LIMNOLOGY
and
OCEANOGRAPHY

ASLO

Limnol. Oceanogr. 9999, 2025, 1–18

doi: 10.1002/lno.12817

RESEARCH ARTICLE

Lake chlorophyll responses to drought are related to lake type, connectivity, and ecological context across the conterminous United States

Xinyu Sun,[1*] **Kendra S. Cheruvelil**,[1,2] **Patrick J. Hanly**,[1] **Patricia A. Soranno**[1,3]
[1]Department of Fisheries and Wildlife, Michigan State University, East Lansing, Michigan, USA; [2]Lyman Briggs College, Michigan State University, East Lansing, Michigan, USA; [3]Department of Integrative Biology, Michigan State University, East Lansing, Michigan, USA

Abstract

Local and regional-scaled studies point to the important role of lake type (natural lakes vs. reservoirs), surface water connectivity, and ecological context (multi-scaled natural settings and human factors) in mediating lake responses to disturbances like drought. However, we lack an understanding at the macroscale that incorporates multiple scales (lake, watershed, region) and a variety of ecological contexts. Therefore, we used data from the LAGOS-US research platform and applied a local water year timeframe to 62,927 US natural lakes and reservoirs across 17 ecoregions to examine how chlorophyll *a* responds to drought across various ecological contexts. We evaluated chlorophyll *a* changes relative to each lake's baseline and drought year. Drought led to lower and higher chlorophyll *a* in 18% and 20%, respectively, of lakes (both natural lakes and reservoirs included). Natural lakes had higher magnitudes of change and probabilities of increasing chlorophyll *a* during droughts than reservoirs, and these differences were particularly pronounced in isolated and highly-connected lakes. Drought responses were also related to long-term average lake chlorophyll *a* in complex ways, with a positive correlation in less productive lakes and a negative correlation in more productive lakes, and more pronounced drought responses in higher-productivity lakes than lower-productivity lakes. Thus, lake chlorophyll responses to drought are related to interactions between lake type and surface connectivity, long-term average chlorophyll *a*, and many other multi-scaled ecological factors (e.g., soil erodibility, minimum air temperature). These results reinforce the importance of integrating multi-scaled ecological context to determine and predict the impacts of global changes on lakes.

Lakes have been termed *sentinels of climate change* because of their wide geographical distribution, high sensitivity to change, and ability to integrate and reflect the dynamics of their catchments and the atmosphere (Pham et al. 2008; Adrian et al. 2009). They can be used to study responses to a range of climate changes, from long-term, gradual warming to extreme events such as droughts and floods (Havens and Jeppesen 2018). However, quantifying the effects of climate change on lakes is complicated because of the many multi-scaled disturbances that affect lakes. Additionally, the ecological context, which is the hydrologic, geologic, land use, and climatic setting of lakes, is also structured at multiple spatial scales (i.e., lake, watershed, region) and plays a role in how lakes respond to climate change (Read et al. 2015; McCullough et al. 2019). In fact, lake responses to disturbance can be related to characteristics of the lake (e.g., lake morphometry), watershed (e.g., land use), region (e.g., climate) (Pham et al. 2008; Read et al. 2015; Farrell et al. 2020), as well as cross-scale interactions among them (e.g., Soranno et al. 2014; Taranu et al. 2015). Thus, to understand and

---

*Correspondence: 16xs6@queensu.ca; sunxiny9@msu.edu

Associate editor: Marie-Elodie Perga

Data Availability Statement: Local water year data and code have been uploaded to the Environmental Data Initiative (EDI) data portal and are available from: https://portal.edirepository.org/nis/mapbrowse?packageid=edi.1547.2. The methods for creating local water year are described in a preprint that can be found on EarthArXiv https://doi.org/10.31223/X5Q121. Data for drought responses and predictors have been uploaded to Zenodo and are available from: https://doi.org/10.5281/zenodo.11244005.

predict lake responses to climate change, we need macroscale studies that incorporate multi-scale natural and human factors.

Although drought has become more frequent and intensified in many regions globally due to climate change (e.g., Easterling et al. 2000; Prein et al. 2016; Oikonomou et al. 2020), we lack an understanding of its potential effects on lakes at macroscales. Meteorological droughts, usually characterized by the combination of decreased precipitation and increased air temperature (Van Loon et al. 2016), can influence lake ecosystem functioning through decreased water levels and increased evaporation. These changes can lead to concentrated nutrients, increases in pollutant concentration, and alterations to biogeochemical processes (Jeppesen et al. 2015; Vicente-Serrano et al. 2020). Algal biomass (often measured as chlorophyll *a*) sometimes increases in response to drought, potentially caused by elevated nutrient concentrations and a shift in phytoplankton community composition toward more toxin-producing cyanobacteria that can further degrade water quality (Oliveira et al. 2019). However, these changes are not universal, and multi-scale ecological context can play a crucial role in determining the magnitude and even direction of changes (Mosley 2015). A global review by Mosley (2015) suggested that although most studies reported increases in lake algal biomass during droughts, some observed declines. For instance, phytoplankton biomass decreased in a shallow lake in semi-arid Brazil during a drought despite a higher nutrient concentration, which was due to the sediment resuspension promoted by water-level reduction that decreased light availability (Da Costa, Attayde, and Becker 2016). Moreover, in lakes that receive large nutrient inputs from watersheds, droughts could cause declines in nutrients and algal biomass due to reduced riverine inflows (Jeppesen et al. 2015). Such inconsistencies in responses reveal the importance of considering multi-scaled factors to understand and forecast the impacts of droughts on lakes at macroscales.

One challenge in developing a deeper understanding of macroscale climate change impacts on lakes is the lack of consideration of *lake type* in past studies. Lake type refers to the origin of the lake, whether it be natural or human-made (i.e., reservoirs), and it is likely to affect lake drought responses (Fergus et al. 2020). Reservoirs are abundant and provide essential ecosystem services for human well-being, but they are also different from natural lakes (Hayes et al. 2017; Rodriguez et al. 2023). For example, reservoirs tend to have higher surface water temperatures (Thornton, Kimmel, and Payne 1990), greater catchment-to-surface area ratio (Doubek and Carey 2017), and shorter water residence time (Beaulieu, Pick, and Gregory-Eaves 2013) than natural lakes. These lake type differences can influence the transport and transformation of energy (e.g., irradiance and heat) and mass (e.g., water, solutes, particles) through the landscape and within waterbodies, resulting in divergent lake chemistry (e.g., nutrient levels) and biota (e.g., productivity) as well as responses to changes (Beaulieu, Pick, and Gregory-Eaves 2013; Hayes et al. 2017; Fergus et al. 2021). Unfortunately, reservoirs are studied far less than natural lakes and we lack a comprehensive understanding of the ecological context of reservoirs (Rodriguez et al. 2023).

There is little consensus on whether and how to integrate lake type into climate change studies. Some existing conceptual frameworks about lake responses to climate change assume that natural lakes and reservoirs share similar responses, thus not considering their differences (e.g., Williamson et al. 2009). In contrast, Hayes et al. (2017) argued that drought effects would differ between lake types as they have distinct catchment and management characteristics. Perhaps because of these potential differences in responses, reservoirs are sometimes excluded from climate change studies (e.g., Adrian et al. 2009). However, since $\sim 46\%$ of lakes ≥ 4 ha in the conterminous United States are reservoirs (Rodriguez et al. 2023), this approach would ignore large numbers of water bodies at continental scales.

Another factor that likely affects lake responses to drought is lake surface water connectivity. Both natural lakes and reservoirs are connected to streams and other lakes via a range of different surface water connections (Fergus et al. 2017; Hu et al. 2017), from entirely isolated natural lakes and reservoirs to natural lakes with both inflow and outflow and run-of-the-river reservoirs (Rodriguez et al. 2023). For example, many lakes receive surface inflow from upstream lakes that can serve as persistent sources of freshwater and/or nutrient supply during droughts, which may alleviate drought impacts on water levels, water quality, and productivity (Spence et al. 2019). On the other hand, lakes without surface inflow may be more sensitive to droughts due to a lack of surface water supply (Webster et al. 2000; Cobbaert, Wong, and Bayley 2015). However, few studies have considered how surface water connectivity may affect lake responses to climate change (Fergus et al. 2017).

Large differences in climate conditions across a continent with different seasonalities also poses challenges for macroscale understanding of drought effects on lakes. Traditionally, the effects of droughts on aquatic systems have been analyzed based on a calendar year (i.e., January–December), which cannot fully capture the asynchrony between precipitation and water fluxes (Vasas et al. 2010; Yang et al. 2016; Kamps and Heilman 2018). A timeframe that takes into account both timing of surface flow and lag effects, such as water year (also called hydrological year), may be more appropriate than the calendar year for understanding lake responses to drought. In the United States, the duration of a water year is standardized from October 1 to September 30 (U.S. Geological Survey 2024). A drawback of this standard is that regional variations in flow seasonality are not considered, which hinders the accuracy and relevance of the water year to continental-scale research (Wasko, Nathan, and Peel 2020). To account for regional discrepancies, Wasko, Nathan, and Peel (2020) used a global study to illustrate that the water year period varies both across and within countries, including the United States, and proposed a local definition of the water year (i.e., local water year, LWY) whereby the LWY of each site is defined as the 12-month period starting from the month with the lowest local streamflow.

In our study, we aim to build an understanding of how natural lakes and reservoirs across the conterminous United States respond to drought. We asked two questions: (1) Do natural lakes and reservoirs differ in their lake chlorophyll *a* responses to drought, and how does surface water connectivity influence the response?; and (2) Which multi-scaled ecological context variables at the lake, watershed, and region scales affect natural lake and reservoir (hereafter, collectively referred to as lake) chlorophyll *a* drought responses? To answer these questions, we applied a LWY for 62,927 lakes ≥ 4 ha across the United States, used lake chlorophyll *a* concentration as the measure of lake productivity for the 10 yr of 2009–2018, and quantified the difference in lake chlorophyll *a* between the maximum drought year and the baseline year to characterize response to drought. To our knowledge, this is the first study that examines the effects of connectivity and lake type on lake chlorophyll *a* drought responses and quantifies the influences of multi-scale natural and human factors on those responses at the continental scale.

Materials and procedures

Study lakes and data sources

The data used in this study were from the LAGOS-US research-ready, open-access platform (Cheruvelil et al. 2021) that includes lake and ecological context data for 479,950 lakes ≥ 1 ha across the conterminous United States. We obtained lake type (natural lake or reservoir) from the LAGOS-US RESERVOIR module that used a machine vision model (ResNet model) trained on lake shapefiles and manual identifications to predict the classification of 137,465 lakes ≥ 4 ha (Polus et al. 2022; Rodriguez et al. 2023). Although validation procedures were conducted on the lake-type classification (about 81% accuracy), the classification includes 7% of natural lakes with a flag for being less than 50 m from a dam (Rodriguez et al. 2023). Additionally, lake types are likely more complex than binary natural lakes and reservoirs. Therefore, we further refined lakes into sub-categories that take into account the critical role that surface water connectivity plays in shaping lakes' ecological context (e.g., Hu et al. 2017). We refined the lake type classification by combining it with four surface water connectivity classes that range from least to most connected (i.e., isolated, headwater, drainage, and drainage-lake [drainageLK]; Fig. S1) from the LAGOS-US LOCUS module (Smith et al. 2021), excluding terminal and terminal-lake classes due to extremely low sample sizes (1823 and 379, respectively). The isolated lakes lack both inflows and outflows, headwater lakes have an outflow but no inflow, drainage lakes have both inflow and outflow and are not connected with an upstream lake that is greater than 10 ha, and drainageLK lakes have both inflow and outflow and are connected with an upstream lake that is greater than 10 ha.

Satellite-inferred chlorophyll *a* concentration data were obtained from the LAGOS-US LANDSAT module (Hanly, Webster, and Soranno 2024a, 2024b). The LANDSAT module used random forest regression model to predict chlorophyll *a* using more than 47 million Landsat 5, 7, and 8 lake and scene combinations from 1984 to 2020 based on 43,755 same-day matchups between in situ sampled chlorophyll *a* from LAGOS-US LIMNO module (Shuvo et al. 2023) and whole-lake surface reflectance retrievals (Hanly, Webster, and Soranno 2024a, 2024b). We extracted all lake-specific chlorophyll *a* data from 2009 to 2018, processed it, and used it in two ways (described below): (1) as lake-specific chlorophyll *a* used for calculating lake responses to drought and (2) as 10-yr average chlorophyll *a* to characterize each lake's long-term average productivity.

