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RESEARCH ARTICLE

Climate-driven alterations of lake thermal regimes

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Abstract

Temperate lakes are undergoing climate-driven alterations in their thermal regimes, changing their ecology. Previous efforts to understand temperature changes have overlooked multi-dimensional temperature dynamics, missing complex shifts at high spatiotemporal resolutions across landscapes. Here, we use simulated daily water temperature profiles from > 11,000 temperate lakes throughout the Midwestern United States to (1) quantify multivariate, landscape-scale patterns in contemporary thermal regimes and (2) contextualize forecasted shifts and identify novel regimes that may emerge with climatic change. Hierarchical clustering and principal component analyses identified six lake clusters with distinct thermal regimes driven by differences in annual warming rates and spring–summer dynamics, with secondary influences from extreme heat events and seasonal variability. Annual temperature variations were influenced by lake-specific physical characteristics, emphasizing distinct thermal profiles and seasonal variability patterns. Projected climate-driven alterations in thermal regimes suggest a homogenization toward warmer and more variable conditions, with the majority of lakes characterized by higher temperatures and increased variability. Few lakes ($n = 310$), particularly in the southern and southeastern Midwest, may experience novel, non-analog conditions by the late 21st century, while others will undergo shifts between clusters but remain within analogous regime frameworks. Projected changes in lake thermal regimes highlight concerns about ecological impacts on aquatic species and habitats, especially as extreme and variable growing season temperatures intensify and periods of stratification become prolonged. Furthermore, we identify thermal regimes that are likely to dominate the region by the late 21st century while identifying those likely to be lost. The ecological consequences of such changes remain unknown.

Lake water temperatures are pivotal in driving biogeochemical processes (Couture et al. 2015; Farrell et al. 2024) and shaping the biology and ecology of aquatic organisms, populations, and communities (Magnuson et al. 1979; Tonn 1990; Edlund et al. 2017). These temperature-driven processes influence habitat conditions, particularly for poikilothermic freshwater fish, whose distributions are often in quasi-equilibrium with thermal conditions due to physiological constraints that define species' boundaries (e.g., Heino et al. 2009; Comte et al. 2013). While air temperature plays a significant role in influencing lake water temperatures, the two are not always directly coupled (e.g., Armitage 2023; Tong et al. 2023), limiting the reliability of air temperature as a proxy for understanding lake thermal dynamics. Because lake temperatures are infrequently measured at the resolution and scale necessary to quantify long-term change, efforts to quantify past and future changes in lake temperatures frequently rely on lake temperatures simulated from either process-based, statistical, or hybrid models (e.g., Woolway et al. 2021a, 2021b; Willard et al. 2022; Corson-Dosch et al. 2023).

Lake water temperatures fluctuate due to surficial heat fluxes, precipitation, groundwater discharge, geothermal heat fluxes, and anthropogenic impacts (e.g., Schmid and Read 2022; Piccolroaz et al. 2023). Lake size and morphology (Kraemer et al. 2015; Toffolon et al. 2014; Calamita et al. 2021), littoral canopy cover (e.g., Schiesari 2006), bathymetry

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Data Availability Statement: Datasets generated and analyzed during the current study are available as a USGS Data Release (Corson-Dosch et al. 2023). Data extraction tools, R functions, and mathematical algorithms used for analyses are all available in published R packages, and the necessary details are provided in the text to enable data replication.

(Winslow et al. 2015), and water clarity (Heiskanen et al. 2015; Rose et al. 2016) influence thermal mixing and stratification, creating lake temperature variability within and across landscapes (Soranno et al. 1999; Edlund et al. 2017; Richardson et al. 2017) and seasons (e.g., Winslow et al. 2017). Climate change is expected to elevate average water temperatures, intensify summer extremes, increase diurnal variability, lengthen stratification periods, and reduce winter ice coverage (e.g., Richardson et al. 2017; Martinsen et al. 2019; Woolway et al. 2021a; Jane et al. 2023; Piccolroaz et al. 2023), though individual lake responses to climate change vary due to lake characteristics (e.g., area, depth, clarity; Toffolon et al. 2014; Kraemer et al. 2015; Rose et al. 2016). Surface temperatures, stratification, and/or degree days are typically the focus of assessments of climate change impacts on lakes (Schupp 1992; Magee and Wu 2017; Winslow et al. 2017), but the complexity of lake thermal dynamics is not always encompassed by annual summaries (e.g., Martinsen et al. 2019), highlighting the need for a more comprehensive approach to evaluating spatiotemporal lake temperature patterns and to predict responses to climate change.

