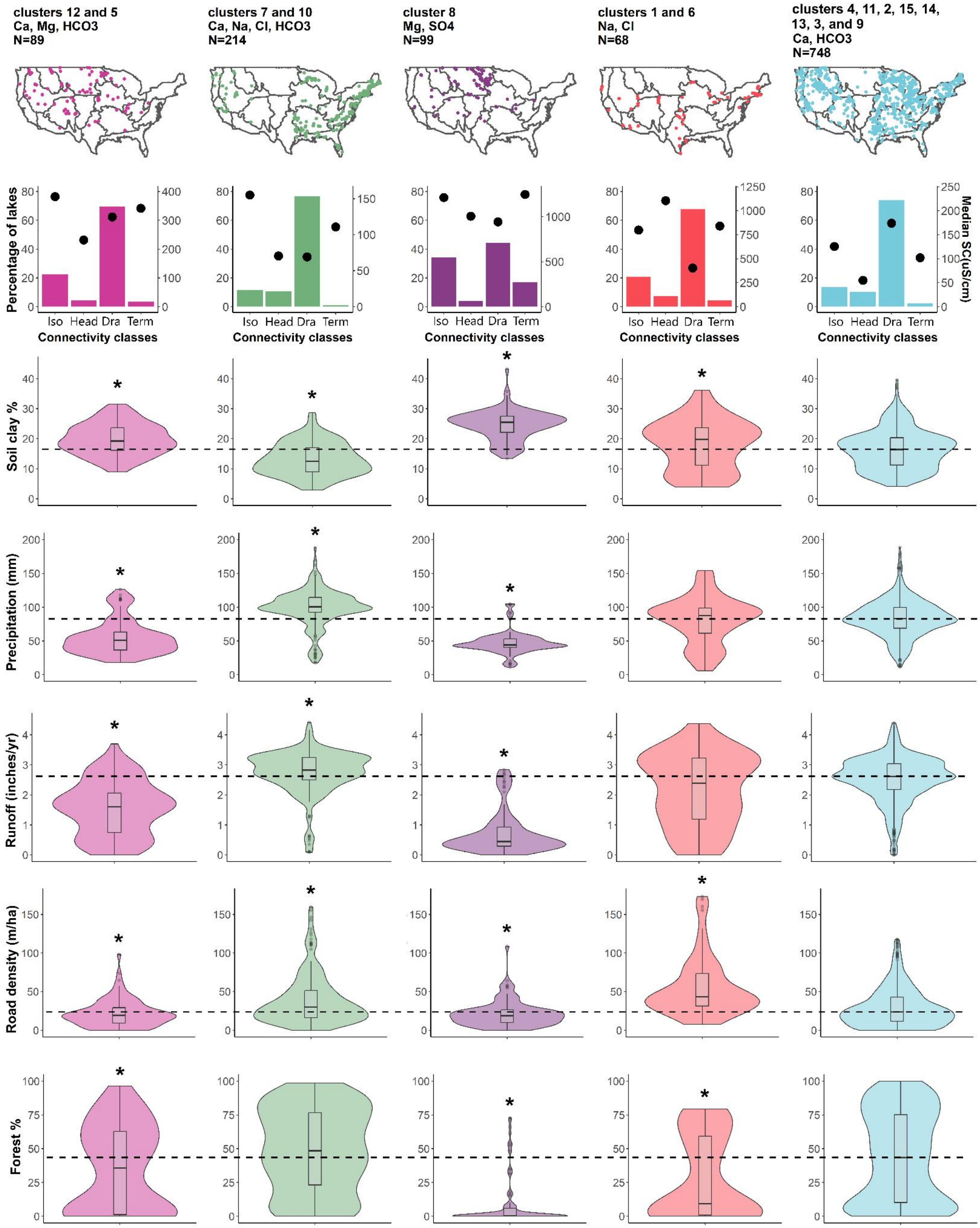


Figure 4. For each cluster, the mean equivalent concentrations (μeq/L) of major ions, mean SC (μS/cm), and proportions of cations and anions. Stacked bars represent ion concentrations with cations above and anions below the zero line, respectively, with corresponding values shown on the left y-axis; black dots represent mean cluster 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 cluster. To aid in visualization, subplot a) shows ion concentrations and SC in clusters 4, 11, 2, and 7.

Table 1. Summary of each cluster's dominant cation(s) and anion(s), percentage of study lakes within each cluster, and average SC of each cluster. Clusters are ordered according to dominant ions.

Cluster	Dominant cation(s)	Dominant anion(s)	Percentage of study lakes	Average SC±SD (μS/cm)
4	Ca^{2+}	HCO_3^-	5	12±4
11	Ca^{2+}	HCO_3^-	2	17±7
2	Ca^{2+}	HCO_3^-	7	32±15
15	Ca^{2+}	HCO_3^-	5	57±26
14	Ca^{2+}	HCO_3^-	12	103±40
13	Ca^{2+}	HCO_3^-	2	134±44
3	Ca^{2+}	HCO_3^-	15	279±75
9	Ca^{2+}	HCO_3^-	13	453±111
12	Ca^{2+}, Mg^{2+}	HCO_3^-	2	255±119
5	Ca^{2+}, Mg^{2+}	HCO_3^-	6	377±172
7	Ca^{2+}, Na^+	HCO_3^-	8	37±18
10	Ca^{2+}, Na^+	Cl^-, HCO_3^-	9	224±113
8	Mg^{2+}	SO_4^{2-}	8	1,201±448
1	Na^+	Cl^-	2	111±40
6	Na^+	Cl^-	3	995±330

The diverse spatial patterns in lake ion composition and cluster assignments of the study lakes were determined by both natural and human factors (GLMNET; Figure 5; Figure S6; Table S3). Ion clusters showed stronger associations with factors in the categories of soil, terrain, climate, human activities, and LU/LC than those in other categories. Hydrology, particularly groundwater-related features, and lake location were only moderately associated with ion composition. Additionally, surface water connectivity was found to be associated with lake membership in only a subset of ion clusters. Below we describe the spatial distribution of each ion cluster as well as their characteristics using the top six natural and human factors (i.e., surface water connectivity, percent clay in the soil, precipitation, runoff, road density, and percent forest land cover) from the GLMNET analysis.



clusters 12 and 5
Ca, Mg, HCO3
N=89
clusters 7 and 10
Ca, Na, Cl, HCO3
N=214
cluster 8
Mg, SO4
N=99
clusters 1 and 6
Na, Cl
N=68
clusters 4, 11, 2, 15, 14, 13, 3, and 9
Ca, HCO3
N=748
Percentage of lakes
Median SC(uS/cm)
Iso Head Dra Term
Connectivity classes
Soil clay %
Precipitation (mm)
Runoff (inches/yr)
Road density (m/ha)
Forest %

326

Figure 5. Maps (top), barplots (middle), and violin plots (bottom) of lakes in clusters aggregated into five major ion cluster groups based on the dominant cation(s) and anion(s). Maps show the location of lakes within each ion group, with the text listing the ion clusters we included in each major ion cluster group, the dominant cations and anions, 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 (Iso=isolated; Head=headwater; Dra=drainage; Term=terminal). Violin plots show data distribution of top natural and human factors by major ion cluster 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 cluster group dominated by Ca^{2+} and HCO_3^- (i.e., the most common ion composition; clusters 4, 11, 2, 15, 14, 13, 3, and 9). The star above the violin plot indicates a significant difference ($p \leq 0.05$) in that factor between the corresponding cluster group and the major ion cluster group dominated by Ca^{2+} and HCO_3^- (the rightmost panel).

Lakes dominated by Ca^{2+} and HCO_3^- (hereafter referred to as the common ion group; clusters 4, 11, 2, 15, 14, 13, 3, and 9) were widely distributed across multiple NEON regions, except for the Northern Plains, Central Plains, Desert Southwest, and Pacific Southwest. Lakes dominated by Mg^{2+}, Ca^{2+}, and HCO_3^- (clusters 12 and 5) were mostly found in the Northern Plains, Prairie Peninsula, Southern Rockies & Colorado Plateau, and Great Basin. Compared to the common ion group, lakes in these clusters had higher percentages of clay in the soil and lower precipitation, runoff, road density, and forest cover (Wilcoxon, $p \leq 0.01$). Lakes dominated by Ca^{2+}, Na^+, Cl^-, and HCO_3^- (clusters 7 and 10) were commonly found in the Northeast, Mid-Atlantic, Southeast, Atlantic Neotropical, Great Lakes, Ozarks Complex, and Great Basin. These lakes had lower percentages of clay and higher precipitation, runoff, and road density than the common ion group ($p<0.001$). Lakes dominated by Mg^{2+} and SO_4^{2-} (cluster 8) were mostly found in the Northern Plains. These lakes were distinct in their surface connectivity classes as, this cluster had the highest proportions of lakes with no inflow and no outflow (i.e., isolated lakes; 34% of all cluster 8 lakes) or with only inflow (i.e., terminal lakes; 17% of all cluster 8 lakes) (Table S4). Additionally, lakes in this cluster had higher percentages of clay and lower precipitation, runoff, road density, and forest cover compared with the common ion group ($p\leq0.003$). Finally, lakes dominated by Na^+ and Cl^- (clusters 1 and 6) were commonly found in the Northeast, Mid-Atlantic, Prairie Peninsula, and Southern Plains. These lakes had higher percentages of clay and road density and lower forest cover than the common ion group ($p\leq0.04$).