To further investigate how drought responses were influenced by multi-scale ecological contexts, we acquired lake location (e.g., latitude and longitude) and morphometric (e.g., lake surface area and elevation) information from the LAGOS-US LOCUS module (Smith et al. 2021) and natural and human factors (e.g., air temperature, hydrology, soil features, and land use) from the LAGOS-US GEO module (Smith et al. 2022). We also incorporated the 17 National Ecological Observatory Network (NEON) regions, which are relatively large (213,800–770,995 km^2) ecoregions in the United States that primarily rely on climate as the basis for classification (Hargrove and Hoffman 1999), as a regional factor. Finally, we used the maximum depth of lakes from the LAGOS-US DEPTH module (Stachelek et al. 2021). We removed highly correlated and redundant variables, resulting in 33 variables (*see* Table S1 for a full list of variables with descriptions).

Local water year and drought index

We quantified drought for 479,950 study lakes across the United States from 2009 to 2018 using an LWY drought index. The LWY timeframe was obtained from Sun and Cheruvelil (2024a, 2024b), which built on the definition proposed by Wasko, Nathan, and Peel (2020) and applied a spatial interpolation method to construct a continental-scale LWY timeframe. We assigned a single LWY to each of the 202 4-digit hydrologic unit (HU4) regions in the conterminous United States that range from 4384 to 134,755 km^2 in area (Seaber, Kapinos, and Knapp 1987), whereby all lakes in each HU4 had the same LWY timeframe. Each LWY is a 12-month period starting from the lowest streamflow month and is named by the calendar year in which it ends (Fig. 1; Sun and Cheruvelil 2024a, 2024b).

We quantified annual lake-specific drought conditions. To do so, we used the Standardized Precipitation Index (SPI), which has been widely used to characterize meteorological drought at various timescales (Guttman 1999; Hayes

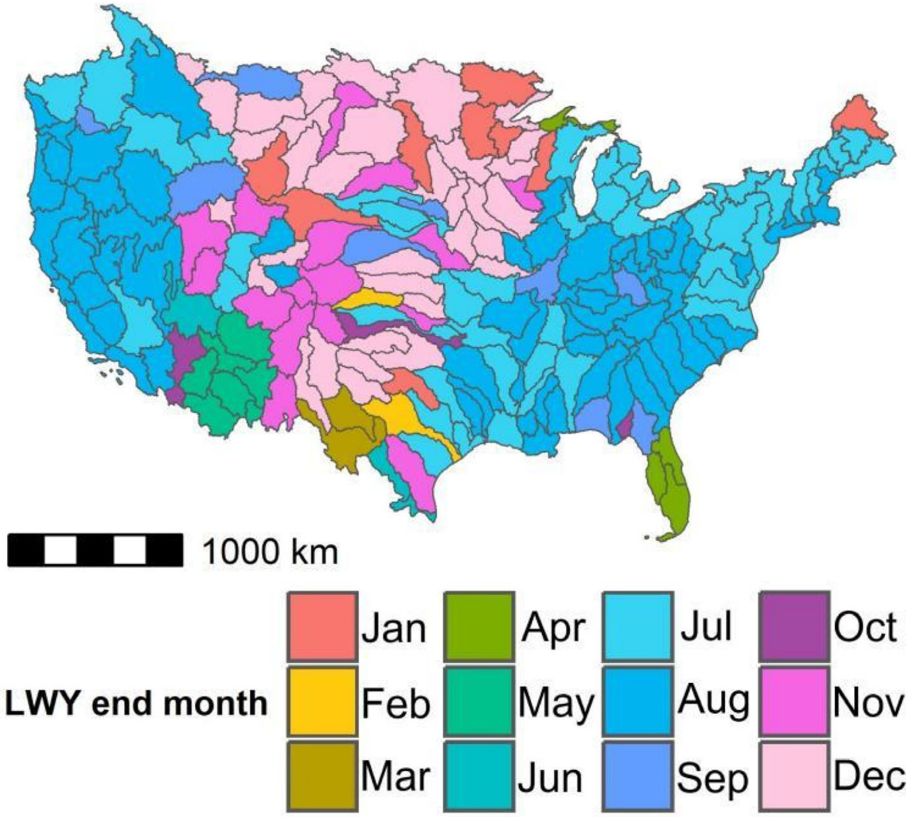


Fig. 1. Map showing the end month of the LWY of each HU4 area. Each color represents a month. This map was adapted from Sun and Cheruvelil (2024b); https://eartharxiv.org/repository/view/7174/. LWY, local water year; HU4, 4-digit hydrologic unit.

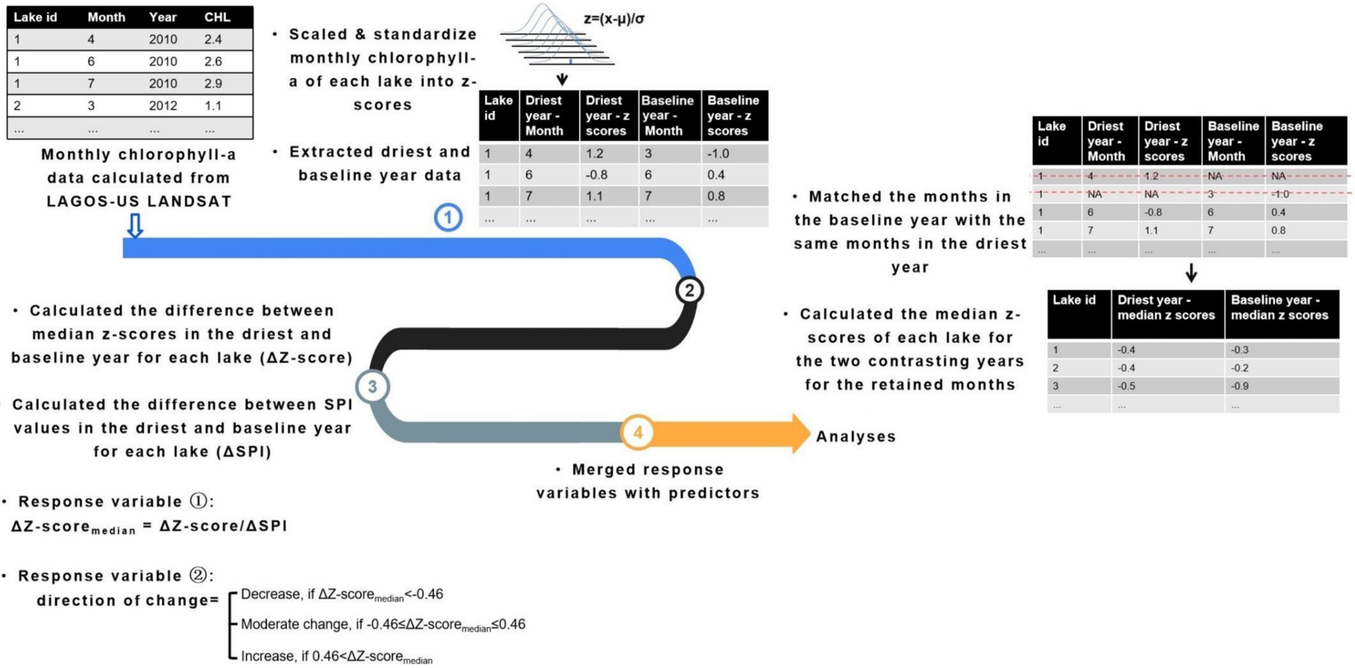
et al. 2011; Ford, Chen, and Schoof 2021). Precipitation data is the only input parameter for the SPI, which is available monthly for each lake at the fine-scale hydrologic areas in the United States (12-digit hydrologic unit, HU12 (Seaber, Kapinos, and Knapp 1987); 54,263 areas that range from 38 to 161 km^2, with 1–564 lakes in each HU12) in the LAGOS-US GEO module. We used a 12-month time scale to examine the medium to long-term drought effects because the duration of drought ranges from several weeks to consecutive months and even to years (Oikonomou et al. 2020; Wu et al. 2020). Monthly precipitation data from 1970 to 2018 were entered into the "SPEI" package (v 1.8.1, Beguería and Vicente-Serrano 2023) in R (v4.3.1, R Core Team 2023) to compute SPI values at the 12-month time-scale using the equation: $\text{SPI} = (P - P^*)/\sigma_\text{p}$, where P is the precipitation, P^* is the mean precipitation of the reference period, and σ_p is the standard deviation (SD) of the precipitation. We set 1970–2000 as the reference period for computation and quantified the precipitation conditions of the latest 10 yr in our dataset (2009–2018 LWY; Beguería and Vicente-Serrano 2023). Standardized Precipitation Index ranges from negative (precipitation is below the mean value of the reference period) to positive (precipitation is above the mean value of the reference period) values. Values between −0.5 and 0.5 were classified as the baseline "normal" condition, greater than 0.5 were "wet" conditions (i.e., more precipitation than baseline), and lower than −0.5 were "drought" conditions (Lloyd-Hughes and Saunders 2002).

Next, using these annual lake-specific LWY SPI values, we identified 2 yr for contrast, the "driest" and the "baseline" for each lake. The driest LWY among the 10-yr study period was the year with the lowest annual SPI value and the baseline LWY was the year with annual SPI closest to zero (i.e., closest to the mean historical precipitation amount for that lake). We further filtered the lakes to keep only lakes with driest year SPI values lower than −0.5 (i.e., true drought year; SPI mean $\pm$ SD $= -1.4 \pm 0.6$) and baseline year values within −0.5 and 0.5 (i.e., true baseline normal condition; SPI mean $\pm$ SD $= 0.01 \pm 0.2$). This filtering process reduced the sample size from 479,950 (all lakes with SPI values) to 406,953 (lakes with true drought and baseline years).

Data processing and analyses

Data processing and analyses were performed in R (R Core Team 2023). The pre-processing of our response variable, chlorophyll *a*, was as follows (Fig. 2). We started with lake-specific monthly average chlorophyll *a* data from 2009 to 2018 LWY. On average, study lakes had 9 ± 2 (SD) years of data, with 6 ± 3 months of data per year. Then, to account for variation among lakes, we scaled and standardized the lake-specific chlorophyll *a* data by converting monthly chlorophyll *a* values to *z*-scores using the formula: $z = (x - \mu)/\sigma$, whereby x is the monthly chlorophyll *a*, μ is the 10-yr average chlorophyll *a* of each individual lake, and σ is the SD. Next, we extracted the monthly *z*-scores for the driest LWY of each lake and the same month in the baseline LWY and, for lakes with multiple observations, calculated the median *z*-scores. Then, we subtracted the median *z*-score of the baseline year from that of the driest year to get median *z*-score difference: $\Delta Z\text{-score} = Z_{\text{dry}} - Z_{\text{base}} = [(x_{\text{dry}} - \mu)/\sigma] - [(x_{\text{base}} - \mu)/\sigma] = (x_{\text{dry}} - x_{\text{base}})/\sigma$, where Z_{dry} and Z_{base} are the median *z*-score of the driest and baseline year, respectively, and x_{dry} and x_{base} are the monthly chlorophyll *a* of each lake in those 2 yr. This step eliminated the 10-yr average chlorophyll *a* (i.e., μ) from the calculation of the response variable, allowing it to be used as a predictor variable later in the analyses. Finally, to take into account the influence of the magnitude of drought on chlorophyll *a* responses, we divided ΔZ-score by the difference between the driest and baseline year SPI values (ΔSPI) using the formula: $\Delta Z\text{-score}_{\text{median}} = \Delta Z\text{-score}/\Delta \text{SPI}$. The ΔZ-score$_{\text{median}}$ was used as the standardized median *z*-score changes for each lake. The absolute value of ΔZ-score$_{\text{median}}$ was used to represent the chlorophyll-based responsiveness of a lake to drought. We further categorized ΔZ-score$_{\text{median}}$ values to represent the directions of each lake's chlorophyll *a* response as: decrease, moderate change, and increase. We used ± 0.46 ΔZ-score$_{\text{median}}$ values (± 0.5 unit of SD for all the lakes; e.g., Zanchettin, Traverso, and Tomasino 2008; Jones et al. 2015; Anderson et al. 2023) as the threshold to define non-moderate changes (increase: above 0.46; decrease: below −0.46).

Pre-processing of natural and human factors included applying a generalized logit transformation to percent data and a natural log transformation to numeric data (Table S1). The 10-yr average chlorophyll *a* (an indication of long-term average lake productivity) was calculated for each lake, and annual mean, minimum, and maximum air temperatures were calculated for each HU12 region. Each ecological context variable was assigned a spatial scale (lake (e.g., 10-yr average chlorophyll *a*), watershed (e.g., soil erodibility), or region (e.g., annual minimum air temperature)), and watershed variables were further refined into three thematic sub-groups: soil (e.g., percent silt in the soil), water supply (e.g., baseflow index that indicates the contribution of groundwater discharge to streamflow), and land use/land cover (e.g., percent of watershed area classified as



Lake id	Month	Year	CHL
1	4	2010	2.4
1	6	2010	2.6
1	7	2010	2.9
2	3	2012	1.1
...	...	...	...