A structured approach to organizing data across various spatial and temporal scales is essential to understanding how lakes and their ecosystems respond to climate change. Examining thermal regimes across multiple dimensions—defining seasonal and annual cycles of water temperatures for specific regions—provides an effective means of characterizing these responses (Caissie 2006; Isaak et al. 2018). Such frameworks categorize environmental variability in terms of magnitude, frequency, timing, rate of change, and duration, quantifying and comparing changes across systems (Caissie 2006). At local scales, this approach can help identify lakes with similar seasonal and annual temperature cycles, providing a baseline for examining lake responses to changing climates (Maheu et al. 2016). At broader scales, it complements traditional large-scale classifications (e.g., by ecoregion; Maberly et al. 2020) and imposes finer-resolute insights into regional variability in water temperature. Furthermore, novel, non-analog thermal patterns in lakes are likely to emerge as climate change progresses (e.g., Ordonez and Williams 2013). A multi-dimensional examination of thermal regimes can serve as a robust tool for detecting unprecedented shifts in lake thermal regimes, predicting ecological impacts on aquatic biota, and assessing spatiotemporal variability in lake temperatures, ultimately improving our understanding of ecological responses to a rapidly changing climate.

Here, we present a broad-scale assessment of temperate lake annual thermal regimes. We define thermal regimes primarily based on the seasonal and annual dynamics of lake surface water temperatures and stratification patterns and related thermal metrics. We focus on the thousands of temperate lakes in the lake-rich upper Midwest, USA, where densities range between 0.358 and 0.826 lakes per km^2 (McDonald et al. 2012). Midwestern lakes are vulnerable to climate-driven thermal shifts (e.g., Hansen et al. 2017; Custer et al. 2024), which may lead to increased productivity and algal blooms (Monteith et al. 2007; Heathcote et al. 2015), reduced dissolved oxygen (Bukaveckas et al. 2024), and shifts in the aquatic community toward warm-water species dominance (Stefan et al. 2001; Graham and Harrod 2009; Hansen et al. 2017, 2022). We employed a comprehensive approach to characterize current thermal regimes and help anticipate their responses to ongoing climate change. Using simulated daily, depth-specific water temperatures simulated for current (1980–2021) and future (2040–2059, 2080–2099) periods for 11,412 Midwestern lakes (Corson-Dosch et al. 2023), we identify lake clusters accounting for annual, seasonal, and event-specific temperature variability across and within lakes and track projected changes associated with climate change. Notably, we anticipate the emergence of novel, non-analogous thermal regimes by the end of the 21st century, underscoring the scale and shape of change facing these ecosystems. Our findings provide critical insights into the multifaceted nature of lake thermal regimes across a vast geographic region and offer a powerful framework for predicting ecological responses under future warming scenarios. Furthermore, we posit that our results can help in informing more precise, targeted conservation strategies for the diverse and vulnerable aquatic communities inhabiting Midwestern lakes.

Methods

Spatial and temporal domain

Supporting Information Fig. S1 provides a conceptual overview of our analytical framework for characterizing lake thermal regimes and projecting future changes to regimes under climate scenarios. Our approach integrates multiple multivariate statistical methods to identify patterns in contemporary thermal regimes and classify future conditions as either shifting between established regimes or developing novel, non-analogous conditions outside historical ranges.

We evaluated thermal regimes across 11,412 temperate lakes in the upper Midwest, including lakes from North Dakota, South Dakota, Minnesota, Iowa, Wisconsin, Illinois, Michigan, and Indiana (Supporting Information Figs. S2, S3). We used simulated daily water temperatures (°C) for lakes within these states from Corson-Dosch et al. (2023), applying the General Lake Model (GLM3.0; Hipsey et al. 2019), as error rates were deemed minimal (RMSE = 2.19; Supporting Information Fig. S4). The GLM is a process-based, one-dimensional model of lake temperatures driven by either daily or hourly meteorological data and parameterized with lake-specific characteristics to predict year-round, mean daily temperatures at various depths from the lake bottom. Model outputs were resampled using interpolation to generate averaged daily temperature for every day of the year, at 0.5 m depth intervals for each lake.

We used simulated temperature data for lakes during 1980–2021, driven by meteorological inputs from the North

American Land Data Assimilation System (NLDAS; Mitchell et al. 2004). Future temperature projections (2040–2059, 2080–2099) were available for 9133 of the 11,412 (80.03%) lakes, and lake temperatures were simulated, driven by downscaled drivers from six Global Circulation Models (GCMs) under a high-emissions scenario (RCP8.5; Notaro et al. 2015, and described in Winslow et al. 2017). To minimize potential bias in water temperatures driven by different meteorological driver datasets between contemporary and future time periods, we used historic projections included with each GCM to calculate lake-specific projected differences in each temperature metric between historical (1980–2000) and projected future periods (2040–2059, 2080–2099) for each lake. These lake-specific differences were then added to contemporary (NLDAS) temperature metrics for each lake (1980–2021). This approach allowed us to use the most complete dataset for estimating contemporary thermal regimes while also projecting future changes in temperatures provided by the GCMs.