Discussion

We describe general spatial patterns in SC and major ion composition across the broad ecoclimatic zones of the conterminous US lakes that help provide context for interpreting the potential for future changes. We also examine the relationships between multi-scaled natural and human factors and SC and major ions that can be used to predict and support the management of lake water quality. Although most lakes had low SC (median=206 µS/cm), 2% of the lakes had SC higher than 2,000 µS/cm. Sixty-one percent of lakes were dominated by Ca^{2+} and HCO_3^- and the remaining were dominated by the cation Mg^{2+} or Na^+ and the anion SO_4^{2-} or Cl^-. SC and ionic composition and concentration were strongly associated with factors including lake elevation, surface connectivity, soil composition, hydrology, climate, and watershed land use that explained the spatial patterns.

Spatial variation in SC and major ions in US lakes

Low SC lakes (SC lower than 10% of all lakes) were mostly found in the Northeast, Mid-Atlantic, Great Lakes, and Northwest regions, which aligns with findings from previous studies on US streams (Griffith 2014; Olson & Cormier 2019). High SC lakes (SC higher than 90% of all lakes) were mainly in the Plains, Desert Southwest, and Southeast regions, particularly Florida. Previous macroscale studies of stream conductivity found relatively high SC in the Plains and Desert Southwest but did not find high SC in the Southeast (Griffith 2014; Olson & Cormier 2019). This difference could demonstrate the water chemistry differences between lakes and streams in the Southeast and/or be attributed to the large difference in the number of systems studied between previous and our research (e.g., 315 Coastal Plain (a National Rivers and Stream Assessment region) stream sites in Olson & Cormier 2019 compared to 1,521 lakes in the Southeast in our dataset). Previous regional studies have suggested that the high SC in the Southeast, specifically in Florida, could be attributed to ion inputs from precipitation and seawater intrusion as they were in or near coastal areas (Kiflai et al. 2022; Haque 2023) as well as from discharges from stormwater pipes and detention ponds (Beckingham et al. 2019). Understanding that high-SC lakes occur in the southeastern US has the potential to change SC prediction and management in this region as further increases could lead to biological responses depending on the dominant cation and anions. Furthermore, differences in regional patterns between our study and the stream study could also be due to temporal variations in SC, as some lakes in the Southeast had relatively high CVs (Figure S4). However, most lakes were only sampled once each year in the summer, which highlights the need for sampling during other seasons in order to obtain a comprehensive understanding of long-term inter- and intra- annual variation in lake SC.

Although SC is an important measure of water quality, major ion concentration and composition are also critical for understanding lake SC. We observed a linear relationship between SC and the total ion concentration (calculated by summing up the concentration of each ion), which could be applied to predict total ion concentration using SC or vice versa. However, these relationships differed among different major ion compositions, particularly in high-SC lakes (Figure S7). Moreover, the same SC levels can be made up of very different major ion compositions and concentrations. For example, clusters 14 and 1 had similar average SC (103μS/cm and 111μS/cm, respectively), but cluster 14 was dominated by Ca^{2+} and HCO_3^- and cluster 1 was dominated by Na^+ and Cl^-. These differences are important because ionic composition can determine the aquatic species present in water, the impacts of SC and ion level changes on organisms (Elphick et al. 2011; Mount et al. 2016; Huber et al. 2024), the usage of water (Tiri et al. 2018; Zaman et al. 2018), and management strategies to mitigate the negative effects of elevated ions in water.

Management agencies in the US responsible for monitoring lake water quality (which is our primary data source) are more likely to measure SC than major ions, perhaps due to the high costs associated with sampling and measuring ions compared to SC. Our results highlight the importance of these agencies considering approaches to supplement their SC data, particularly for lakes with high SC and those in the Southeast (e.g., Florida) and Central Plains. Researchers can also help fill this 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. Our estimation of the relationships between major ions and SC and our models, which will be discussed later, that documented relationships between major ion composition and key natural and human features provide an important first step in this direction.

We found that ion concentration and composition varied greatly within and among regions. As expected (Dugan 2024), Ca^{2+}, and sometimes Na^+, was the dominant cation in many lakes. However, in about 16% of lakes located mostly in the Northern Plains, Mg^{2+} was the dominant cation or equally abundant to Ca^{2+} (a few others were located in the Prairie Peninsula and West regions). We also found substantial within-region variation in ion levels, which is intriguing because earlier stream studies suggested that the composition of ions was directly controlled by natural mechanisms (e.g., precipitation, rock dominance, and evaporation), which often vary regionally (Griffith 2014; Olson & Cormier 2019). However, previous regional lake studies also found heterogeneity in ion composition that they attributed to both natural processes and human activities (e.g., groundwater, soil texture, and acid deposition) (Baker et al. 1991; DeSellas et al. 2023). Our research findings that each NEON region included multiple ion clusters further support the idea that major ions are influenced by multiple multi-scaled natural and human factors that vary both locally and regionally.

Multi-scaled natural and human factors related to SC and major ions

SC, major ion concentrations, and ion composition were related to both natural and human factors. This result suggests that factors such as geology, hydrology, and climate are key determinants of ion inputs from natural sources and that, in combination with the water balance in the lake, control background SC and ions. Human disturbances that influence export ions to lakes cause ions to deviate from those background levels and vary across lakes within the region. For example, Cl^- was strongly and mostly influenced by human activities (Figure S8). Therefore, effective management strategies designed to manage water quality and lake ecosystems should target specific measures of SC and specific ions.

We found that a range of multi-scaled natural factors were important for understanding SC and major ions. For example, at the lake scale, elevation was negatively related to SC. However, because these low-elevation and high SC lakes also had higher percentages of developed land use and road density in their catchments, this relationship could be signaling greater human ion inputs to low-elevation lakes compared to those at higher elevations (Table

S5). A similar pattern of higher SC in lower-elevation lakes was observed by Müller et al. (1998), which was attributed to higher rock weathering and dissolution rates and lower relative water inputs from rainfall with decreasing elevations. Additionally, our lakes with low elevation and high SC were mostly in Florida and the Atlantic Neotropical region and had relatively high proportions of Na^+ and Cl^-, which could also be related to current or past seawater intrusion (Kiflai et al. 2022).

We anticipated surface connectivity, such as measures of landscape position, to be important for explaining differences in SC and major ions because it influences the relative importance of water and ion inputs from precipitation, surface water, and groundwater sources (Riera et al. 2000; Bennett et al. 2007; Dumelle et al. 2024). However, it was only strongly associated with lake membership in some ion clusters. For instance, cluster 8 (high SC, dominated by Mg^{2+} and SO_4^{2-}) had the highest proportions of terminal (only surface inflows) and isolated (no surface inflow or outflow) lakes among all clusters; and 41% of all terminal lakes and 20% of all isolated lakes were in cluster 8 (Table S4). Previous research found that isolated and terminal lakes can be ion sinks for the catchment, particularly in evaporative regions (Saleem et al. 2015; Cotner et al. 2022; Ding et al. 2024). We also found that the SC of drainage lakes (those with both inflows and outflows) was higher than that of other connectivity classes in the most common ion group (i.e., clusters dominated by Ca^{2+} and HCO_3^-), but SC for drainage lakes was lower than that of other connectivity classes in other cluster groups (Figure 5). This result implies that although the water inputs from tributaries can import ions into lake (e.g., from rock weathering) and increase ionic concentrations, other stronger natural and human processes (e.g., groundwater discharge and human land use) may mask this effect by causing greater increases, in which case tributary water inputs could have a dilution effect on SC and ion concentrations.