Monthly chlorophyll-a data calculated from LAGOS-US LANDSAT

- Scaled & standardize monthly chlorophyll-a of each lake into z-scores
- Extracted driest and baseline year data

Lake id	Driest year - Month	Driest year - z scores	Baseline year - Month	Baseline year - z scores
1	4	1.2	3	-1.0
1	6	-0.8	6	0.4
1	7	1.1	7	0.8
...	...	...	...	...

- Matched the months in the baseline year with the same months in the driest year

Lake id	Driest year - Month	Driest year - z scores	Baseline year - Month	Baseline year - z scores
~~1~~	~~4~~	~~1.2~~	~~NA~~	~~NA~~
~~1~~	~~NA~~	~~NA~~	~~3~~	~~-1.0~~
1	6	-0.8	6	0.4
1	7	1.1	7	0.8
...	...	...	...	...

- Calculated the median z-scores of each lake for the two contrasting years for the retained months

Lake id	Driest year - median z scores	Baseline year - median z scores
1	-0.4	-0.3
2	-0.4	-0.2
3	-0.5	-0.9
...	...	...

- Calculated the difference between median z-scores in the driest and baseline year for each lake (ΔZ-score)
- Calculated the difference between SPI values in the driest and baseline year for each lake (ΔSPI)
- Merged response variables with predictors
- Response variable ①: $\Delta Z\text{-score}_{\text{median}} = \Delta Z\text{-score}/\Delta \text{SPI}$
- Response variable ②: direction of change=
  - Decrease, if $\Delta Z\text{-score}_{\text{median}} < -0.46$
  - Moderate change, if $-0.46 \leq \Delta Z\text{-score}_{\text{median}} \leq 0.46$
  - Increase, if $0.46 < \Delta Z\text{-score}_{\text{median}}$

Fig. 2. Processing steps taken when calculating the response variable, lake chlorophyll *a* response to drought (ΔZ-score$_{\text{median}}$). We started with monthly chlorophyll *a* data from each lake's 2009–2018 local water year (LWY). (1) We scaled and standardized chlorophyll *a* data into *z*-scores for each lake and extracted the driest and baseline LWY *z*-scores for each lake. (2) We extracted the month in the baseline year and the same month in the driest year and, for lake-months with multiple measurements, we calculated the median *z*-score of each lake for the 2 contrasting years. (3) We calculated the difference between median *z*-score in the driest and baseline year for each lake (ΔZ-score) and calculated the difference between lake-specific drought values (SPI) in the driest and baseline year for each lake (ΔSPI). Using these, we computed the change in *z*-score per unit change in SPI values for each lake, which is our response variable (ΔZ-score$_{\text{median}}$). We also created a second response variable by categorizing ΔZ-score$_{\text{median}}$ values, representing the direction of each lake's chlorophyll *a* response: decrease, moderate change, and increase. (4) We merged these response variables with independent variables (i.e., predictors) for further analyses.

wetlands). The final dataset of complete predictors (excluding lake depth) and ΔZ-score$_{\text{median}}$ values contained 62,927 lakes (full dataset; 34,422 natural lakes and 28,505 reservoirs). Owing to the limnological importance but the sparsity of lake depth data and the difficulty associated with estimating lake depths (Taranu and Gregory-Eaves 2008; Oliver et al. 2016; Stachelek, Hanly, and Soranno 2022), we created a subset of the full dataset with maximum lake depth, which included 8994 lakes (depth data subset; 4820 natural lakes and 4174 reservoirs).

The full dataset was used to examine natural lake and reservoir responses to drought. A generalized linear model with the gamma distribution (log link function) was employed to examine relationships between the absolute value of ΔZ-score$_{\text{median}}$ and lake type and connectivity classes ("car" package, v3.1-2, Fox et al. 2023). The model included two categorical predictors, lake type (natural lake/reservoir) and connectivity class (ordinally ranked by connectivity), and an interaction term between them. A multinomial logistic regression model ("nnet" package, v7.3-19, Ripley and Venables 2023) on the categorical ΔZ-score$_{\text{median}}$ response (decrease, moderate change, and increase) was utilized to explore the relationships between the direction of chlorophyll *a* response to drought and lake type, connectivity class, and their interaction. Post hoc analyses were performed using Tukey's contrasts on generalized linear model and multinomial logistic regression model ("multcomp" package, v1.4-25, Hothorn et al. 2023; "lsmeans" package, v2.30-0, Lenth 2018).

The full dataset (33 independent variables) and the depth data subset (32 independent variables) were each used to investigate the effects of lake characteristics and multi-scaled ecological context factors on lake chlorophyll *a* responses to drought. We applied random forest ("randomForest" package, v4.7-1.1, Cutler and Wiener 2022) and Boruta feature selection ("Boruta" package, v8.0.0, Kursa and Rudnicki 2022) to four models identifying lake, watershed, and region factors that affect ΔZ-score$_{\text{median}}$ with either the ΔZ-score$_{\text{median}}$ values (continuous) or direction of response (categorical) as the response variable and either the full dataset or the depth data subset (Fig. S2). First, Boruta feature selections with a maximum of 1000 runs were performed to identify relevant predictor variables. All the predictor variables were selected by Boruta when using the full dataset, and one factor (connectivity fluctuates) was rejected when using the depth data subset. Second, we input data (response variable and Boruta-selected predictor variables [32 predictor variables for both the full dataset and the depth data subset]) to random forest models that used five-fold repeated cross-validation. The mean importance scores from Boruta and the percentage increase in mean squared error (i.e., %IncMSE) and decrease in impurity (i.e., Gini) from random forest were used to assess the importance of variables. The effects of the top variable of each spatial scale and sub-group (lake, soil, water supply, land use/land cover, and region) were assessed through partial dependence plots ("pdp" package, v0.8.1, Greenwell 2022) and two-sample Wilcoxon tests.

Results

Profile of study lakes

Across the United States, we observed spatial patterns in lake drought occurrences for 11 of the 17 NEON regions for the 2009–2018 period, but there was no clear pattern for baseline years (Fig. 3). For example, the driest years in the Northeast were LWY 2015 or 2016. For most lakes in the Mid-Atlantic, Southeast, Atlantic Neotropical, Ozarks Complex, Southern Plains, and southern Central Plains, LWY 2011 was the driest. Local water year 2012 was the driest for the Prairie Peninsula, southern Northern Plains, and northern Central Plains, while LWY 2017 was the driest for lakes in northern Northern Plains. Finally, the driest LWY in the Southern Rockies and Colorado Plateau was 2018, whereas LWY 2014 was the driest in the Pacific Southwest.

Across the United States, natural lakes and reservoirs were differ in surface connectivity and productivity. Although there were more natural lakes than reservoirs in our dataset, both lake types were abundant across the conterminous United States. However, the lake types were not equally common across the surface water connectivity classes: natural lakes were predominant in isolated and headwater classes and reservoirs were predominant in drainage and drainageLK classes (Fig. 4a). Note that although reservoirs without an inflowing stream are not included in many definitions of reservoirs, we included them in our study because Rodriguez et al. (2023) found that human-made systems exist as either isolated (no inflow and outflow) or headwater (only has outflow) waterbodies in the conterminous United States. Background chlorophyll *a* concentrations in reservoirs were higher than in natural lakes (median concentration = 8.7 and 8.0 μg L^{-1}, respectively; Wilcoxon test, $p < 0.001$). For both lake types, isolated and drainage lakes had the highest median chlorophyll *a* concentration (8.7 μg L^{-1}), whereas headwater lakes had the lowest median chlorophyll *a* (7.1 μg L^{-1}). When considering lake classification jointly with connectivity class, we found that the median chlorophyll *a* was highest in drainage reservoirs (9.1 μg L^{-1}) and lowest in headwater natural lakes (6.6 μg L^{-1}) (Fig. 4b; Table S2).

Lake-specific drought responses

Across all lakes, the SPI values of the baseline and driest LWYs were 0.01 ± 0.16 (mean ± SD) and -1.45 ± 0.67, respectively, and the average standardized lake drought response was an increase of 0.3 ± 5.8 μg L^{-1} chlorophyll *a* (ΔZ-score$_{\text{median}} = 0.05 \pm 0.92$; Fig. S3a). Using the 0.5 unit of SD value as the threshold, 17.8% and 20.5% of lakes showed decreases or increases in chlorophyll *a*, respectively, during drought (11,224 and 12,934 lakes, respectively), whereas

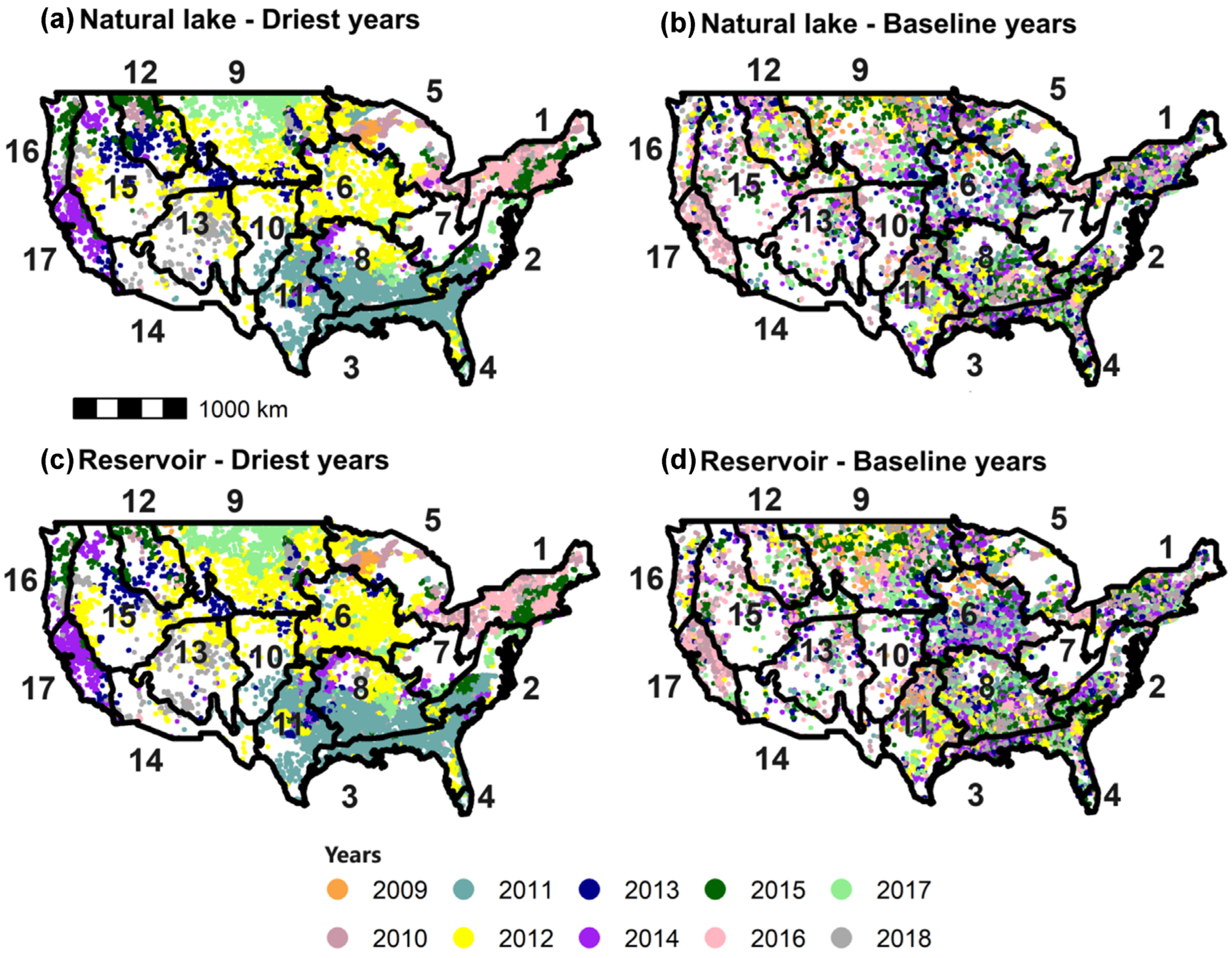


Fig. 3. Maps showing the driest and baseline years of natural lakes (**a** and **b**) and reservoirs (**c** and **d**) by NEON regions. Each dot represents a lake, and each color represents a year. (NEON ecoregions: 1 = Northeast, 2 = Mid-Atlantic, 3 = Southeast, 4 = Atlantic Neotropical, 5 = Great Lakes, 6 = Prairie Peninsula, 7 = Appalachians and Cumberland Plateau, 8 = Ozarks Complex, 9 = Northern Plains, 10 = Central Plains, 11 = Southern Plains, 12 = Northern Rockies, 13 = Southern Rockies and Colorado Plateau, 14 = Desert Southwest, 15 = Great Basin, 16 = Pacific Northwest, 17 = Pacific Southwest). NEON, National Ecological Observatory Network.