Defining and calculating thermal metrics

Using mean daily water temperatures, both surface and depth-integrated, for each lake, we derived thermal metrics representing various facets of lake thermal regimes. Sub-zero predicted water temperatures were set to zero, assuming ice formation occurs when air temperatures drop below freezing, rendering surface temperatures relatively stable (e.g., Crisp and Howson 1982). We summarized daily temperature data across annual periods (e.g., monthly, seasonal) to capture diverse thermal properties. For example, average July water temperatures for 1980–2021 illustrate the thermal heterogeneity across lakes in the study area (Supporting Information Figs. S2, S3). In total, we computed 34 thermal metrics that capture six aspects of annual thermal regimes: magnitude, variability, frequency, timing, duration, and rate of change (Supporting Information Table S1). We calculated most metrics (31 out of 34) using surface water temperatures (0.0 m depth) to align with common in situ temperature observations. We extracted three metrics across entire depth profiles from Winslow et al. (2015) to describe vertical temperature variations (Supporting Information Table S1). Thermal metrics were calculated annually, and we then calculated mean values for each period (contemporary, 1980–2021; mid-century, 2040–2059; and late century, 2080–2099). Subsequent analyses use both daily temperatures and annual temperature metrics as inputs.

Identifying contemporary patterns in temperate lake thermal regimes

Principal component analysis

We used principal component analysis (PCA) to explore relationships among metrics for contemporary thermal regimes in temperate lakes, reducing the dimensionality of non-normal, multi-scalar data into *n* interpretable axes that reveal underlying patterns (Maćkiewicz and Ratajczak 1993). To prepare data for the PCA, we checked for multicollinearity among thermal metrics using the variation inflation factor (VIF) using the "vif" function from the "car" tools package (Fox et al. 2007) in Program R (version 4.3.2; R Development Core Team 2024) and removed highly correlated (VIF < 5.0) and ecologically similar metrics (nine removed; Supporting Information Table S1). Our input matrix included 11,412 lakes as rows and the remaining 25 thermal metrics as columns. The PCA produced principal components (PCs), with each axis representing linear combinations of the data weighted by eigenvector coefficients (Maćkiewicz and Ratajczak 1993). The first PC captured the highest variance in the dataset, with subsequent PCs capturing decreasing variance while remaining orthogonal to prior PCs. We deemed PC axes significant if they explained over 10.0% of variation and had eigenvalues > 1.0. We ran the PCA using the "prcomp" function from the "stats" tools package and assessed significant correlations between lake-specific characteristics and PC axes using Pearson's *r* (via "rcorr" function in the "Hmisc" package; Harrell Jr and Harrell Jr 2019).

To identify groups of lakes with similar thermal regimes during 1980–2021, we applied hierarchical cluster analysis on the PCA scores, using Ward's linkage method based on Euclidean distances. We evaluated cluster stability with the "Elbow Method," plotting within-cluster sum of squares (WSS) against cluster numbers to identify distinct clusters. We then mapped these clusters to the 11,412 Midwestern lakes, visualizing regions with shared thermal characteristics across the Midwest. We used the "hclust" function from the "cluster" tools package to perform the analysis (Maechler et al. 2013). Using the first two PCs, we constructed a convex hull around each identified cluster to delineate multivariate boundaries with the "chull" function from the "geometry" package (Grasman and Gramacy 2010).

T-mode principal component analysis

For each unique cluster, we performed a T-mode PCA analysis (Richman 1986) to examine annual spatial phases in water temperatures that may emerge at a landscape scale. A T-mode PCA analyzes variations across time (e.g., daily temperatures) rather than specific metrics, simplifying continuous time-series observations. A spatial phase herein represents how the spatial distribution of lake temperatures shifts temporally across lakes and, thus, the landscape, reflecting different spatial patterns at different times of the year. The input data matrix comprised mean daily water temperatures with columns for each of the 366 d (starting January 1) in a year and rows for the temperate lakes in each cluster. The number of PC axes explaining significant variation (> 10.0%) reflects distinct spatial phases in lake temperature patterns, with crossing PC vectors indicating phase transitions (Gallacher et al. 2017). One or more significant PCs suggest shifts in spatial patterns over time, while a single dominant PC implies stable spatial temperature patterns across lakes throughout the year. Eigenvector loadings for each PC axis, thus, capture temporal signals in dominant spatial temperature patterns. For instance, similar-magnitude loadings with the same sign indicate an average spatial pattern, such as a consistent latitudinal temperature gradient, while variable or sign-changing loadings suggest seasonal spatial shifts (e.g., strong summer gradients but minimal winter variation). Multiple PCs that do not cross imply distinct aspects of spatial temperature variability among periods, with certain lakes differently contributing throughout the year. To visualize temporal shifts in spatial phases, we plotted eigenvector loadings from dominant PCs for each day and mapped select mean daily water temperatures during these phases across the Midwest (*see* Supporting Information). This analysis provides insight into distinct, time-varying spatial patterns of lake thermal regimes within each cluster across the region.