At the watershed and regional scales, soil composition variables, measures of overland surface water flow and groundwater recharge, and precipitation were important in models of lake SC and ion composition. We found that lakes with high percentages of clay tend to have higher SC and/or Mg^{2+} concentrations than other lakes. This result could be explained by the higher levels of agricultural activities in areas with higher clay in the soil along with the finding that soil with a higher proportion of clay often contains higher amounts of cations such as Mg^{2+} (Ross et al. 2008). We found negative relationships between SC and groundwater recharge and runoff, which may indicate greater influence of precipitation and surface water inputs for low SC lakes (Webster et al. 2006) compared to the influences of groundwater as a source of ions to high SC lakes in many regions (Li et al. 2020; Dugan 2024). Additionally, runoff and regional precipitation were both lower in lakes with high proportions of Mg^{2+} (clusters 12, 5, and 8), suggesting that other factors such as evaporation may be more important for these lakes (La Baugh et al. 2000). These findings imply the significant, complex roles that watershed geology and hydrology and regional climate play in affecting lake hydrologic and chemical budgets.

Lake SC and major ions were also related to multi-scaled human factors (and those that indicate the lack of disturbance), including watershed land use/cover and road density. For example, forest land cover, which can be used to identify lakes with fewer human disturbances, was negatively related to SC and was lower in clusters 12, 5, 8, 1, and 6, which were not dominated by Ca^{2+} and HCO_3^-. Moreover, one of the most crucial factors that affected ion composition was road density, which was higher in clusters 7, 10, 1, and 6. These same clusters, which are located in regions where winter road salt applications happen (e.g., the Northeast, Mid-Atlantic, Great Lakes, and Prairie Peninsula regions; Dugan et al. 2017), also had higher concentrations and proportions of Na^+ and Cl^- than other clusters. Therefore, this pattern is likely due to road deicing salt applications in winter that are retained in lakes, causing increases in salt concentrations throughout the year (Kaushal et al. 2021; Solomon et al. 2023). Supplementing 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 demonstrate the importance of reducing road salt applications in regions with high impervious surface area and road density near lakes.

Although our models considered the effects of all the natural and human factors, we did not examine the joint effects of these factors or the influence of temporal changes in those factors on SC and ions. Very few studies have looked at the combined effects of such factors on other water quality parameters (Kernan & Helliwell 2001; Nobre et al. 2020; Lin et al. 2021), and no or limited information exists on SC and major ions, despite the likely complex interactive effects. Additionally, human activities can influence some of the natural factors and cause them to change through time (Meybeck 2003), which may affect these factors' relationships with ions. Therefore, future research efforts should attempt to disentangle the complex underlying mechanisms affecting SC and ion concentrations and composition in lakes.

Conclusion

We documented spatial variation in specific conductance (SC) and major ion concentration and composition in 9,784 and 1,218 lakes, respectively, across the continental US. We found substantial spatial variation in ion composition and that lakes with similar SC values can have very different ion composition, which can result in differential effects on lake biota, may change differently in the future, and likely require different strategies to manage. These findings highlight the importance of considering all major ions when studying lake water chemistry. We also found that variation in SC was related to a wide range of local, watershed, and regional factors, such as lake elevation, soil texture, hydrology, precipitation, and forest land cover. Major ions were strongly associated with both human and natural factors. In particular, elevated Cl^- levels were predominantly related to road density and urban development, which can be managed to address issues such as freshwater salinization. Our results suggest that while geology, hydrology, surface connectivity, and climate control ion inputs from natural sources, human disturbances directly and indirectly alter ion export to lakes, causing SC and major ions to deviate from their background levels.

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Supplementary Figures

Paper title: Natural and human drivers of specific conductance and major ion composition in United States lakes

Authors: Xinyu Sun, Kendra Spence Cheruvelil, Patrick J. Hanly, Katherine E. Webster, & Patricia A. Soranno

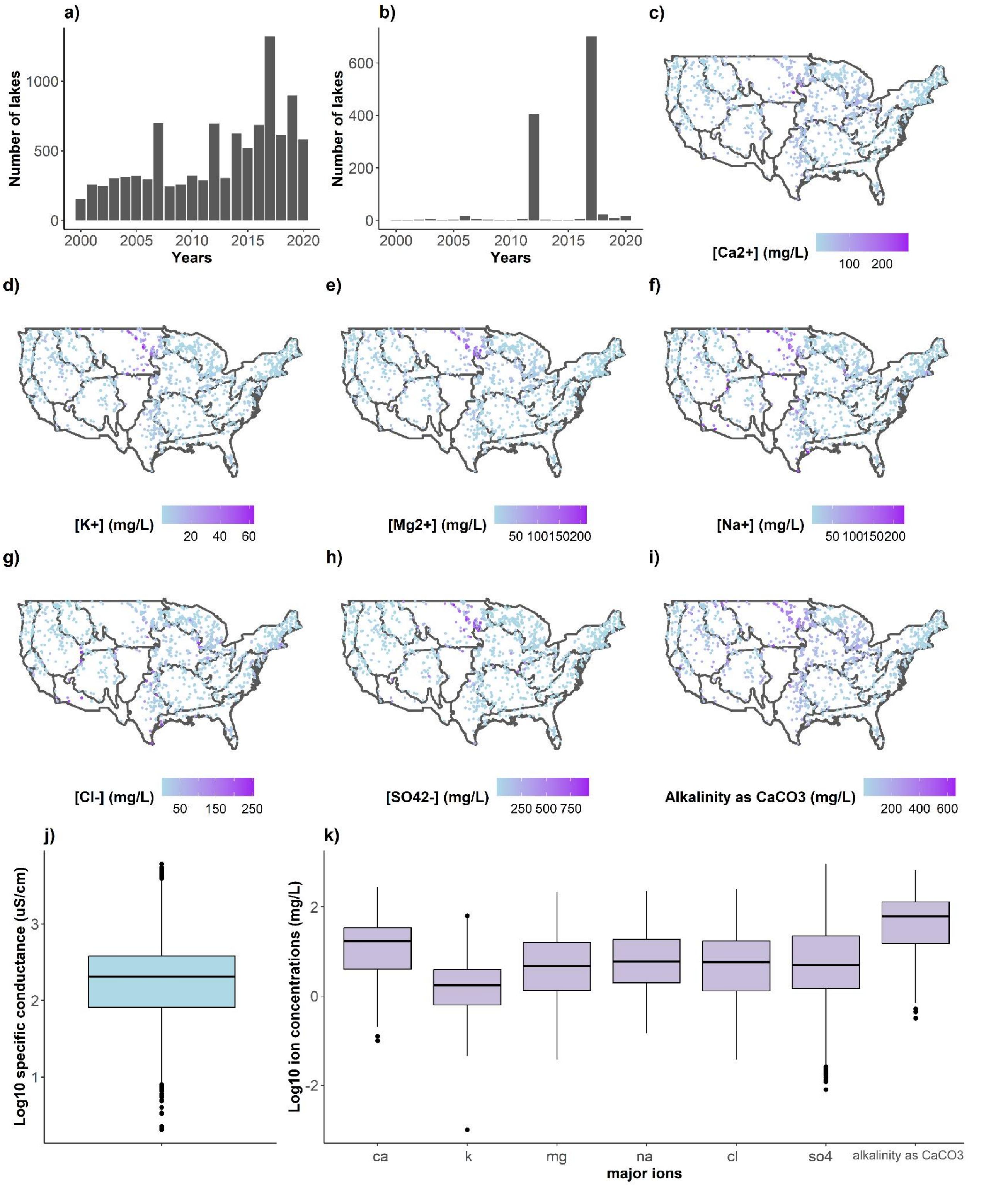


Figure S1. Summary of specific conductance (SC) and major ion data: a) number of lakes sampled in each latest SC sampling year; b) number of lakes sampled in each latest major ion sampling year; c) - i) maps showing major ion concentrations and alkalinity levels as $CaCO_3$ (mg/L) by NEON region; j) 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.