61.6% showed moderate changes ($-0.46 < \Delta Z\text{-score}_{\text{median}} < 0.46$, 38,769 lakes; Fig. 5).

We found that lake type and connectivity individually and interactively affected lake chlorophyll *a* responses to drought, measured by the absolute value of $\Delta Z\text{-score}_{\text{median}}$ (generalized linear model, $p \leq 0.001$; Fig. 6a; Table S3). Overall, natural lakes were more responsive to droughts than reservoirs (generalized linear model, $p < 0.001$). The magnitudes of change in response to drought were greater in natural lakes (0.59 ± 0.78 $\Delta Z\text{-score}_{\text{median}}$, $4.0 \pm 5.3\ \mu\text{g L}^{-1}$ chlorophyll *a* changes) than in reservoirs (0.50 ± 0.68 $\Delta Z\text{-score}_{\text{median}}$, $2.9 \pm 3.9\ \mu\text{g L}^{-1}$ chlorophyll *a* changes). The differences in the absolute value of $\Delta Z\text{-score}_{\text{median}}$ between lake types were particularly pronounced between isolated and the two classes of highly-connected lakes (drainage and drainageLK; Tukey, $p < 0.001$; Fig. 6a). Specifically, the standardized chlorophyll *a* changes (per unit change in SPI) were $0.8\ \mu\text{g L}^{-1}$ ($\Delta Z\text{-score}_{\text{median}} = 0.4$), $0.6\ \mu\text{g L}^{-1}$ (0.8), and $1.1\ \mu\text{g L}^{-1}$ (0.8) chlorophyll *a* higher in isolated, drainage, and drainageLK natural lakes than reservoirs of those same three connectivity classes, respectively. Moreover, isolated lakes, especially isolated natural lakes, were more responsive to drought ($5.0 \pm 6.6\ \mu\text{g L}^{-1}$ chlorophyll *a* changes) than natural lakes and reservoirs of other connectivity classes (Tukey, $p < 0.001$).

We also found that the directions of lake response to drought (decrease, moderate change, and increase) differed by lake type, connectivity class, and sometimes interactively (multinomial logistic regression model, $p < 0.001$; Fig. 6b,c; Table S3). For example, natural lakes were more likely to have increased chlorophyll *a* in response to drought than reservoirs (multinomial logistic regression model, $p < 0.001$), but there

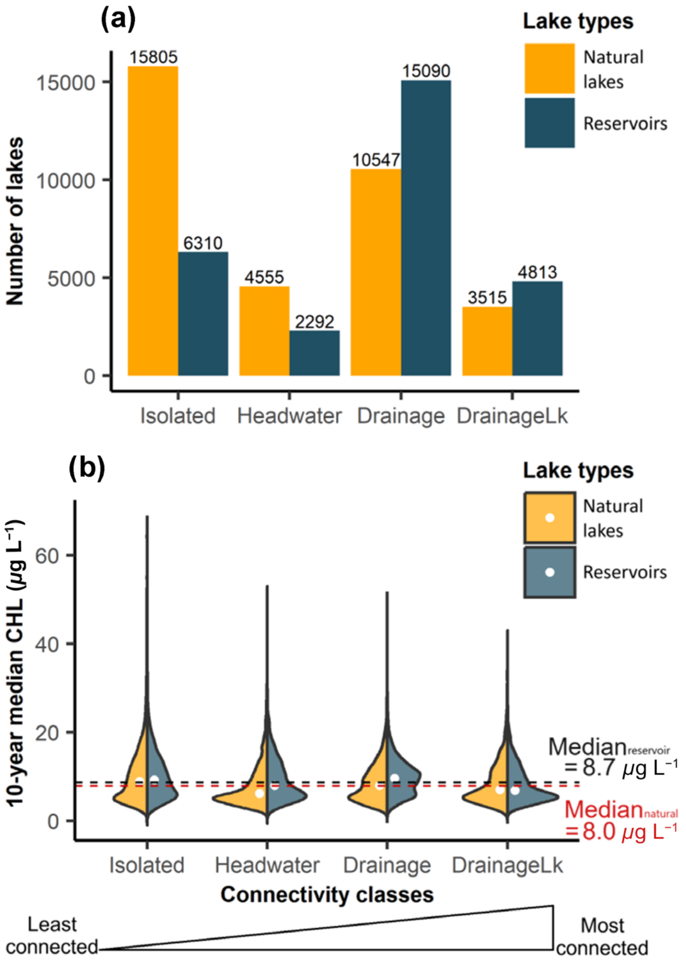


Fig. 4. Bar and violin plots showing the number of lakes in each lake type (natural lake and reservoir) and surface connectivity class (**a**) and 10-yr median lake chlorophyll *a* (**b**). Above each bar in plot (a) are the numbers of lakes. In plot (b), the red and black dashed lines indicate the median chlorophyll *a* (CHL) values of natural lakes and reservoirs, respectively, and white dots represent median values for each lake type and connectivity class combination. Lake types are ranked from the least to most connected based on the number of streams and upstream lakes (Fig. S1).

was no difference in the probability of a decreased chlorophyll *a* ($p = 0.113$) between the two lake types. Isolated natural lakes (24%) and drainageLK natural lakes (20%) had the highest probabilities of having increased and decreased chlorophyll *a* during drought, respectively; and drainageLK reservoirs had the lowest probabilities of having both increased (16%) and decreased (15%) chlorophyll *a* during drought. With the exception of drainageLK natural lakes, the probabilities of changing chlorophyll *a* decreased with increasing surface connectivity.

Multi-scaled ecological context effects on drought responses

Continuous lake drought response and full dataset

We found that 12% of the out-of-bag variance in ΔZ-score$_{\text{median}}$ was explained in the random forest using the full dataset ($n = 62{,}927$ lakes). The 10-yr average chlorophyll *a* concentration (long-term average productivity) was the most important variable, followed by soil erodibility and annual minimum air temperature (Figs. 7a, S4). Although the effect of lake type and connectivity classes on drought responses was confirmed by the Boruta feature selection algorithm for both the regression and classification models, they were not among the top explanatory variables.

Our examination of the effects of the top variables within each spatial scale and sub-group (10-yr average lake chlorophyll *a*, watershed soil erodibility, topographic wetness, and wetlands, regional minimum air temperature) on the continuous lake drought response found that lake drought responses and 10-yr average chlorophyll *a* had a positive relationship until about 25 μg L^{-1} chlorophyll *a*, beyond which the relationship became negative (Fig. 7b). Although initially relatively consistent, when erodibility of watershed soil became higher than about 1.5, there was a strong positive association between soil erodibility and drought responses (Fig. 7c). The partial dependence plot curves were close to positive linear for topographic wetness (Fig. 7d) and percent wetland in the watershed (Fig. 7e). Finally, as regional minimum air temperature increased, the relationships changed from positive (until about −22°C), to negative (until about −19°C; Fig. 7f). However, there was another breakpoint at about −15°C, whereby the relationship between temperature and drought responses switched from positive to negative once the minimum temperature was warmer than −15°C.

Categorical lake drought response and full dataset

The classification random forest model of the direction of change had 96% accuracy in correctly assigning lakes to response categories (i.e., decrease, moderate change, or increase in chlorophyll *a* in response to drought). All lakes with decreased- and increased-chlorophyll *a* responses were correctly classified, while about 4% of lakes with moderate change were misclassified, with there being more lake misclassified as increased- than as decreased-chlorophyll *a*. The 10-yr average chlorophyll *a* was again the top explanatory variable, and longitude and latitude (lake location) were the next two most important variables (Fig. 8a).

A range of natural and human factors at multiple scales were related to the categorical lake response to drought (Fig. 8b–f). For example, we found that lakes with increased-chlorophyll *a* responses to drought had significantly higher 10-yr average chlorophyll *a* (median = 11.8 μg L^{-1}) than those with decreased-chlorophyll *a* responses (11.3 μg L^{-1}) or moderate change (10.8 μg L^{-1}) (Wilcoxon test, $p < 0.001$). This result was consistent with the finding from the regression random forest model, despite that the ΔZ-score$_{\text{median}}$ and 10-yr average chlorophyll *a* were negatively associated when chlorophyll *a* was higher than 25 μg L^{-1} (Fig. 7b). In contrast, lakes with increased-chlorophyll *a* responses to drought had significantly lower percent watershed forest (29.1%) than lakes with

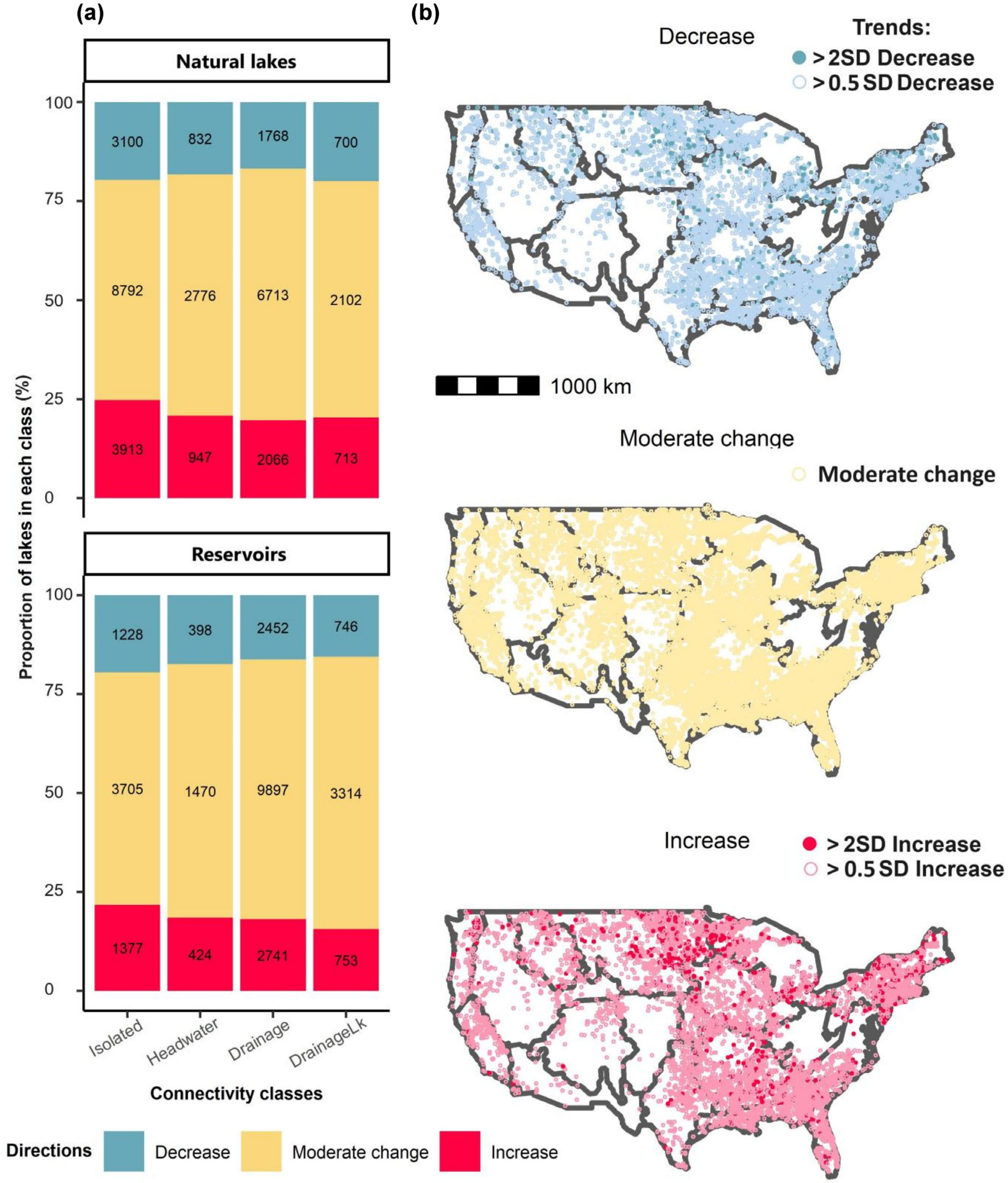


Fig. 5. Bar plots showing the number and proportion (**a**) and maps showing the spatial distribution by NEON regions (**b**) of lakes with increases, moderate change, or decreases in chlorophyll *a* in response to droughts. The numbers of lakes in each class are labeled on each bar in plot (a). In plot (b), each circle or dot represents a lake (including both natural lakes and reservoirs). Blue dots or circles represent lakes with decreased chlorophyll *a* (i.e., more than 2 and between 0.5 and 2 units of SD decreases in ΔZ-score$_{\text{median}}$, respectively). Red dots or circles represent lakes with increases in chlorophyll *a* (i.e., more than 2 and between 0.5 and 2 units of SD increases in ΔZ-score$_{\text{median}}$, respectively). NEON, National Ecological Observatory Network; SD, standard deviation.