S-mode principal component analysis

We conducted an S-mode PCA (Richman 1986) to evaluate temporal covariance in water temperature regimes within each lake cluster. The S-mode PCA eigenvector loadings reveal lakes with similar temporal patterns in water temperature, adjusted for spatiotemporal correlations. This analysis enables us to examine lake-specific characteristics when temporal temperature patterns do not co-vary. The number of PC axes explaining significant variation (> 10.0%) indicates distinct periods where temperature dynamics among lakes either covary or diverge, with crossing PC vectors marking transitions between these periods (e.g., Isaak et al. 2018). Typically, the first PC captures most of the data's variation due to seasonal water temperature dynamics (e.g., Supporting Information Fig. S3), but if another PC explains comparable variation, it implies that temperature patterns diverge among lakes, which could be driven by localized conditions during transitional periods (e.g., fall or spring). Further, influential PC axes that do not cross or separate when plotted suggest that localized conditions do not differentially impact temperature patterns year-round. For S-mode analysis, we transposed the T-mode data matrix for each lake cluster, with lakes as columns and daily mean temperatures as rows, disaggregating by year to capture hydroclimatic variation. This matrix comprised over 15,000 daily temperature values (one for each day from 1980 to 2021) across the lake clusters. We explored the influence of lake-specific characteristics on temporal covariance in temperature using a generalized linear model ("glm" function) on S-mode PC2 scores, with log-transformed lake characteristics from Supporting Information Table S1 as continuous, fixed effects and cluster identity as a categorical, fixed effect, identifying characteristics impacting thermal regimes across clusters.

Projected climate-driven shifts in temperate lake thermal regimes

We inferred climate-driven alterations in thermal regimes using a discriminant analysis of principal components (DAPC). A DAPC is similar to a PCA but uses a supervised method to maximize the separation among predefined clusters while reducing dimensionality (e.g., Chorak et al. 2019). We used DAPC to determine which thermal metrics are causing multivariate changes in regimes across time periods within each lake cluster we identified. We used a priori groupings of lakes by previously identified lake clusters and periods (1980–2021, 2040–2059, and 2080–2099) to initiate the analysis. We used the "dapc" function from the "adegenet" tools package (V2.0.1) to perform the analysis (Jombart et al. 2010). To assess the contribution of individual thermal metrics to these multivariate shifts, we extracted variable contributions from the linear discriminant (LD) axes to determine their influence on cluster differentiation. We compared absolute differences in LD scores between periods and clusters using the "MCMCglmm" function from the "MCMCglmm" package (V.2.35) and default priors (Hadfield 2010), providing robust estimates of uncertainty around changing LD scores. This provides a cluster-focused assessment of changing LD scores, showing how the combination of thermal metrics differs across time periods and contributes to the broader understanding of cluster thermal stability or shifts. We extracted the mean eigenvalue for the first LD axis for each lake cluster to visualize the absolute magnitude of shifts in multivariate space, and thereby thermal regimes, across periods.

Identifying transitional and novel, non-analog temperate lake thermal regimes

To quantify transitional and novel, non-analog lake thermal regimes, we analyzed thermal regimes across time periods (1980–2021, 2040–2059, and 2080–2099). Using the first two PCs from the original analysis, we constructed convex hulls around the six lake clusters identified and a general convex hull around all clusters with the "chull" function (Grasman and Gramacy 2010) to delineate multivariate boundaries defined by these PCs. We then projected the thermal regime data from both future periods onto the PC space of current regimes using the "predict" function. We used standardized Euclidean Distances (SEDs) to quantify the degree of dissimilarity between current (1980–2021) and future (2040–2059 and 2080–2099) lake thermal regimes:

$$SED_{k,j} = \sqrt{\sum_{k=1}^{n} \left(b_{k,j} - a_{k,j}^2\right) / S_{k,j}^2}$$

Here, n determines the number of thermal regime metrics used to estimate similarity, and $a_{k,i}$ and $b_{k,i}$ represent the current and future thermal regimes for the i^{th} lake. We standardized distances using the current thermal regime variability ($S^2{}_{k,j}$) to scale all variables, enabling analog or non-analog identification across multiple metrics (Ordonez and Williams 2013).

We analyzed projected climate-driven changes in lake thermal regimes by comparing SEDs against a 95^{th} percentile threshold, ensuring conservative climate analog determinations (Ordonez and Williams 2013). Using these projections, we assessed shifts in lake positions relative to each historical cluster's convex hulls and into nearby PC space, reflecting potential changes in thermal regimes under future climate scenarios. Lakes were classified as either shifting cluster identity, transitional, or non-analogous. Cluster shifting was defined as lakes moving from their original cluster (based on 1980–2021 temperatures) to another cluster in PC space, indicating shifts in multivariate thermal properties. We defined transitional lakes as those occupying PC space in between historical convex hulls but not outside the hull over the aggregate of clusters. These transitions inherently involve minor shifts in lake conditions due to changing gradients and covariances rather than absolute changes in individual variables. Non-analogous lakes, in contrast, occupied novel PC space outside the bounds of all historical clusters, indicating unprecedented and novel thermal regimes. We identified thermal metrics driving non-analogous changes by calculating each lake's deviation from the PC mean and creating a vector of contributions for each variable, where more extreme values indicate a stronger influence on dominant PCs. This lake-specific approach differs from the DAPC by focusing on individual lake transitions within the multivariate space, offering a detailed perspective on how non-analogous lakes arise from historical thermal regimes over time.