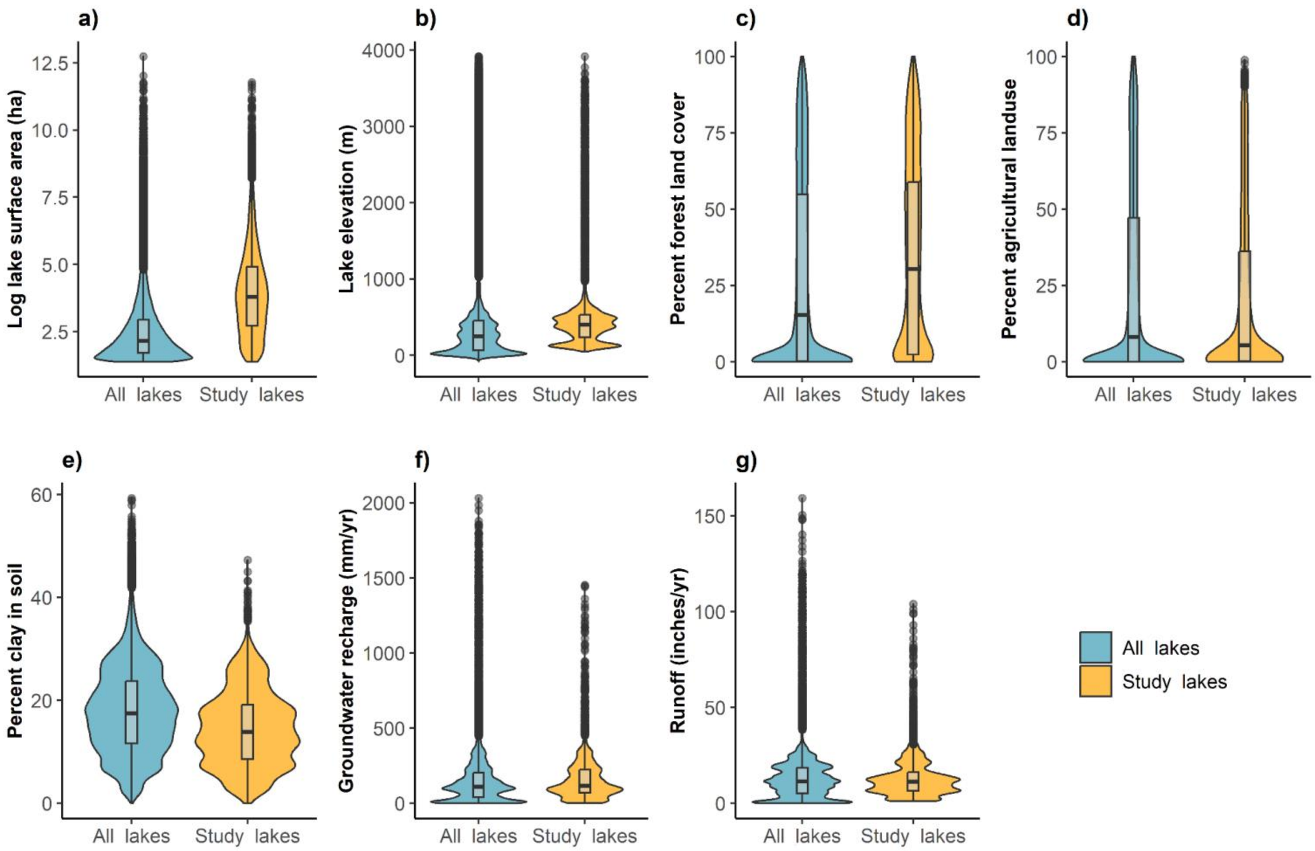


Figure S2. Comparison of all lakes > 4 ha in the U.S. (All lakes, blue) relative to the study lake population (Study lakes, orange). The violin plots show all data for the two groups of lakes, and the boxes within the violin plots are the interquartile ranges with the median. The ‘All lakes’ category was derived from the LAGOS lake population > 4 ha.

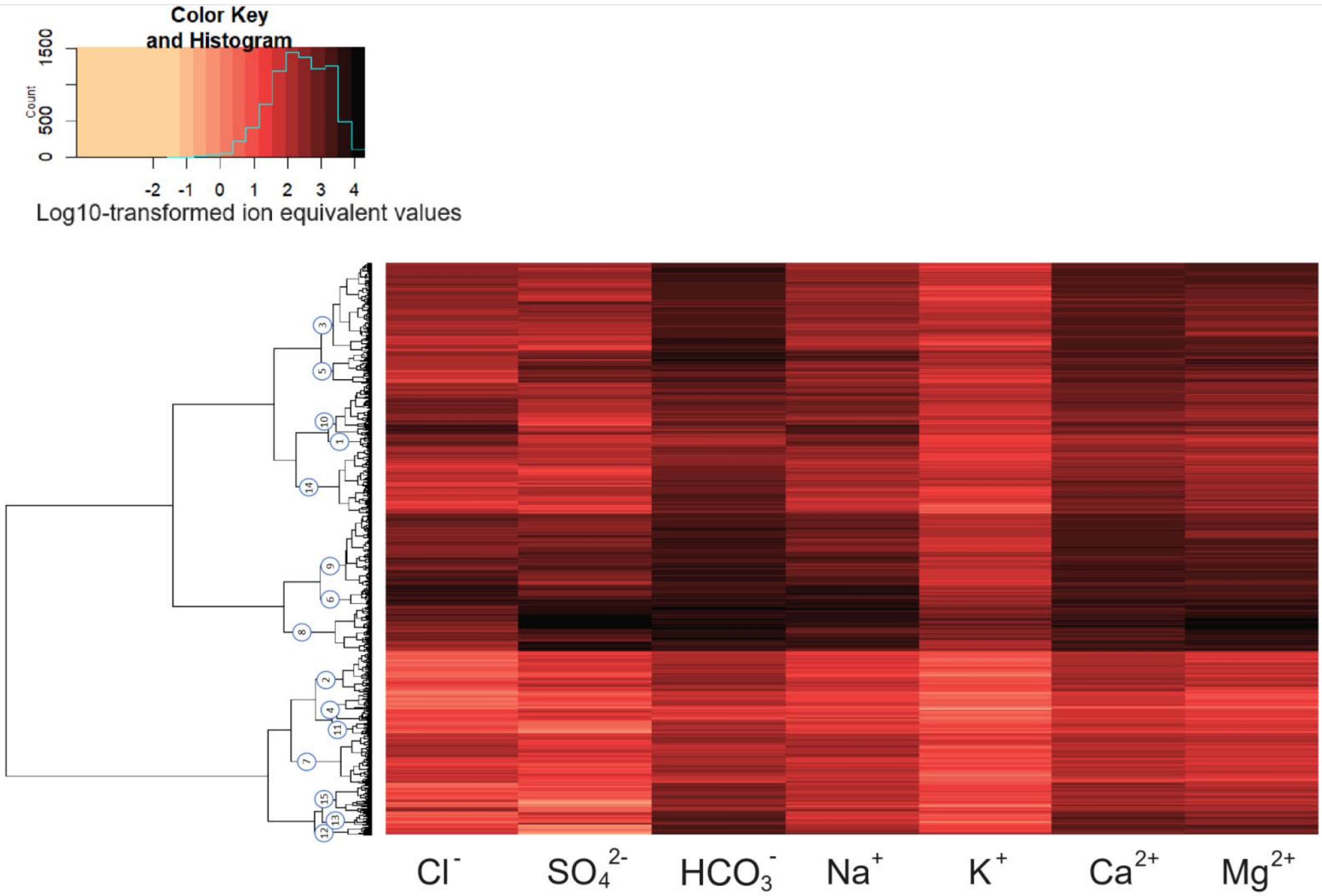


Figure S3. Heatmap showing log_{10}-transformed major ion equivalent values grouped by clusters with a dendrogram (output of the hierarchical clustering using the Ward's method) on the left edge. The histogram at the top shows the color key and distribution of data.

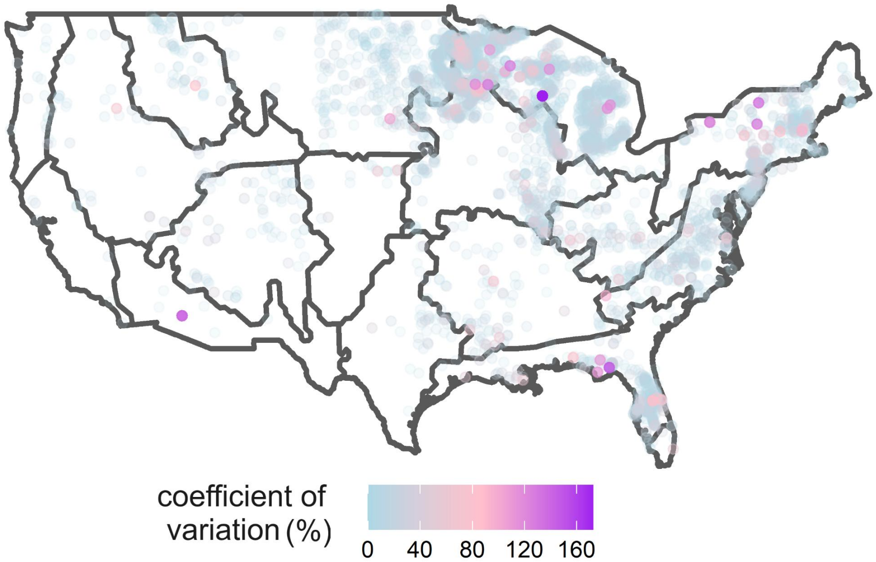


Figure S4. Map showing the intra-year SC coefficient of variation (N=4,581) of each lake by NEON region. Each dot represents a lake. See Figure 1 caption for NEON region names.