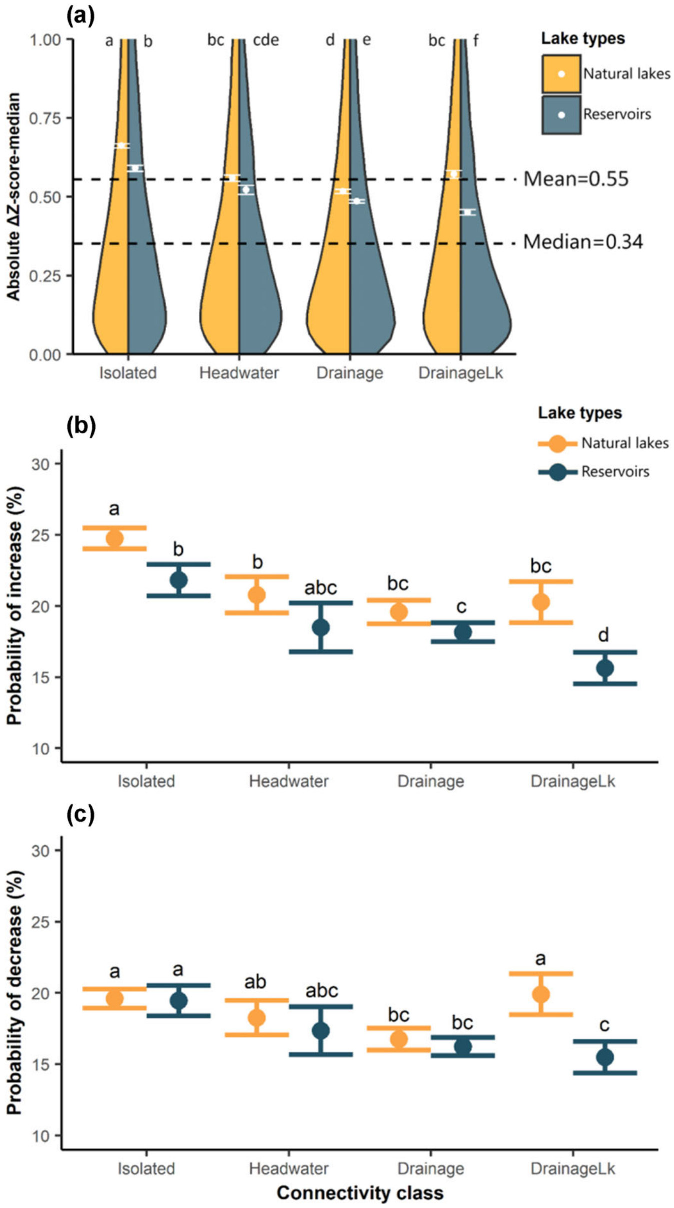


Fig. 6. Plots showing the magnitude of lake chlorophyll *a* response to drought (ΔZ-score$_{\text{median}}$) in all the lakes (**a**) and the probability of having increased (**b**) or decreased (**c**) chlorophyll *a* in response to droughts by lake type and connectivity class. Plot (a) only presents the ΔZ-score$_{\text{median}}$ from 0 to 1 to aid in visualization. A plot with the full range can be found in the supplementary material (Fig. S3). In plot (a), white dots represent mean values, and the bars are standard errors. In plots (b) and (c), each dot represents the estimated probability of increased or decreased chlorophyll *a* and the bars are lower and upper 95% confidence intervals. The letters above each violin and bar indicate the results of Tukey's contrasts post hoc tests. In each plot, the groups with the same letter(s) have similar ΔZ-score$_{\text{median}}$ values or probabilities ($p > 0.05$). Lake types are ranked from the least to most connected based on the number of streams and upstream lakes (Fig. S1).

decreased-chlorophyll *a* responses (31.2%) and moderate change lakes (31.8%; Wilcoxon test, $p < 0.001$). Additionally, lakes with increased-chlorophyll *a* responses to drought had statistically significantly lower mean watershed percent baseflow (42.4%) than those with decreased-chlorophyll *a* responses (44.5%) and moderate change (43.8%) (Wilcoxon test, $p < 0.001$). Lakes with either increased- or decreased-chlorophyll *a* responses to drought had similar watershed median percent silt in soil (37.6% and 37.5% respectively), which were statistically significantly higher than moderate-change lakes (36.1%) (Wilcoxon test, $p < 0.001$). Finally, lakes with increased-chlorophyll *a* responses to drought were further west (median longitude = −93.2) than lakes with decreased-chlorophyll *a* responses (−92.2) and moderate-change lakes (− 91.5) (Wilcoxon test, $p < 0.001$).

The effect of lake depth on lake drought responses

Lake maximum depth passed the Boruta feature selection and was one of the top variables in both models (i.e., continuous and categorical response variables; Fig. S4). When using the depth data subset ($n = 8994$ lakes), the random forest regression model explained 10% of the out-of-bag variance in lake drought response and the classification random forest model had 87% accuracy in correctly assigning equal-weighted categories. Lake type and connectivity were still included as important variables but had low importance. We observed lower chlorophyll *a* increases in deeper lakes until the maximum depth reached 3 m, beyond which chlorophyll *a* decreased in response to drought (negative predicted ΔZ-score$_{\text{median}}$; Fig. 7g). Lakes with increased-chlorophyll *a* responses to drought were significantly shallower (max depth = 9.6 m) than those with decreased-chlorophyll *a* responses (10.2 m) and moderate change lakes (11.6 m; Wilcoxon test, $p < 0.001$; Fig. 8g).

Discussion

This research extends our understanding of lake responses to climate change. Using a lake-specific LWY to study 62,927 lakes across the conterminous United States, we found that lake chlorophyll *a* responds to meteorological drought. However, by studying tens of thousands of lakes, we found that lakes differ in their responses by lake type (natural lakes and reservoirs) and surface water connectivity, as well as according to long-term average lake productivity. In addition, we determined that ecological factors from multiple scales affected lake chlorophyll *a* responses to drought.

This research advances scientific understanding in two main ways. First, we fill an existing knowledge gap about how lake type and surface water connectivity individually and interactively affect lake responses to drought. Reservoirs in general, and their responses to climate change in particular, have been understudied compared to natural lakes despite their abundance and important role in providing diverse ecosystem services (Ho and Goethals 2020; Rodriguez et al. 2023). Reservoirs in our study had higher baseline productivity (measured by median chlorophyll *a*) than natural lakes, and we found that their drought responses differed by connectivity

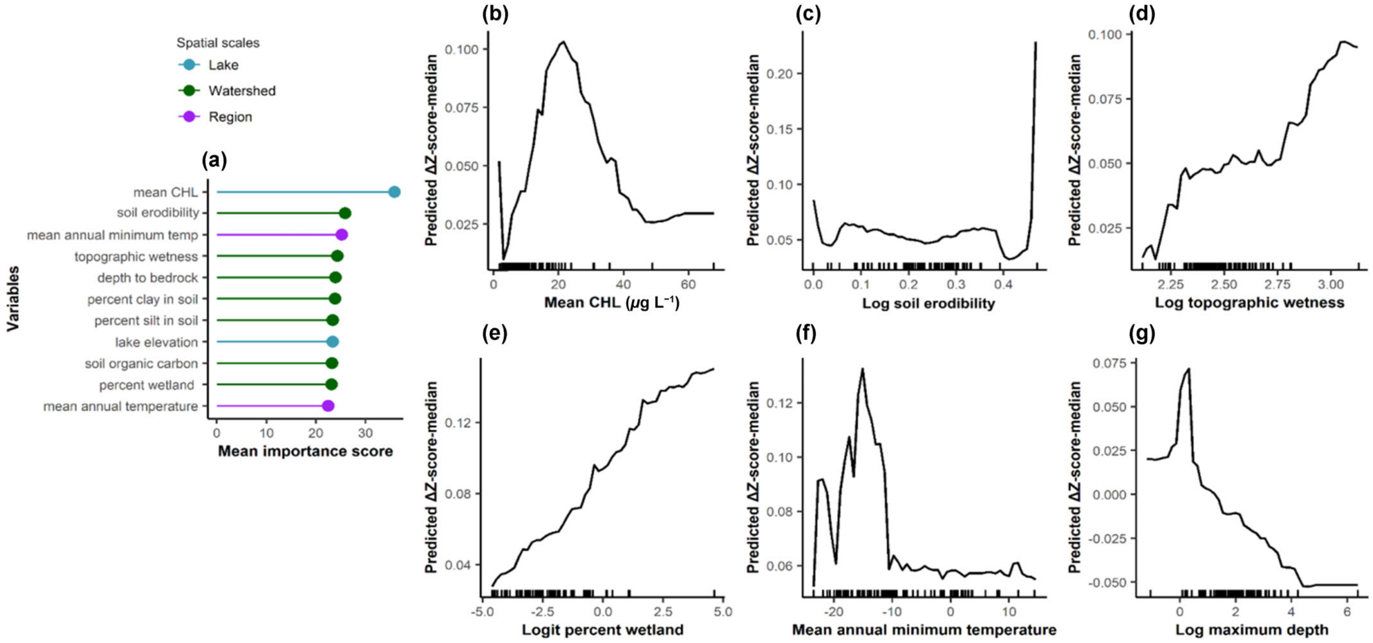


Fig. 7. Random forest Boruta feature selection (**a**) and partial dependence plots (PDPs; **b–g**) demonstrating the top multi-scale context variables for predicting the continuous lake drought chlorophyll *a* responses to drought using the full dataset. Plot (a) shows the mean importance scores of the top variables for predicting $\Delta Z\text{-score}_{\text{median}}$. Plots (b–g) are PDPs of the top variable for each scale (lake, watershed, region) and by sub-group for the watershed scale: 10-yr average lake chlorophyll *a*, watershed soil erodibility, topographic wetness, and percent wetland, regional minimum air temperature, and for the depth data subset, maximum depth. The PDP curves indicate the associations between the response variable and top predictor variables. The Boruta importance scores were determined by the loss of model accuracy due to the random permutation of variables. In plots (b–g), denser vertical tick-marks (percent of input data) on x-axes indicate more data points.

class. For example, headwater natural lakes and reservoirs had similar drought responses, whereas less connected (i.e., isolated) and more connected (i.e., drainage and drainageLK) lakes differed in their drought responses by lake type. Although our study cannot get at causation, these differences between natural lakes and reservoirs could be affected by multiple factors. For instance, lake elevation could be an influential factor since isolated natural lakes have higher elevations, on average, than isolated reservoirs (Fig. S5a). A previous study found that high-altitude lakes responded to climate change differently than low-altitude lakes due to differences in snow and ice-cover conditions that are sensitive to changes in temperature and precipitation and can affect lake ecosystems (Thompson, Kamenik, and Schmidt 2005).

At the other end of the connectivity spectrum, drainage and drainageLK reservoirs may experience a moderation of the impacts of drought (either increased or decreased chlorophyll) by riverine inflows and upstream lakes, which provided water and/or nutrient supply (Fig. S5b; Jeppesen et al. 2015; Spence et al. 2019). However, the moderation afforded by these inputs may be less effective or non-existent during extreme droughts when streams dry up. We also observed a greater sensitivity to drought in isolated natural lakes than in headwater natural lakes and reservoirs. Although neither group receives surface inflow, headwater lakes receive higher groundwater inputs compared to isolated lakes (Fig. S5c,d), which can alleviate water level declines during droughts (Cobbaert, Wong, and Bayley 2015) and may be contributing to the differences we found. These results are taken within the context of a study documenting how human regulation of reservoir water levels can greatly affect their drought responses (Fergus et al. 2022) and the conceptual model proposed by Hayes et al. (2017) that natural lakes and reservoirs respond differently to climate change due to impacts from catchment and management features that affect energy and mass transport and transformation within waterbodies and through the landscape. Our findings highlight the necessity of including reservoirs in lake climate change studies, accounting for lake type, including measures of surface water connectivity.