Results

Identifying contemporary patterns in temperate lake thermal regimes

Principal component analysis

Water temperatures across Midwestern lakes exhibited substantial spatial and temporal variability in their physical characteristics and thermal regimes. Most lakes were relatively small (median ≈ 0.28 km^2), with moderate maximum depths (6.71 m), mid-range elevations (374.0 m), and shallow light extinction values (0.69 m; Supporting Information Fig. S2). Annual temperature patterns differed widely, with lakes in the southern portion of our study region (Illinois and Indiana) experiencing warmer conditions and extended growing seasons compared to those in northern regions (e.g., Minnesota, Wisconsin, and Michigan; Supporting Information Figs. S2, S3). For example, mean annual surface water temperatures across lakes ranged from 7.34 to 18.91°C, and the frequency of hot days (no. days with water temperatures > 20.0°C) ranged from 17.19 to 169.60 d (*see* Supporting Information Table S2 for a complete summary).

Most variation in lake thermal regimes was driven by seasonal temperature patterns, and influenced by elevation, latitude, and lake depth. Two PCs accounted for 80.23% of the variation among the 25 lake temperature metrics. The first PC (PC1) explained 62.17% of the variation (standard deviation = 3.94) and was negatively associated with the duration of cold water temperature days and the date of 50% of the annual degree days, and positively associated with the average July, spring, and summer water temperatures and the growing season length (Fig. 1). First PC scores were positively correlated with light extinction (Pearson's $r = 0.84$, $p = 0.02$) and negatively correlated with both elevation ($r = -0.94$, $p = 0.002$) and latitude ($r = -0.98$, $p = < 0.001$), which were both correlated with each other ($r = 0.93$, $p = 0.002$; Table 1). The second PC (PC2) explained 18.08% of variation (standard deviation = 2.13) and was positively associated with the warming rate of water temperatures, the standard deviation of summer temperatures, and the date of stratification, and negatively associated with the average Julian date at which 50% and 75% of the annual degree days were accumulated and the mean fall daily water temperatures (Fig. 1). The PC2 was positively correlated with the maximum lake depth ($r = -0.96$, $p = < 0.001$; Table 1). Subsequent PCs did not explain significant variation in the temperature metrics (≤ 4.99%). Maps of PC1 and PC2 scores indicated a spatial patterning in temperature metrics across the Midwest (Fig. 1). The PC1 shows a consistent spatial patterning where PC scores decrease with increasing latitude, whereas patterning for PC2 shows a more heterogeneous mix of PC scores scattered throughout the Midwest given their association with lake-specific maximum depth (Table 1; Fig. 1).

We identified six distinct clusters of lakes with unique thermal regimes and little overlap in two-dimensional space (Fig. 2a). Of the 11,412 Midwestern lakes, we classified 4258 (37.3%) as Cluster 1, 1759 (15.4%) as Cluster 2, 2003 (17.6%) as Cluster 3, 950 (8.3%) as Cluster 4, 2138 (18.7%) as Cluster 5, and 304 (2.7%) as Cluster 6 (Table 2). Convex hulls for each lake cluster showed little overlap in multivariate space, indicating distinct thermal regimes with minimal similarity among clusters (Fig. 2a). Spatial patterning of clusters across the 11,412 Midwestern lakes highlighted several areas where clusters are geographically restricted (e.g., Cluster 6 in southern regions throughout Illinois and Indiana) and others where many cluster types are present in a geographically proximal areas (e.g., Clusters 2, 3, and 4 in central Minnesota; Fig. 2b). We provide descriptions of thermal characteristics and basic characterizations of lakes thermal regimes assigned to each cluster in Table 2. We provided normalized calculations of the 25 included water temperature metrics for each lake cluster in Supporting Information Fig. S12.