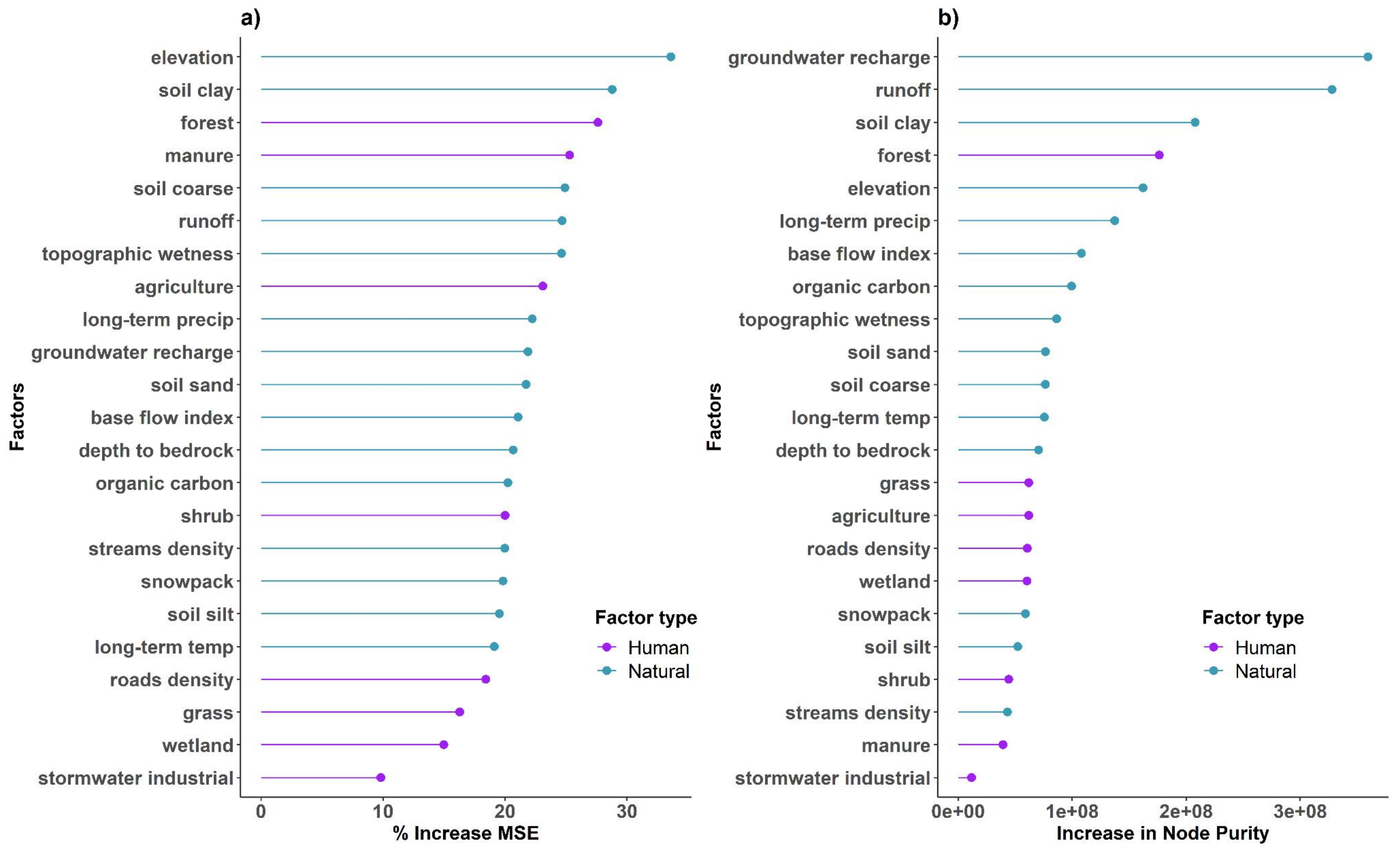


Figure S5. Results from random forest regression model (N=9,784) of natural and human factors and their relationships to lake SC: a) importance scores of important natural and human factors based on the percentage increase in mean squared error (MSE); b) importance scores of important natural and human factors based on the increase in node purity (from Gini Index).

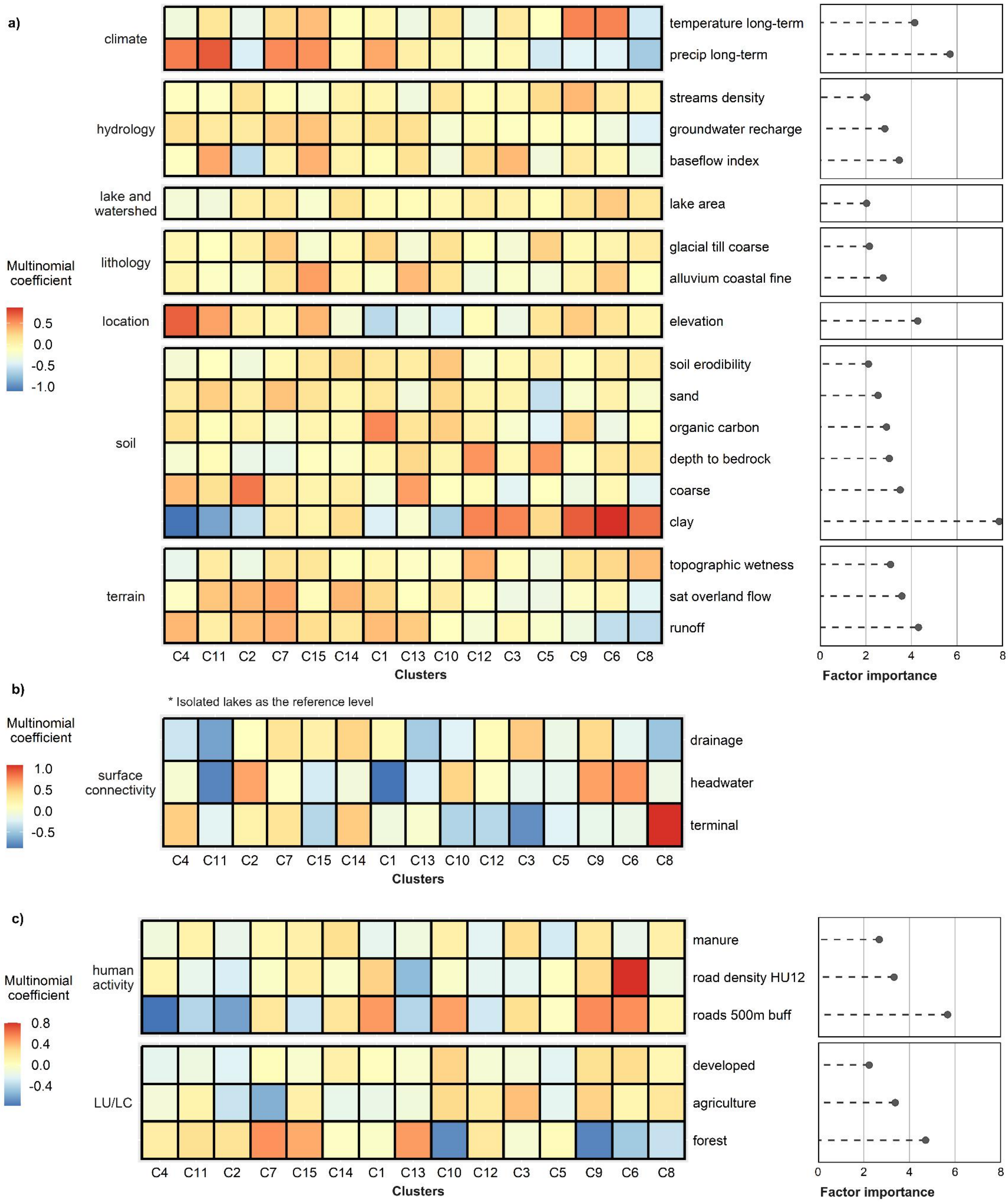


Figure S6. Heatmaps showing multinomial coefficients generated from a single GLMNET model predicting ion composition cluster assignment based on each natural (a,b) and human factor (c), with the factor importance plotted on the right (lollipop plots) that was calculated as the absolute sum of the cluster-specific 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 ≥2 were plotted (18 of 30 inputted natural factors, surface connectivity was counted as one factor, and 6 of 12 inputted human factors). A full table of coefficients can be found in Table S3.