Second, we include a large suite of multi-scaled ecological context variables in our models to determine which natural and human factors are affecting lake chlorophyll *a* drought responses. Although our random forest model explained a small proportion of variance (12%), the top variables in the random forest included all three scales (lake, watershed, and region), demonstrating the importance of incorporating multi-scaled ecological context into climate change impact assessment and prediction. The most important variable for both chlorophyll *a* response to drought and the direction of that response was 10-yr average chlorophyll *a*, which gets at long-term productivity and has been found to be a primary

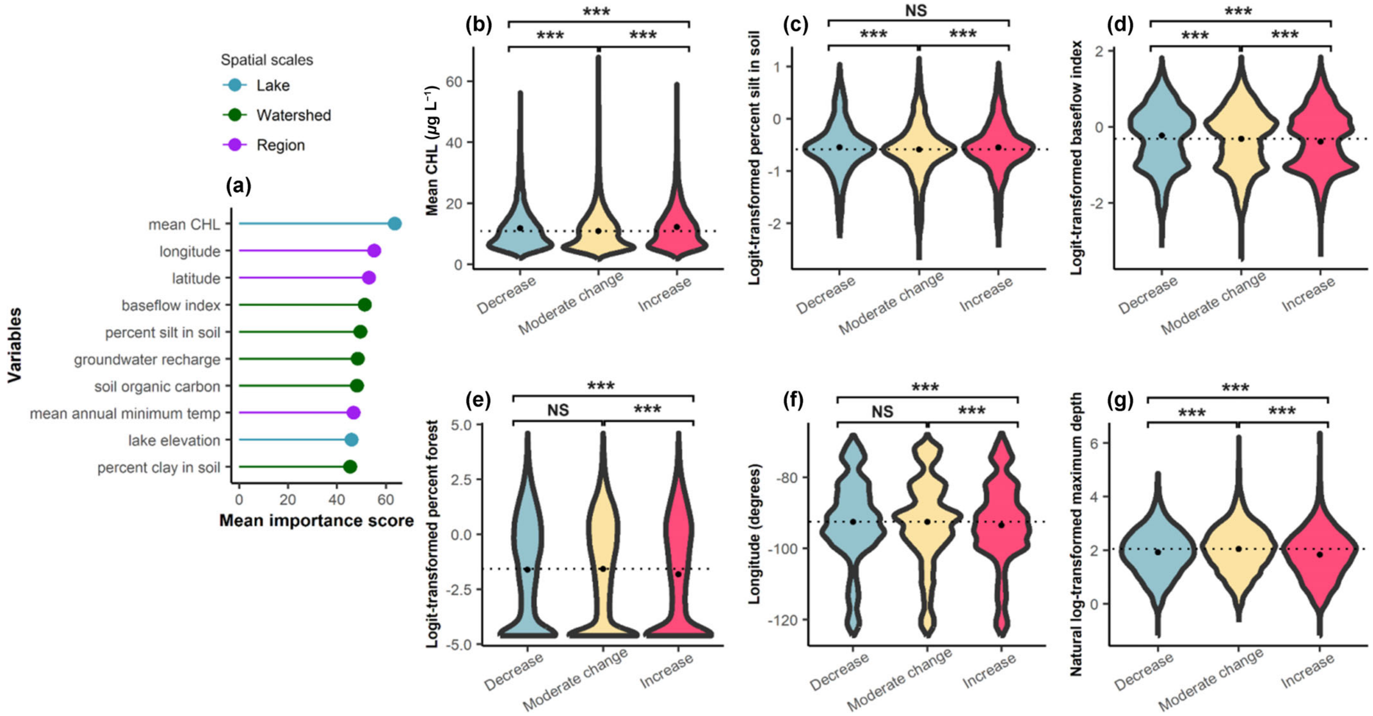


Fig. 8. Random forest Boruta feature selection (**a**) and violin plots (**b**–**g**) demonstrating the top multi-scale context variables for predicting the categorical lake drought chlorophyll *a* responses to drought using the full dataset. Plot (a) shows the mean importance scores of the top variables for predicting the relationship between directional lake chlorophyll *a* responses and droughts. Plots (b–g) show values of the top variable for each spatial scale (lake, watershed, region) and by sub-group for the watershed scale: 10-yr average lake chlorophyll *a*, percent silt in soil, baseflow index, percent forest, longitude, and, for the depth data subset, maximum depth. In plots (b–g), the black dots represent median values, and the dotted lines are the median values in the moderate change class. NS = non-significant ($p > 0.05$), ***$p < 0.001$.

driver of lake response to other measures of climate change (e.g., temperature variations, Nõges et al. 2011; warming temperature, Farrell et al. 2020). Using standardized changes in chlorophyll *a* allowed us to document the complicated nature of these relationships. Although lakes with greater 10-yr average productivity were, on average, likely to show greater increases in chlorophyll *a* during droughts, that pattern reversed when 10-yr average chlorophyll *a* exceeded about 25 μg L^{-1}, which is on the upper end of eutrophic and approaching hypereutrophic conditions (U.S. EPA 2022). This non-linear relationship could be related to differential watershed nutrient loading, or to an, as-of-yet documented, upper limit on the relationship between chlorophyll *a* and drought. In oligotrophic and mesotrophic lakes, decreased water levels can concentrate nutrients, which increases nutrient availability and induces algae growth during droughts (Mosley 2015). In contrast, in more eutrophic lakes that rely heavily on watershed inputs, droughts could reduce nutrient loadings to lakes, which decreases algal growth (Vanni et al. 2006). However, if droughts coincide with fewer storms during the growing season, then for stratified lakes, internal nutrient loading could be reduced during drought years, further decreasing nutrient inputs into meso- to eutrophic lakes (Soranno, Carpenter, and Lathrop 1997; Orihel et al. 2017).

Our findings also demonstrated that other multi-scaled ecological context variables influence lake chlorophyll *a* drought responses. For example, we demonstrated that deeper lakes are less sensitive to droughts than shallower ones. Lake depth has been found to regulate climate change impacts (Woolway et al. 2020), perhaps because shallow lakes may experience a greater proportional water volume loss during droughts, leading to greater water temperature increases and sediment (and associated nutrients) resuspension, which can cause reduced light availability (decreasing productivity) or nutrient enrichment (increasing productivity) (Brasil et al. 2016; Seitz et al. 2020).

At the watershed scale, we found soil erodibility and texture to be important, which may point to eroded particles as a source of nutrient and organic matter inputs and the composition of soil determining soil infiltration rates and capacity of water storage (Cleophas et al. 2022), which can buffer water volume decline during droughts. On the one hand, we found that lakes receiving considerable amounts of water inflows from catchments (i.e., higher topographic wetness index values indicating large catchment areas that can provide higher levels of surface water flow) were more responsive to drought. This result may indicate that these lakes are sinks of dissolved organic matter and nutrients (Guillemette et al. 2017), which can be accentuated during droughts and facilitate algae growth. On the other hand, lakes with higher contributions of groundwater discharge to streamflow (i.e., higher baseflow index indicating groundwater inputs) were less responsive to drought, perhaps because these groundwater inputs act as a vital water sources that can mitigate ecological disruptions caused by drought (Cobbaert, Wong, and Bayley 2015). The fact that these two measures of water supply were both important, but had different relationships with lake drought responses highlights the complex hydrological processes (e.g., surface water and groundwater supply) that influence lake responses to drought. Moreover, we found that variables describing land use/land cover characteristics were important to lake chlorophyll *a* drought responses. For instance, compared to other drought response groups, the increased-chlorophyll *a* response group had fewer lakes with high watershed forest cover (about 70% forest cover) and more lakes with extremely low forest cover (about 2% forest cover). Previous studies have shown that land use/land cover factors (e.g., forest and wetland cover and agricultural land use) affect dissolved organic matter and nutrient inputs (Sankar et al. 2020), which could contribute to divergent lake chlorophyll *a* responses to droughts (Fergus et al. 2022).

Finally, regional air temperatures, especially minimum air temperatures, were associated with lake chlorophyll *a* drought responses. However, the direction of the association changed from positive to negative with an increase of minimum temperatures (until about -10°C), suggesting that there could be other factors (e.g., lake geographical location; Adrian et al. 2009) collectively affecting the responses, particularly in areas with extremely low temperatures. Although lake location (via longitude and latitude) was important in the random forests, obvious spatial patterns of lake chlorophyll *a* responses to drought did not emerge across the conterminous United States. The complexity of the lake chlorophyll *a* responses to droughts that we found, as well as the fact that a range of lake, watershed, and regional ecological context variables were important for understanding those relationships, demonstrate the importance of further macroscale studies that take into account a wide range of multi-scaled ecological context variables to account for complex underlying mechanisms.

We used a LWY timeframe (Sun and Cheruvelil 2024b) to study lake chlorophyll *a* responses to droughts at the continental scale. Doing so allowed us to capture the relationships between precipitation and chlorophyll *a* on temporally appropriate scales that account for regional variation in hydroclimate. However, due to the broad scale of this study and lack of snow/ice melt-relevant data, we did not specifically identify areas where snow is the dominant water source. According to Tedesche, Dahl, and Giovando (2023), snow-dominated areas occupy a small proportion of the conterminous United States, mainly in the Great Basin and Northern Plains regions (NEON 15 and 9 ecoregions). In our study, snow in late fall and winter has likely been taken into account in the Great Basin region because that area has an LWY end month in summer or early fall. However, since the LWYs in some areas in the Northern Plains region commonly have end months of January and December, the LWYs may not have fully covered the snow period, leading to the drought intensity (i.e., SPI values) being overestimated in this region. Future research could further refine the LWY with snow data and examine lake drought responses in these snow-dominant areas.

Our models and results explained part of the variance among lake chlorophyll *a* drought responses, implying that additional variables (e.g., water nutrient levels, light availability, or water column stability) and interactions among them and ecological contexts should be considered in future studies to improve our understanding of these responses. We studied algal biomass (chlorophyll *a*) because those data are available across the conterminous United States for both baseline and drought years. However, it is essential to study a range of biotic and abiotic responses to understand the effects of climate change on lakes. Variables such as phosphorus (Shuvo et al. 2021), salinity (Jeppesen et al. 2015), zooplankton (Meerhoff et al. 2022), and water management (Fergus et al. 2022) have all been found to influence lake responses to drought and ought to be considered in future studies. Additionally, we used the change in median *z*-score per unit change in SPI as our response variable as we expected that a greater drought magnitude (i.e., greater SPI value) would lead to a greater lake chlorophyll *a* change. Further research could be conducted to investigate the relationship between drought magnitude and lake responses and the multiscale factors affecting the relationship at the macroscale, which would improve the assessment and prediction of drought impacts on lakes. Moreover, previous research suggests that interactions among ecological context variables across scales can sometimes cause unexpected results (i.e., cross-scale interactions; Peters, Bestelmeyer, and Turner 2007; Soranno et al. 2014; Fischer 2018). For example, Soranno et al. (2014) found that local wetlands were positively associated with lake phosphorus concentrations in regions with low percent agricultural land use, but negatively associated in regions with high percent agricultural land use. Therefore, further investigation is needed to understand these nuanced interactions between multiple factors across scales (e.g., latitude and long-term average chlorophyll *a*; Fig. S6) and to better disentangle the complex relationships between ecological context variables and lake drought responses.

Conclusion

Our study applied a lake-specific LWY timeframe to examine 62,927 lake chlorophyll *a* responses to droughts at the continental scale from 2009 to 2018. We examined the individual and interactive effects of lake type (natural lake and reservoir) and surface water connectivity on lake chlorophyll *a* drought responses, and included a large suite of lake characteristics and multi-scaled ecological context variables in models to determine which natural and human factors drive lake chlorophyll *a* drought responses. Our findings suggest that headwater natural lakes and reservoirs respond similarly to drought, whereas more and less-connected lakes respond differently according to lake type (i.e., natural lakes are more responsive to drought than reservoirs). We also found that features across spatial scales, such as 10-yr average lake productivity, watershed soil texture, groundwater, and land use/cover, and regional air temperature, all determined lake chlorophyll *a* responses to drought. These results point to the import of including lake type and surface connectivity, as well as a wide range of lake characteristics and multi-scaled ecological context variables when studying lake responses to droughts. Doing so will improve the prediction and management of lake responses to droughts as well as other anthropogenic and climate change disturbances. Thus, there is an urgent need to integrate multi-scale factors into impact analyses and forecasting to bolster our understanding of how these invaluable ecosystems respond to future changes at regional, continental, and global scales.