T-mode principal component analysis

Lake clusters exhibited distinct seasonal dynamics in water temperature spatial phases, with some exhibiting stable temperature dynamics and others undergoing seasonal shifts. Most clusters exhibit stable temperature patterns across the Midwest during certain periods of the year, while others, like Clusters 1 and 2, experience pronounced seasonal spatial phases (Fig. 3). Results from the T-mode PCA showed that the first three PCs explained 84.56% of the variation for Cluster 1and 78.92% of the variation for Cluster 3. We also found that the first two axes explained 81.09% of the variation for Cluster 2, 80.18% of the variation for Cluster 4, 80.73% of the

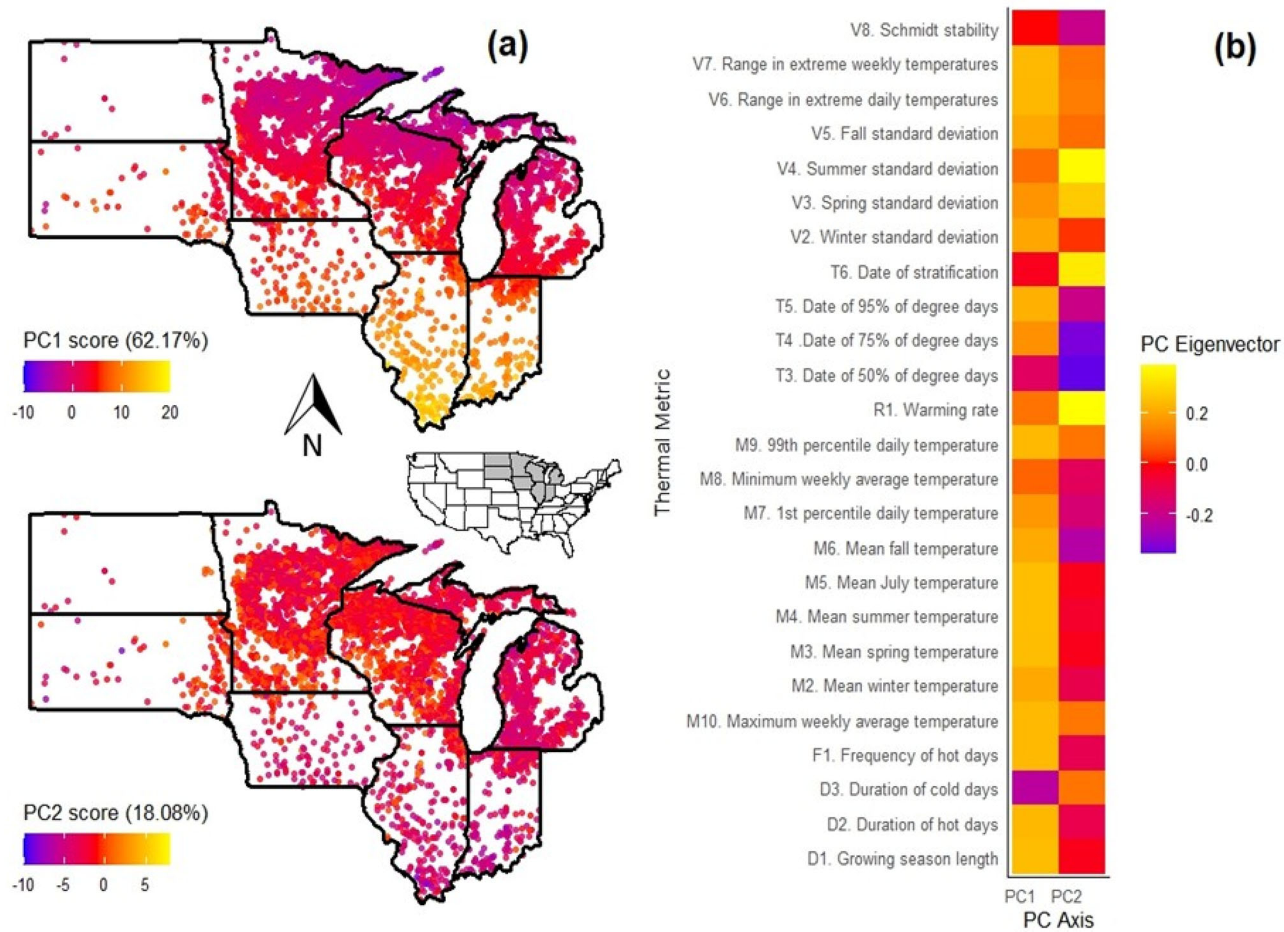

Fig. 1. Principal component scores for the first two PC axes mapped to the 11,412 lakes throughout the Midwest during 1980–2021 (**a**). Eigenvector loadings of the thermal metrics on the first two principal components in the PCA (**b**).

Table 1. Pearson's correlation coefficients and *p*-values for correlations among lake temperature principal components and characteristics of the 11,412 lakes throughout the Midwestern United States. We calculated statistics from the predicted time series and mean daily values between 1980 and 2021.