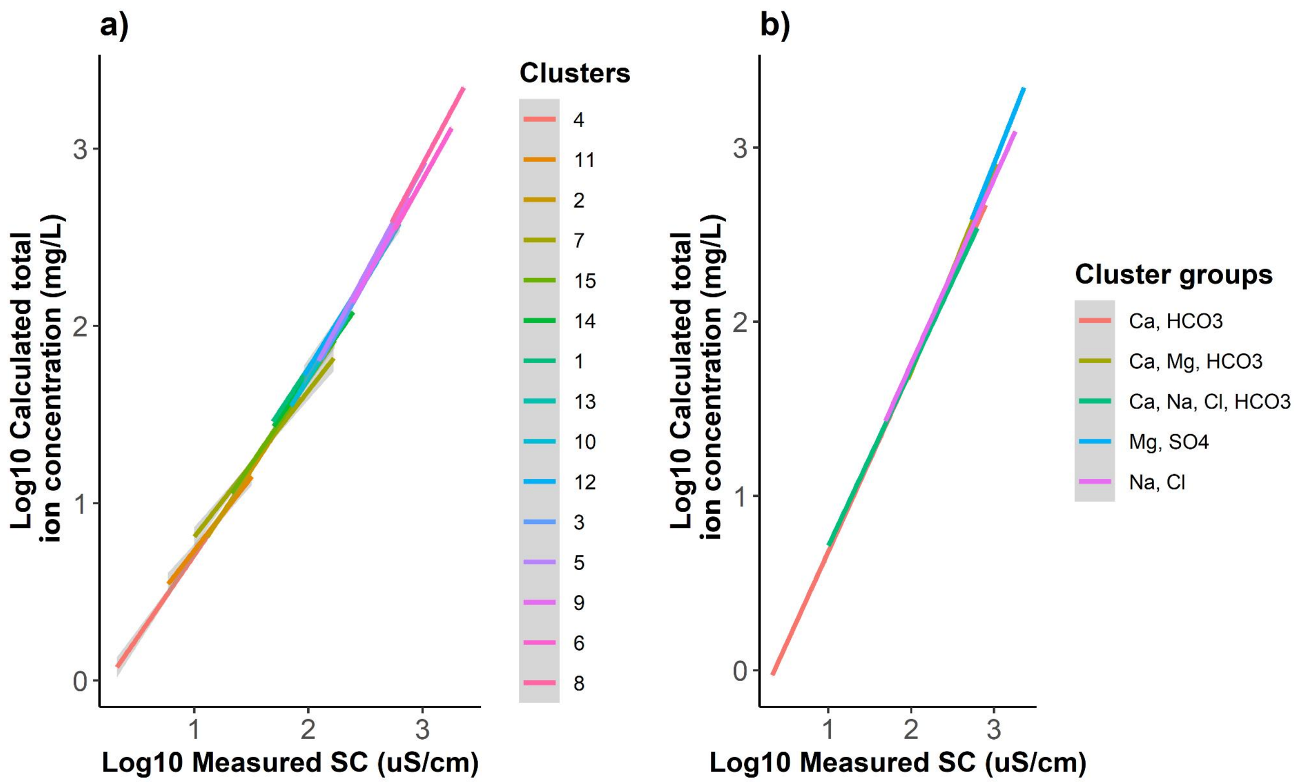
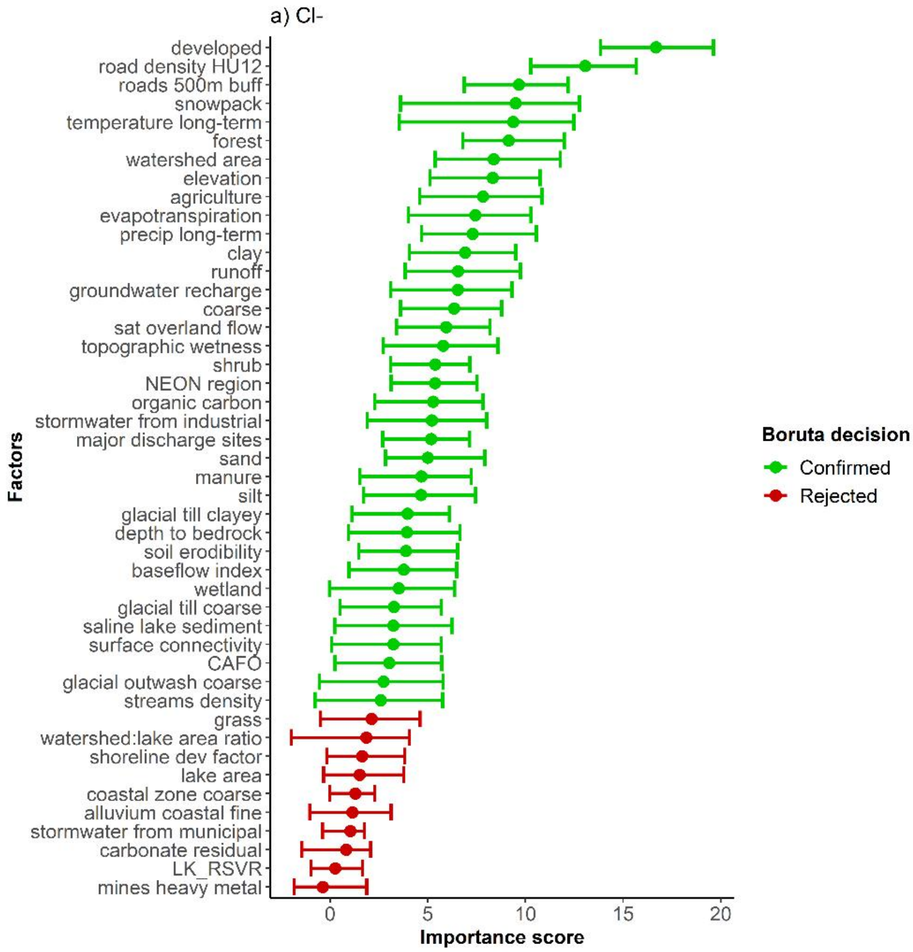
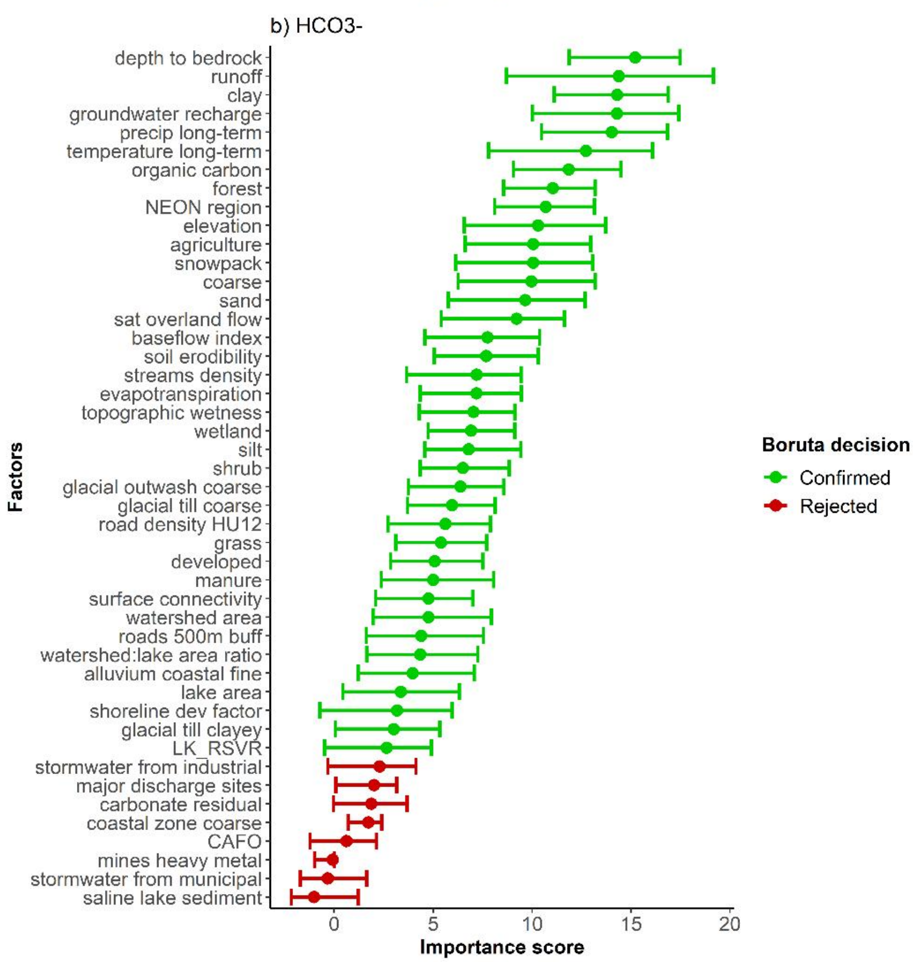