Author Contributions

Xinyu Sun and Kendra S. Cheruvelil conceived the project. Xinyu Sun, Kendra S. Cheruvelil, Patrick J. Hanly, and Patricia A. Soranno designed the analyses. Xinyu Sun and Patrick J. Hanly gathered and processed data. Xinyu Sun performed analyses, made figures, tables, and supplements. All authors interpreted the results. Xinyu Sun wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

Acknowledgments

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

Conflicts of Interest

None declared.

References

Adrian, R., C. M. O'Reilly, H. Zagarese, et al. 2009. "Lakes as Sentinels of Climate Change." *Limnology and Oceanography* 54, no. 6part2: 2283–2297. https://doi.org/10.4319/lo.2009.54.6_part_2.2283.

Anderson, M. G., M. Clark, A. P. Olivero, et al. 2023. "A Resilient and Connected Network of Sites to Sustain Biodiversity under a Changing Climate." *Proceedings of the National Academy of Sciences* 120, no. 7: e2204434119. https://doi.org/10.1073/pnas.2204434119.

Beaulieu, M., F. Pick, and I. Gregory-Eaves. 2013. "Nutrients and Water Temperature Are Significant Predictors of Cyanobacterial Biomass in a 1147 Lakes Data Set." *Limnology and Oceanography* 58, no. 5: 1736–1746. https://doi.org/10.4319/lo.2013.58.5.1736.

Beguería, S., and S. M. Vicente-Serrano. 2023. SPEI: Calculation of the Standardized Precipitation-Evapotranspiration Index (1.8.1). https://cran.r-project.org/web/packages/SPEI/index.html.

Brasil, J., J. L. Attayde, F. R. Vasconcelos, D. D. F. Dantas, and V. L. M. Huszar. 2016. "Drought-Induced Water-Level Reduction Favors Cyanobacteria Blooms in Tropical Shallow Lakes." *Hydrobiologia* 770, no. 1: 145–164. https://doi.org/10.1007/s10750-015-2578-5.

Cheruvelil, K. S., P. A. Soranno, I. M. McCullough, K. E. Webster, L. K. Rodriguez, and N. J. Smith. 2021. "LAGOS-US LOCUS v1.0: Data Module of Location, Identifiers, and Physical Characteristics of Lakes and Their Watersheds in the Conterminous U.S." *Limnology and Oceanography Letters* 6, no. 5: 270–292. https://doi.org/10.1002/lol2.10203.

Cleophas, F., F. Isidore, B. Musta, et al. 2022. "Effect of Soil Physical Properties on Soil Infiltration Rates." *Journal of Physics: Conference Series* 2314, no. 1: 012020. https://doi.org/10.1088/1742-6596/2314/1/012020.

Cobbaert, D., A. S. Wong, and S. E. Bayley. 2015. "Resistance to Drought Affects Persistence of Alternative Regimes in Shallow Lakes of the Boreal Plains (Alberta, Canada)." *Freshwater Biology* 60, no. 10: 2084–2099. https://doi.org/10.1111/fwb.12633.

Cutler, F., and R. Wiener. 2022. randomForest: Breiman and Cutler's Random Forests for Classification and Regression (4.7-1.1). https://cran.r-project.org/web/packages/randomForest/index.html.

Da Costa, M. R. A., J. L. Attayde, and V. Becker. 2016. "Effects of Water Level Reduction on the Dynamics of Phytoplankton Functional Groups in Tropical Semi-Arid Shallow Lakes." *Hydrobiologia* 778, no. 1: 75–89. https://doi.org/10.1007/s10750-015-2593-6.

Doubek, J. P., and C. C. Carey. 2017. "Catchment, Morphometric, and Water Quality Characteristics Differ Between Reservoirs and Naturally Formed Lakes on a Latitudinal Gradient in the Conterminous United States." *Inland Waters* 7, no. 2: 171–180. https://doi.org/10.1080/20442041.2017.1293317.

Easterling, D. R., G. A. Meehl, C. Parmesan, S. A. Changnon, T. R. Karl, and L. O. Mearns. 2000. "Climate Extremes: Observations, Modeling, and Impacts." *Science* 289, no. 5487: 2068–2074. https://doi.org/10.1126/science.289.5487.2068.

Farrell, K. J., N. K. Ward, A. I. Krinos, et al. 2020. "Ecosystem-Scale Nutrient Cycling Responses to Increasing Air Temperatures Vary With Lake Trophic State." *Ecological Modelling* 430: 109134. https://doi.org/10.1016/j.ecolmodel.2020.109134.

Fergus, C. E., J. R. Brooks, P. R. Kaufmann, et al. 2020. "Lake Water Levels and Associated Hydrologic Characteristics in the Conterminous U.S." *JAWRA Journal of the American Water Resources Association* 56, no. 3: 450–471. https://doi.org/10.1111/1752-1688.12817.

Fergus, C. E., J. R. Brooks, P. R. Kaufmann, et al. 2021. "National Framework for Ranking Lakes by Potential for Anthropogenic Hydro-Alteration." *Ecological Indicators* 122: 107241. https://doi.org/10.1016/j.ecolind.2020.107241.

Fergus, C. E., J. R. Brooks, P. R. Kaufmann, et al. 2022. "Natural and Anthropogenic Controls on Lake Water-Level Decline and Evaporation-To-Inflow Ratio in the Conterminous United States." *Limnology and Oceanography* 67, no. 7: 1484–1501. https://doi.org/10.1002/lno.12097.

Fergus, C. E., J. Lapierre, S. K. Oliver, et al. 2017. "The Freshwater Landscape: Lake, Wetland, and Stream Abundance and Connectivity at Macroscales." *Ecosphere* 8, no. 8: e01911. https://doi.org/10.1002/ecs2.1911.

Fischer, A. P. 2018. "Forest Landscapes as Social-Ecological Systems and Implications for Management." *Landscape and Urban Planning* 177: 138–147. https://doi.org/10.1016/j.landurbplan.2018.05.001.

Ford, T. W., L. Chen, and J. T. Schoof. 2021. "Variability and Transitions in Precipitation Extremes in the Midwest United States." *Journal of Hydrometeorology* 22, no. 3: 533–545. https://doi.org/10.1175/JHM-D-20-0216.1.

Fox, J., S. Weisberg, B. Price, et al. 2023. car: Companion to Applied Regression (3.1-2). https://cran.r-project.org/web/packages/car/index.html.

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

Guillemette, F., E. Von Wachenfeldt, D. N. Kothawala, D. Bastviken, and L. J. Tranvik. 2017. "Preferential Sequestration of Terrestrial Organic Matter in Boreal Lake Sediments." *Journal of Geophysical Research: Biogeosciences* 122, no. 4: 863–874. https://doi.org/10.1002/2016JG003735.

Guttman, N. B. 1999. "Accepting the Standardized Precipitation Index: A Calculation Algorithm." *Journal of the American Water Resources Association* 35, no. 2: 311–322. https://doi.org/10.1111/j.1752-1688.1999.tb03592.x.

Hanly, P. J., K. E. Webster, and P. A. Soranno. 2024*a*. "LAGOS-US LANDSAT: Data Module of Remotely-Sensed Water Quality Estimates for U.S. Lakes Over 4 Ha From 1984 to 2020." Environmental Data Initiative. https://portal.edirepository.org/nis/mapbrowse?packageid=edi.1427.1.

Hanly, P. J., K. E. Webster, and P. A. Soranno. 2024*b*. LAGOS-US LANDSAT: Remotely Sensed Water Quality Estimates for U.S. Lakes Over 4 ha From 1984 to 2020 https://doi.org/10.1101/2024.05.10.593626.

Hargrove, W. W., and F. M. Hoffman. 1999. "Using Multivariate Clustering to Characterize Ecoregion Borders." *Computing in Science & Engineering* 1, no. 4: 18–25. https://doi.org/10.1109/5992.774837.

Havens, K., and E. Jeppesen. 2018. "Ecological Responses of Lakes to Climate Change." *Water* 10, no. 7: 917. https://doi.org/10.3390/w10070917.

Hayes, M., M. Svoboda, N. Wall, and M. Widhalm. 2011. "The Lincoln Declaration on Drought Indices: Universal Meteorological Drought Index Recommended." *Bulletin of the American Meteorological Society* 92, no. 4: 485–488. https://doi.org/10.1175/2010BAMS3103.1.

Hayes, N. M., B. R. Deemer, J. R. Corman, N. R. Razavi, and K. E. Strock. 2017. "Key Differences Between Lakes and Reservoirs Modify Climate Signals: A Case for a New Conceptual Model." *Limnology and Oceanography Letters* 2, no. 2: 47–62. https://doi.org/10.1002/lol2.10036.

Ho, L., and P. Goethals. 2020. "Research Hotspots and Current Challenges of Lakes and Reservoirs: A Bibliometric Analysis." *Scientometrics* 124, no. 1: 603–631. https://doi.org/10.1007/s11192-020-03453-1.

Hothorn, T., F. Bretz, P. Westfall, R. M. Heiberger, A. Schuetzenmeister, and S. Scheibe. 2023. multcomp: Simultaneous Inference in General Parametric Models (1.4-25). https://cran.r-project.org/web/packages/multcomp/index.html.

Hu, R., X. Duan, L. Peng, B. Han, and L. Naselli-Flores. 2017. "Phytoplankton Assemblages in a Complex System of Interconnected Reservoirs: The Role of Water Transport in Dispersal." *Hydrobiologia* 800, no. 1: 17–30. https://doi.org/10.1007/s10750-017-3146-y.

Jeppesen, E., S. Brucet, L. Naselli-Flores, et al. 2015. "Ecological Impacts of Global Warming and Water Abstraction on Lakes and Reservoirs Due to Changes in Water Level and Related Changes in Salinity." *Hydrobiologia* 750, no. 1: 201–227. https://doi.org/10.1007/s10750-014-2169-x.

Jones, B. M., G. Grosse, C. D. Arp, et al. 2015. "Recent Arctic Tundra Fire Initiates Widespread Thermokarst Development." *Scientific Reports* 5, no. 1: 15865. https://doi.org/10.1038/srep15865.

Kamps, R. H., and J. L. Heilman. 2018. "A Method to Calculate a Locally Relevant Water Year for Ecohydrological Studies Using Eddy Covariance Data." *Ecohydrology* 11, no. 7: e1980. https://doi.org/10.1002/eco.1980.

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

Lenth, R. 2018. lsmeans: Least-Squares Means (2.30-0). https://cran.r-project.org/web/packages/lsmeans/index.html.

Lloyd-Hughes, B., and M. A. Saunders. 2002. "A Drought Climatology for Europe." *International Journal of Climatology* 22, no. 13: 1571–1592. https://doi.org/10.1002/joc.846.

McCullough, I. M., K. S. Cheruvelil, S. M. Collins, and P. A. Soranno. 2019. "Geographic Patterns of the Climate Sensitivity of Lakes." *Ecological Applications* 29, no. 2: e01836. https://doi.org/10.1002/eap.1836.

Meerhoff, M., J. Audet, T. A. Davidson, et al. 2022. "Feedback Between Climate Change and Eutrophication: Revisiting the Allied Attack Concept and How to Strike Back." *Inland*

Waters 12, no. 2: 187–204. https://doi.org/10.1080/20442041.2022.2029317.

Mosley, L. M. 2015. “Drought Impacts on the Water Quality of Freshwater Systems; Review and Integration.” *Earth-Science Reviews* 140: 203–214. https://doi.org/10.1016/j.earscirev.2014.11.010.

Nõges, P., T. Nõges, M. Ghiani, et al. 2011. “Increased Nutrient Loading and Rapid Changes in Phytoplankton Expected With Climate Change in Stratified South European Lakes: Sensitivity of Lakes With Different Trophic State and Catchment Properties.” *Hydrobiologia* 667, no. 1: 255–270. https://doi.org/10.1007/s10750-011-0649-9.

Oikonomou, P. D., C. A. Karavitis, D. E. Tsesmelis, E. Kolokytha, and R. Maia. 2020. “Drought Characteristics Assessment in Europe Over the Past 50 Years.” *Water Resources Management* 34, no. 15: 4757–4772. https://doi.org/10.1007/s11269-020-02688-0.