	PC1	PC2	Lake area (km^2)	Maximum depth (m)	Elevation (m)	Light extinction (m)	Latitude
PC1	1						
PC2	0.027 (0.95)	1					
Lake area (km^2)	−0.006 (0.99)	−0.35 (0.49)	1				
Maximum depth (m)	0.22 (0.63)	**−0.96 (< 0.001)**	0.26 (0.57)	1			
Elevation (m)	**−0.94 (0.006)**	0.13 (0.79)	−0.13 (0.79)	0.04 (0.93)	1		
Light extinction (m)	**0.84 (0.02)**	0.46 (0.30)	−0.19 (0.68)	−0.60 (0.16)	−0.69 (0.09)	1	
Latitude	**−0.98 (< 0.001)**	0.12 (0.80)	−0.07 (0.89)	0.09 (0.86)	**0.93 (0.002)**	−0.75 (0.052)	1

variation for Cluster 5 and 89.08% of the variation for Cluster 6. Daily eigenvalue loadings indicated when distinct spatial phases occur for each lake cluster (i.e., phase shift occurs when PC lines intersect; Fig. 3). For example, a spatial phase transition in Cluster 2 occurred around 23 February (Julian day 54) and 12 December (346), suggesting that the average spatial patterning of water temperatures across sites remained stable (indicated by largely positive and stable loading values) for the majority of the year but changed for approximately 2.5 months (Fig. 3). Principal component vectors did not cross for a

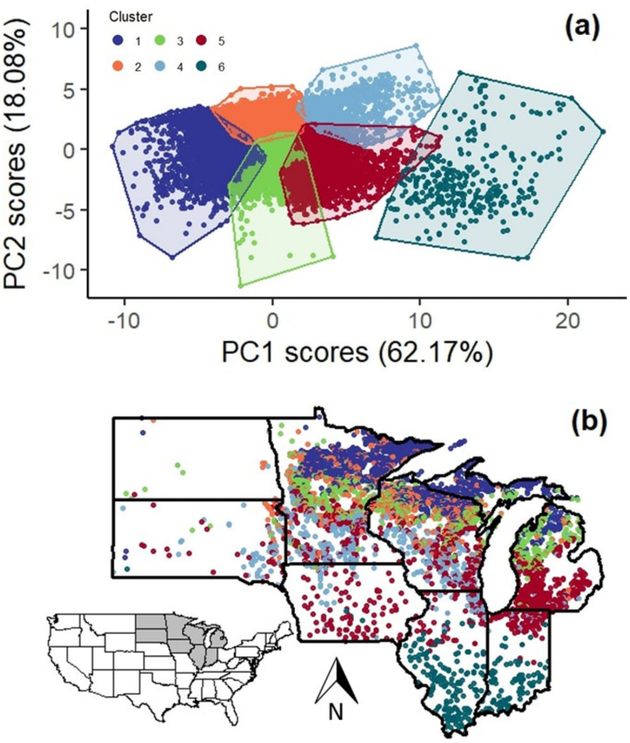

Fig. 2. Ordination plot showing the principal component scores by identified cluster for the first two PC axes derived from annual water temperature data measured at 11,412 lakes across the Midwest during 1980–2021 (**a**) and principal component scores mapped to lake locations (**b**).

significant amount of time in Clusters 4 and 6, indicating that only a minority of lakes within each cluster have strong seasonal temperature changes. *See* Supporting Information Figs. S5–S10 for example maps of distinct spatial phases in temperature patterns for each unique lake cluster.

S-mode principal component analysis

Water temperature dynamics across lake clusters were strongly seasonal, with lake-specific conditions driving deviations from general seasonal trends during transitional periods. S-mode PC1 explained over 97.50% of the temporal covariance and reflected broad seasonal temperature changes across lake clusters (Fig. 4). The PC2, on the other hand, captured localized influences on water temperature temporal covariance during transitional periods such as spring-to-summer and summer-to-fall, particularly in clusters with loop structures (e.g., Clusters 1, 3, and 6; Fig. 4). Late fall to early spring months exhibited minimal variation and were grouped within similar multivariate spaces, whereas transitional periods showed pronounced shifts along PC1, with PC2 variation evident in specific clusters (Fig. 4). Specifically, loop structures in Clusters 1, 3, and 6 suggested that localized drivers influence annual temperature patterns during transitional periods (Fig. 4; Supporting Information Fig. S11). Reconstructed annual water temperature dynamics visualize when shifts in temperature covariance occurred, typically when PC lines intersect (Fig. 5). For example, in Clusters 1 and 3 where a loop structure is present (Fig. 4), PC1 dominated and peaked mid-summer, likely reflecting seasonal warming; in spring and fall, PC2 dominance suggested transitional periods driven by local conditions (Fig. 5). In Cluster 6, PC1's summer dominance extended into late fall, while PC2 governed from winter through summer, indicating that only warming patterns are strongly influenced by localized conditions. In clusters without loop structures, relatively minimal PC line separation suggested that seasonal air temperature trends primarily drove water temperature covariance through time. Finally, broader separation in Clusters 1 and 5 during spring and fall indicated lower water temperature covariance, showing distinct temperature dynamics during these periods (Figs. 4, 5).