Figure S7. Relationships between log10-transformed measured SC and calculated total ion concentration by clusters (a; 15 clusters; ordered based on SC, from the lowest (cluster 4) to the highest (cluster 8)) and cluster groups (b; 5 groups based on dominant cations and anions). The prediction lines were fitted with linear models.


a) Cl-
developed
road density HU12
roads 500m buff
snowpack
temperature long-term
forest
watershed area
elevation
agriculture
evapotranspiration
precip long-term
clay
runoff
groundwater recharge
coarse
sat overland flow
topographic wetness
shrub
NEON region
organic carbon
stormwater from industrial
major discharge sites
sand
manure
silt
glacial till clayey
depth to bedrock
soil erodibility
baseflow index
wetland
glacial till coarse
saline lake sediment
surface connectivity
CAFO
glacial outwash coarse
streams density
grass
watershed:lake area ratio
shoreline dev factor
lake area
coastal zone coarse
alluvium coastal fine
stormwater from municipal
carbonate residual
LK_RSVR
mines heavy metal
Factors
Importance score
0
5
10
15
20
Boruta decision
Confirmed
Rejected


b) HCO3-
depth to bedrock
runoff
clay
groundwater recharge
precip long-term
temperature long-term
organic carbon
forest
NEON region
elevation
agriculture
snowpack
coarse
sand
sat overland flow
baseflow index
soil erodibility
streams density
evapotranspiration
topographic wetness
wetland
silt
shrub
glacial outwash coarse
glacial till coarse
road density HU12
grass
developed
manure
surface connectivity
watershed area
roads 500m buff
watershed:lake area ratio
alluvium coastal fine
lake area
shoreline dev factor
glacial till clayey
LK_RSVR
stormwater from industrial
major discharge sites
carbonate residual
coastal zone coarse
CAFO
mines heavy metal
stormwater from municipal
saline lake sediment
Factors
Importance score
0
5
10
15
20
Boruta decision
Confirmed
Rejected

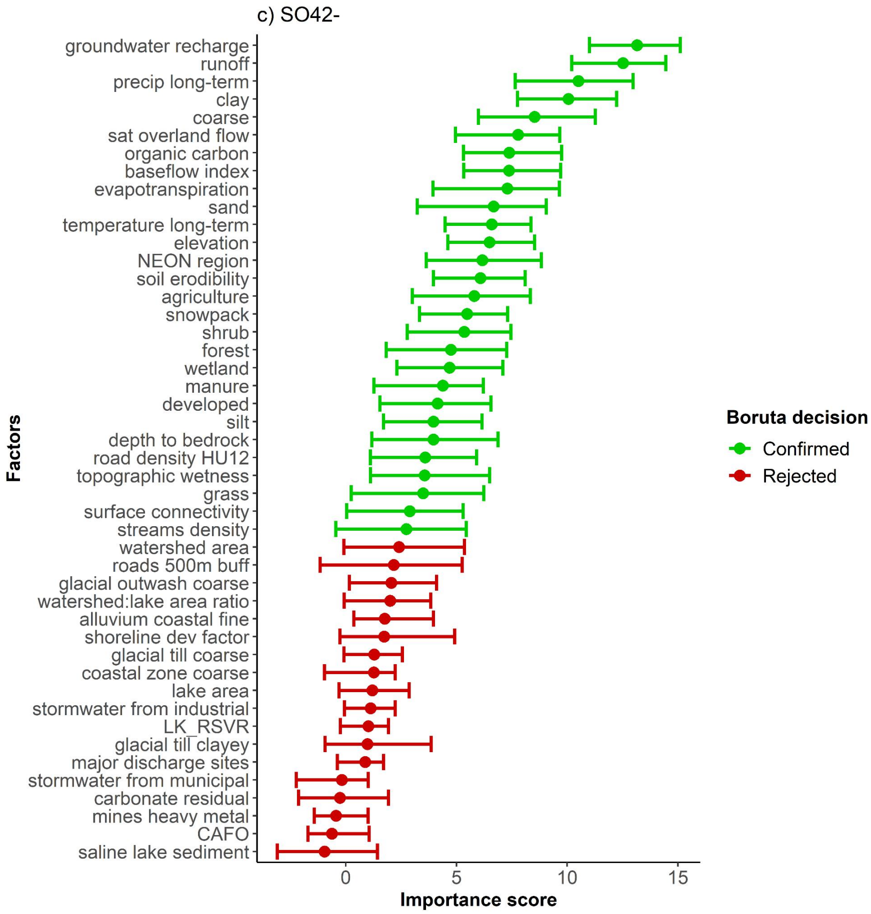


Figure S8. Importance scores from Boruta feature selection for the three anions: Cl^- (a), HCO_3^- (b), and $SO4^{2-}$ (c). Green dots and bars indicate that the factors were identified as ‘important’ by Boruta and red dots and bars indicate that Boruta rejected the factors. Dots are the mean Boruta 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).

Kursa, M. B., A. Jankowski, and W. R. Rudnicki. 2010. Boruta—A system for feature selection. Fundam. Inform. 101: 271–285. doi:10.3233/FI-2010-288

Supplementary Tables

Paper title: Natural and human drivers of specific conductance and major ion composition in United States lakes

Authors: Xinyu Sun, Kendra Spence Cheruvelil, Patrick J. Hanly, Katherine E. Webster, & Patricia A. Soranno

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

Factors name in figure	Factors original name	Spatial scale of measurement	Group	Natural Human	Data sources	Explanation	Transformation in RF
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 activity	H	LAGOS-US GEO	Road density in 500 m buffer around the shoreline of a LAGOS-US lake polygon	natural log
temperature long-	NA, calculated	HU12	climate	N	LAGOS-US	Long-term average air temperature	NA

term					GEO	data (5 years before sampling year)	
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_heavymetal_n	HU12	human activity	H	LAGOS-US GEO	Count of heavy metal mines active in 2003 within the zone	natural log
CAFO	value.npdes_cafo_n	HU12	human activity	H	LAGOS-US GEO	Count of concentrated animal feed operations within the zone	natural log
major discharge sites	value.npdes_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 GEO	Mean topographic wetness index of cells within the zone	natural log
watershed area	ws_area_ha	watershed	lake and	N	LAGOS-US	Area of zone polygon	natural log

			watershed		LOCUS		
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. Converting factors applied to convert major ion concentrations from mg/L to ueq/L and to calculate SC. Converting factors were extracted from Hem (1985).

Ions	Converting factor (from mg/L to ueq/L)	Converting 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 CaCO3)	19.98	(as HCO_3^-) 43

Hem, J.D. 1985. Study and Interpretation of the Chemical Characteristics of Natural Water. U.S. Geological Survey, Water Supply Paper 2254. Retrieved from https://pubs.usgs.gov/wsp/wsp2254/html/pdf.html

Table S3. Multinomial coefficients from a GLMNET model predicting ion composition cluster assignment. C1-C15 indicate ion clusters. Groups indicate natural and human factor categories.