Oliveira, C. Y. B., C. D. L. Oliveira, A. J. G. Almeida, A. O. Gálvez, and D. M. Dantas. 2019. “Phytoplankton Responses to an Extreme Drought Season: A Case Study at Two Reservoirs From a Semiarid Region, Northeastern Brazil.” *Journal of Limnology* 78, no. 2: 176–184. https://doi.org/10.4081/jlimnol.2019.1869.

Oliver, S. K., P. A. Soranno, C. E. Fergus, et al. 2016. “Prediction of Lake Depth Across a 17-State Region in the United States.” *Inland Waters* 6, no. 3: 314–324. https://doi.org/10.1080/IW-6.3.957.

Orihel, D. M., H. M. Baulch, N. J. Casson, et al. 2017. “Internal Phosphorus Loading in Canadian Fresh Waters: A Critical Review and Data Analysis.” *Canadian Journal of Fisheries and Aquatic Sciences* 74, no. 12: 2005–2029. https://doi.org/10.1139/cjfas-2016-0500.

Peters, D. P. C., B. T. Bestelmeyer, and M. G. Turner. 2007. “Cross-Scale Interactions and Changing Pattern–Process Relationships: Consequences for System Dynamics.” *Ecosystems* 10, no. 5: 790–796. https://doi.org/10.1007/s10021-007-9055-6.

Pham, S. V., P. R. Leavitt, S. McGowan, and P. Peres-Neto. 2008. “Spatial Variability of Climate and Land-Use Effects on Lakes of the Northern Great Plains.” *Limnology and Oceanography* 53, no. 2: 728–742. https://doi.org/10.4319/lo.2008.53.2.0728.

Polus, S. M., P. J. Hanly, L. K. Rodriguez, et al. 2022. “LAGOS-US RESERVOIR: Data Module Classifying Conterminous U.S. Lakes 4 Hectares and Larger as Natural Lakes or Reservoirs.” Environmental Data Initiative https://doi.org/10.6073/PASTA/F9AA935329A95DFD69BF895015BC5161.

Prein, A. F., G. J. Holland, R. M. Rasmussen, M. P. Clark, and M. R. Tye. 2016. “Running Dry: The U.S. Southwest's Drift Into a Drier Climate State.” *Geophysical Research Letters* 43, no. 3: 1272–1279. https://doi.org/10.1002/2015GL066727.

Read, E. K., V. P. Patil, S. K. Oliver, et al. 2015. “The Importance of Lake-Specific Characteristics for Water Quality Across the Continental United States.” *Ecological Applications* 25, no. 4: 943–955. https://doi.org/10.1890/14-0935.1.

Ripley, B., and W. Venables. 2023. nnet: Feed-Forward Neural Networks and Multinomial Log-Linear Models (7.3-19). https://cran.r-project.org/web/packages/nnet/index.html.

Rodriguez, L. K., S. M. Polus, D. I. Matuszak, et al. 2023. “LAGOS-US RESERVOIR: A Database Classifying Conterminous U.S. Lakes 4 Ha and Larger as Natural Lakes or Reservoir Lakes.” *Limnology and Oceanography Letters* 8, no. 2: 267–285. https://doi.org/10.1002/lol2.10299.

Sankar, M. S., P. Dash, Y. Lu, et al. 2020. “Land Use and Land Cover Control on the Spatial Variation of Dissolved Organic Matter Across 41 Lakes in Mississippi, USA.” *Hydrobiologia* 847, no. 4: 1159–1176. https://doi.org/10.1007/s10750-019-04174-0.

Seaber, P. R., F. P. Kapinos, and G. L. Knapp. 1987. Hydrologic Unit Maps: US Geological Survey Water-Supply Paper 2294. Denver, CO: U.S. Geological Survey. https://pubs.usgs.gov/wsp/wsp2294/html/pdf.html.

Seitz, C., F. Scordo, A. J. Vitale, M. I. Vélez, and G. M. E. Perillo. 2020. “The Effects of Extreme Drought Events on the Morphometry of Shallow Lakes: Implications for Sediment Resuspension and Littoral and Pelagic Zone Distribution.” *Journal of South American Earth Sciences* 103: 102743. https://doi.org/10.1016/j.jsames.2020.102743.

Shuvo, A., C. M. O'Reilly, K. Blagrave, et al. 2021. “Total Phosphorus and Climate Are Equally Important Predictors of Water Quality in Lakes.” *Aquatic Sciences* 83, no. 1: 16. https://doi.org/10.1007/s00027-021-00776-w.

Shuvo, A. K., N. R. Lottig, K. E. Webster, et al. 2023. “LAGOS-US LIMNO: Data Module of Surface Water Chemistry From 1975–2021 for Lakes in the Conterminous U.S.” Environmental Data Initiative https://doi.org/10.6073/PASTA/2C58F5A50AB813919F99CC1F265F271C.

Smith, N. J., K. E. Webster, L. K. Rodriguez, K. S. Cheruvelil, and P. A. Soranno. 2021. “LAGOS-US LOCUS v1.0: Data Module of Location, Identifiers, and Physical Characteristics of Lakes and Their Watersheds in the Conterminous U.S.” Environmental Data Initiative https://doi.org/10.6073/PASTA/E5C2FB8D77467D3F03DE4667AC2173CA.

Smith, N. J., K. E. Webster, L. K. Rodriguez, K. S. Cheruvelil, and P. A. Soranno. 2022. “LAGOS-US GEO v1.0: Data Module of Lake Geospatial Ecological Context at Multiple Spatial and Temporal Scales in the Conterminous U.S.” Environmental Data Initiative https://doi.org/10.6073/pasta/0e443bd43d7e24c2b6abc7af54ca424a.

Soranno, P. A., S. R. Carpenter, and R. C. Lathrop. 1997. “Internal Phosphorus Loading in Lake Mendota: Response to External Loads and Weather." *Canadian Journal of Fisheries and Aquatic Sciences* 54, no. 8: 1883–1893. https://doi.org/10.1139/f97-095.

Soranno, P. A., K. S. Cheruvelil, E. G. Bissell, et al. 2014. "Cross-Scale Interactions: Quantifying Multi-Scaled Cause–Effect Relationships in Macrosystems." *Frontiers in Ecology and the Environment* 12, no. 1: 65–73. https://doi.org/10.1890/120366.

Spence, C., G. Ali, C. J. Oswald, and C. Wellen. 2019. "An Application of the T-TEL Assessment Method to Evaluate Connectivity in a Lake-Dominated Watershed After Drought." *JAWRA Journal of the American Water Resources Association* 55, no. 2: 318–333. https://doi.org/10.1111/1752-1688.12702.

Stachelek, J., P. J. Hanly, and P. A. Soranno. 2022. "Imperfect Slope Measurements Drive Overestimation in a Geometric Cone Model of Lake and Reservoir Depth." *Inland Waters* 12, no. 2: 283–293. https://doi.org/10.1080/20442041.2021.2006553.

Stachelek, J., L. K. Rodriguez, J. Díaz Vázquez, et al. 2021. "LAGOS-US DEPTH v1.0: Data Module of Observed Maximum and Mean Lake Depths for a Subset of Lakes in the Conterminous U.S." Environmental Data Initiative https://doi.org/10.6073/PASTA/64DDC4D04661D9AEF4BD702DC5D8984F.

Sun, X., and K. S. Cheruvelil. 2024*a*. Local Water Year Values for the Conterminous United States. EarthArXiv. https://doi.org/10.31223/X5Q121.

Sun, X., and K. S. Cheruvelil. 2024*b*. Local Water Year for 4-Digit Hydrologic Unit Areas across the Conterminous United States. Environmental Data Initiative. https://doi.org/10.6073/PASTA/94185D860444092A1D358D02DBC6BB40.

Taranu, Z. E., and I. Gregory-Eaves. 2008. "Quantifying Relationships Among Phosphorus, Agriculture, and Lake Depth at an Inter-Regional Scale." *Ecosystems* 11, no. 5: 715–725. https://doi.org/10.1007/s10021-008-9153-0.

Taranu, Z. E., I. Gregory-Eaves, P. R. Leavitt, et al. 2015. "Acceleration of Cyanobacterial Dominance in North Temperate-Subarctic Lakes During the Anthropocene." *Ecology Letters* 18, no. 4: 375–384. https://doi.org/10.1111/ele.12420.

Tedesche, M. E., T. Dahl, and J. J. Giovando. 2023. Changing Snow Regime Classifications Across the Contiguous United States https://doi.org/10.22541/essoar.167340718.86199797/v1.

Thompson, R., C. Kamenik, and R. Schmidt. 2005. "Ultra-Sensitive Alpine Lakes and Climate Change." *Journal of Limnology* 64, no. 2: 139. https://doi.org/10.4081/jlimnol.2005.139.

Thornton, K. W., B. L. Kimmel, and F. E. Payne. 1990. Reservoir Limnology: Ecological Perspectives. New York: John Wiley & Sons.

U.S. Environmental Protection Agency. 2022. National Lakes Assessment: The Third Collaborative Survey of Lakes in the United States. (No. EPA 841-R-22-002). Washington, DC: U.S. Environmental Protection Agency, Office of Water and Office of Research and Development. https://nationallakesassessment.epa.gov/webreport/.

U.S. Geological Survey. 2024. "USGS Surface-Water Data for the Nation." National Water Information System: Web Interface. https://waterdata.usgs.gov/nwis/sw.

Van Loon, A. F., K. Stahl, G. Di Baldassarre, et al. 2016. "Drought in a Human-Modified World: Reframing Drought Definitions, Understanding, and Analysis Approaches." *Hydrology and Earth System Sciences* 20, no. 9: 3631–3650. https://doi.org/10.5194/hess-20-3631-2016.

Vanni, M. J., A. M. Bowling, E. M. Dickman, et al. 2006. "Nutrient Cycling by Fish Supports Relatively More Primary Production as Lake Productivity Increases." *Ecology* 87, no. 7: 1696–1709. https://doi.org/10.1890/0012-9658(2006)87[1696:NCBFSR]2.0.CO;2.

Vasas, G., I. Bácsi, G. Surányi, et al. 2010. "Isolation of Viable Cell Mass From Frozen Microcystis Viridis Bloom Containing Microcystin-RR." *Hydrobiologia* 639, no. 1: 147–151. https://doi.org/10.1007/s10750-009-0025-1.

Vicente-Serrano, S. M., S. M. Quiring, M. Peña-Gallardo, S. Yuan, and F. Domínguez-Castro. 2020. "A Review of Environmental Droughts: Increased Risk Under Global Warming?" *Earth-Science Reviews* 201: 102953. https://doi.org/10.1016/j.earscirev.2019.102953.

Wasko, C., R. Nathan, and M. C. Peel. 2020. "Trends in Global Flood and Streamflow Timing Based on Local Water Year." *Water Resources Research* 56, no. 8: e2020WR027233. https://doi.org/10.1029/2020WR027233.

Webster, K. E., P. A. Soranno, S. B. Baines, et al. 2000. "Structuring Features of Lake Districts: Landscape Controls on Lake Chemical Responses to Drought." *Freshwater Biology* 43, no. 3: 499–515. https://doi.org/10.1046/j.1365-2427.2000.00571.x.

Williamson, C. E., J. E. Saros, W. F. Vincent, and J. P. Smol. 2009. "Lakes and Reservoirs as Sentinels, Integrators, and Regulators of Climate Change." *Limnology and Oceanography* 54, no. 6part2: 2273–2282. https://doi.org/10.4319/lo.2009.54.6_part_2.2273.

Woolway, R. I., B. M. Kraemer, J. D. Lenters, C. J. Merchant, C. M. O'Reilly, and S. Sharma. 2020. "Global Lake Responses to Climate Change." *Nature Reviews Earth and Environment* 1, no. 8: 388–403. https://doi.org/10.1038/s43017-020-0067-5.

Wu, Z., L. Yu, Z. Du, H. Zhang, X. Fan, and T. Lei. 2020. "Recent Changes in the Drought of China From 1960 to

2014." *International Journal of Climatology* 40, no. 7: 3281–3296. https://doi.org/10.1002/joc.6397.

Yang, Y., C. Stenger-Kovács, J. Padisák, and K. Pettersson. 2016. "Effects of Winter Severity on Spring Phytoplankton Development in a Temperate Lake (Lake Erken, Sweden)." *Hydrobiologia* 780, no. 1: 47–57. https://doi.org/10.1007/s10750-016-2777-8.

Zanchettin, D., P. Traverso, and M. Tomasino. 2008. "Po River Discharges: A Preliminary Analysis of a 200-Year Time Series." *Climatic Change* 89, no. 3–4: 411–433. https://doi.org/10.1007/s10584-008-9395-z.

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Submitted 14 June 2024
Revised 28 October 2024
Accepted 19 January 2025