Factors	Group	N_H	C1	C10	C11	C12	C13	C14	C15	C2	C3	C4	C5	C6	C7	C8	C9
drainage	surface connectivity	N	0.16	-0.21	-0.67	0.14	-0.47	0.47	0.25	0.10	0.52	-0.31	-0.11	-0.17	0.37	-0.51	0.45
headwater	surface connectivity	N	-0.88	0.47	-0.81	0.07	-0.24	-0.05	-0.27	0.66	-0.16	-0.01	-0.15	0.72	0.08	-0.11	0.68
terminal	surface connectivity	N	-0.07	-0.42	-0.20	-0.40	0.03	0.51	-0.40	0.23	-0.76	0.50	-0.22	-0.12	0.37	1.08	-0.15
elevation	location	N	-0.61	-0.49	0.45	-0.08	-0.32	-0.25	0.37	0.04	-0.33	0.70	0.14	0.15	-0.03	-0.03	0.29
shoreline dev factor	lake and watershed	N	0.33	0.12	-0.10	-0.25	-0.04	-0.07	-0.33	-0.01	0.05	0.02	-0.05	0.07	-0.02	0.15	0.14
lake area	lake and watershed	N	-0.07	-0.04	-0.27	0.07	-0.08	0.17	-0.21	0.06	0.01	-0.26	-0.08	0.30	0.12	0.13	0.17
manure	human activity	H	-0.20	0.13	0.12	-0.23	-0.13	0.27	0.13	-0.18	0.27	-0.12	-0.29	-0.18	0.07	0.13	0.21
evapotranspirat ion	climate	N	0.05	0.07	0.06	-0.05	0.15	-0.05	-0.21	0.11	0.11	0.03	0.00	-0.11	0.19	-0.10	-0.27

snowpack	climate	N	-0.06	-0.06	-0.05	-0.05	0.18	-0.13	0.15	0.05	-0.10	0.06	0.09	-0.01	0.05	-0.05	-0.08
NEON region	location	N	0.00	-0.03	0.10	0.07	0.01	0.02	0.09	-0.01	0.01	-0.07	-0.05	-0.02	-0.04	-0.04	-0.05
precip long-term	climate	N	0.43	0.00	0.73	-0.18	0.04	-0.07	0.51	-0.47	-0.05	0.60	-0.51	-0.44	0.54	-0.70	-0.43
road density 500m buff	human activity	H	0.50	0.48	-0.40	-0.30	-0.40	0.22	-0.32	-0.62	0.26	-0.78	-0.01	0.53	0.21	0.09	0.55
temperature long-term	climate	N	-0.02	0.14	0.13	-0.34	-0.32	-0.10	0.34	-0.36	0.10	-0.29	-0.12	0.57	0.23	-0.51	0.57
baseflow index	hydrology	N	-0.08	-0.27	0.42	0.22	0.17	0.02	0.39	-0.60	0.36	-0.14	-0.28	-0.03	0.04	-0.34	0.10
groundwater recharge	hydrology	N	0.19	-0.23	0.10	-0.06	0.19	0.07	0.32	0.09	-0.14	0.19	-0.11	-0.30	0.27	-0.46	-0.12
alluvium coastal fine	lithology	N	-0.18	0.15	-0.16	-0.29	0.35	-0.03	0.46	-0.18	-0.17	0.00	-0.26	0.28	0.14	-0.10	-0.01
carbonate residual	lithology	N	-0.03	-0.02	-0.04	0.02	0.15	0.10	0.07	0.03	0.08	-0.03	-0.12	-0.12	-0.06	-0.05	0.03
coastal zone coarse	lithology	N	0.24	0.24	-0.04	-0.01	0.00	-0.15	-0.10	-0.02	-0.07	0.00	0.00	0.00	-0.01	0.00	-0.07

glacial outwash coarse	lithology	N	0.15	-0.13	0.01	0.03	0.06	-0.11	-0.04	0.04	0.09	-0.03	-0.11	-0.06	-0.08	-0.11	0.28
glacial till clayey	lithology	N	0.05	0.01	-0.06	-0.10	0.18	-0.12	0.02	-0.06	-0.01	0.00	-0.14	0.36	-0.17	-0.15	0.19
glacial till coarse	lithology	N	0.24	0.18	-0.12	-0.10	-0.24	-0.05	-0.22	0.04	-0.25	-0.03	0.26	-0.01	0.29	0.08	-0.06
saline lake sediment	lithology	N	0.00	0.04	0.12	-0.04	-0.02	-0.06	-0.06	-0.06	0.06	-0.03	-0.09	0.20	-0.01	0.00	-0.05
major discharge sites	human activity	H	0.01	0.00	-0.05	-0.04	-0.05	-0.08	0.01	-0.06	0.04	0.01	-0.15	0.27	-0.03	0.05	0.08
stormwater from industrial	human activity	H	0.14	-0.02	-0.06	-0.04	-0.03	0.20	0.02	-0.06	-0.06	0.12	-0.07	-0.14	-0.11	-0.01	0.11
stormwater from municipal	human activity	H	-0.05	0.01	0.00	0.00	0.00	0.09	-0.03	0.00	0.18	0.00	0.00	-0.10	-0.06	0.08	-0.10
road density HU12	human activity	H	0.32	-0.04	-0.19	-0.21	-0.53	-0.04	0.15	-0.28	-0.21	0.10	0.00	0.81	-0.03	-0.14	0.29
runoff	terrain	N	0.35	-0.14	0.05	-0.24	0.29	0.13	0.20	0.33	-0.05	0.37	-0.19	-0.58	0.40	-0.60	-0.32
sat overland flow	terrain	N	0.23	0.08	0.31	-0.15	-0.13	0.37	-0.09	0.37	-0.32	-0.16	-0.33	-0.02	0.43	-0.43	-0.16

clay	soil	N	-0.47	-0.67	-0.89	0.57	-0.21	0.20	0.01	-0.57	0.56	-1.11	0.23	0.86	0.13	0.64	0.72
coarse	soil	N	-0.22	-0.13	0.19	-0.08	0.46	0.06	-0.01	0.62	-0.42	0.35	-0.12	-0.05	0.08	-0.41	-0.32
depth to bedrock	soil	N	-0.03	0.00	-0.08	0.50	0.23	-0.16	-0.11	-0.35	-0.05	-0.22	0.49	0.12	-0.37	0.17	-0.14
soil erodibility	soil	N	0.12	0.30	-0.13	-0.19	0.07	0.22	0.13	-0.29	-0.06	-0.24	0.09	0.06	-0.06	0.06	-0.09
organic carbon	soil	N	0.55	0.28	-0.10	0.02	0.15	-0.05	-0.02	0.02	-0.20	0.17	-0.44	-0.33	-0.24	-0.08	0.27
sand	soil	N	0.13	0.23	0.27	0.00	-0.28	-0.01	0.16	0.05	0.00	0.09	-0.57	0.01	0.32	-0.20	-0.20
silt	soil	N	-0.11	-0.14	0.00	-0.12	0.18	0.00	-0.08	0.01	0.16	0.01	0.04	-0.01	-0.07	0.12	0.00
streams density	hydrology	N	-0.03	0.14	-0.15	-0.08	-0.30	0.01	-0.20	0.18	-0.05	-0.12	0.22	0.10	-0.09	0.00	0.36
topographic wetness	terrain	N	-0.04	-0.16	0.08	0.40	-0.15	-0.10	0.14	-0.33	-0.08	-0.37	-0.30	0.23	0.17	0.35	0.17
watershed area	lake and watershed	N	-0.03	0.18	-0.13	-0.09	0.04	0.02	-0.11	-0.04	0.01	-0.25	-0.04	0.25	0.00	0.11	0.10
watershed:lake area ratio	lake and watershed	N	0.01	0.17	0.02	-0.10	0.07	-0.06	0.01	-0.06	0.00	-0.09	0.00	0.07	-0.06	0.03	0.00

agriculture	LU/LC	H	-0.17	0.29	0.11	0.17	-0.12	-0.18	0.13	-0.33	0.38	-0.11	-0.21	0.09	-0.57	0.21	0.31
grass	LU/LC	H	0.04	-0.16	-0.06	-0.20	0.00	0.09	-0.07	0.06	-0.07	0.12	0.07	0.11	0.10	0.04	-0.10
shrub	LU/LC	H	-0.03	0.40	0.14	0.02	-0.04	0.13	-0.07	-0.11	-0.23	0.14	-0.01	-0.05	0.00	-0.13	-0.16
developed	LU/LC	H	0.02	0.31	-0.15	-0.08	-0.06	0.13	-0.06	-0.24	-0.10	-0.21	-0.23	0.28	0.03	0.08	0.26
forest	LU/LC	H	-0.03	-0.70	0.26	0.20	0.50	-0.02	0.45	0.24	-0.08	0.15	0.04	-0.46	0.53	-0.34	-0.72
wetland	LU/LC	H	0.03	-0.08	-0.10	0.11	-0.13	0.02	0.07	0.00	0.00	-0.12	0.06	-0.02	0.00	0.02	0.14

Table S4. A table showing the number of lakes in each surface connectivity class within each cluster.

Cluster	Isolated	Headwater	Drainage	Terminal	Total
4	8	17	34	3	62
11	12	2	12	1	27
2	6	17	60	3	86
7	7	12	84	1	104
15	13	6	43	1	63
14	11	8	118	4	141
1	4	0	23	0	27
13	7	4	16	1	28
10	18	11	80	1	110
12	8	2	10	0	20
3	31	10	145	1	187
5	12	2	52	3	69
9	14	12	125	3	154
6	10	5	23	3	41
8	34	4	44	17	99
Total	195	112	869	42	1218

Table S5. 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