Lake-specific characteristics (maximum depth, surface area, light extinction, and elevation) influenced PC2 eigenvalue loadings from the S-mode PCA across lake clusters (Supporting Information Table S3; Fig. 4). In Clusters 4 and 5, at least one characteristic was not a significant predictor of PC2 loadings, potentially strengthening temporal covariance in water temperature dynamics (*see* Fig. 4). In contrast, all characteristics influenced PC2 eigenvalue loadings in Clusters 1, 3, and 6 where the loop structure was present (Fig. 4), suggesting that localized conditions influenced seasonal water temperature warming and cooling patterns. Lake cluster was the most influential predictor of PC2 loadings for Clusters 1–5, while maximum depth ($\beta = -0.149$) influenced loadings most prominently for Cluster 6 (*see* Supporting Information Table S3 for all β estimates).

Projected climate-driven shifts in temperate lake thermal regimes

Lake thermal regimes were predicted to change in response to climate change (all $p_{MCMC} < 0.001$; Fig. 6). The most informative discriminant axis, LD1, explained 78.89% of the variation in thermal regime shifts across time periods, whereas subsequent axes explained ≤ 15.50%. Increasing LD1 values represent shifts toward warmer, more variable thermal conditions, primarily driven by three key metrics with high variable contributions: frequency of hot water temperature days (DAPC variable contribution = 0.413), duration of hot water temperature days (0.375), and growing season length (0.081; Fig. 6b). The rate of thermal regime shifts in multivariate space differed by cluster, with Clusters 1 and 2 showing more pronounced changes between 1980–2021 and 2040–2059 compared to Clusters 4 and 5, which showed relatively smaller shifts (Supporting Information Table S4). Between 2040–2059 and 2080–2099, multivariate shifts in regimes were less pronounced for Clusters 4–6 (Supporting Information Table S4). Lakes from Cluster 6 showed moderate shifts in LD1 values, particularly for the late-century projection, but overall distributions remained clustered around central LD1 values.

Table 2. Description of thermal regimes and lake characteristics of the six clusters of temperate lakes across the Midwestern lakes during 1980–2021. Normalized values of thermal metrics for each unique lake cluster, which aided cluster descriptions, can be found in Supporting Information Fig. S12. Relatively stable thermal regimes exhibit consistent temperature patterns within seasons with minimal variability, while variable regimes experience greater fluctuations within and across seasons.

Lake cluster	Descriptors	Characterization	Proportion of lakes		
			1980–2021	2040–2059*	2080–2099*
1	Cool, stable, slowly warming annual thermal regimes with short growing seasons; early timing of stratification; three distinct spatial phases in water temperatures focused around late spring and fall; annual temporal cycles in water temperatures are largely modified by lake characteristics; lakes located in northern Minnesota, Wisconsin, and Michigan	Cool, stable lakes with short growing seasons	37.31%	14.76%	1.17%
2	Cool and quickly warming annual thermal regimes with short growing seasons; moderately variable, but summers are highly variable; late stratifying; two distinct spatial phases in water temperatures where the winter is distinct from the rest of the year; lakes located in the central, upper Midwest	Cool, variable lakes with short growing seasons	15.41%	57.34%	35.74%
3	Cool, moderately variable, slowly warming annual thermal regimes with short growing seasons and balanced number of cold and hot days; moderate stratification date; three distinct spatial phases in water temperatures; water temperatures are covarying across lakes, but to a lesser degree during spring and fall; lakes located in central Minnesota, Wisconsin, and Michigan	Cool, balanced lakes with moderate warming	17.55%	3.07%	2.44%
4	Warm, variable, and quickly warming thermal regimes with frequent and quick heat events; variable spring, summer, and fall water temperatures, late stratifying; two distinct spatial phases in water temperatures but some individual lakes contribute to the spatial pattern differentially during the late spring to late fall; lakes sparsely located throughout the Midwest, including southern Minnesota and Wisconsin	Warm, variable lakes with rapid warming and stratification	8.32%	15.24%	50.01%
5	Moderately cool and variable annual thermal regimes are warmer later into the year with moderate heat events and few cold days; two distinct spatial phases in water temperatures where mid-winter is distinct from the more stable remainder of the year; water temperatures are covarying across lakes, but to a lesser degree during spring and fall; lakes located throughout the central Midwest	Moderately cool, variable lakes with a warm fall	18.73%	4.36%	4.38%
6	Very warm and quickly warming thermal regimes with frequency heat events with long growing seasons and warm winters; water temperatures are highly variable but stable during the summer; early stratifying; two distinct spatial phases in water temperatures but some individual lakes contribute to the spatial pattern differentially during the late fall to mid-winter; annual temporal cycles in water temperatures are heavily modified lake-specific characteristics; lakes located in the southern Midwest	Very warm and variable lakes with long growing seasons	2.66%	0.07%	0.12%

*Column percentages do not add up to 100% given the presence of lakes classified as either "transitional" or "non-analogous."

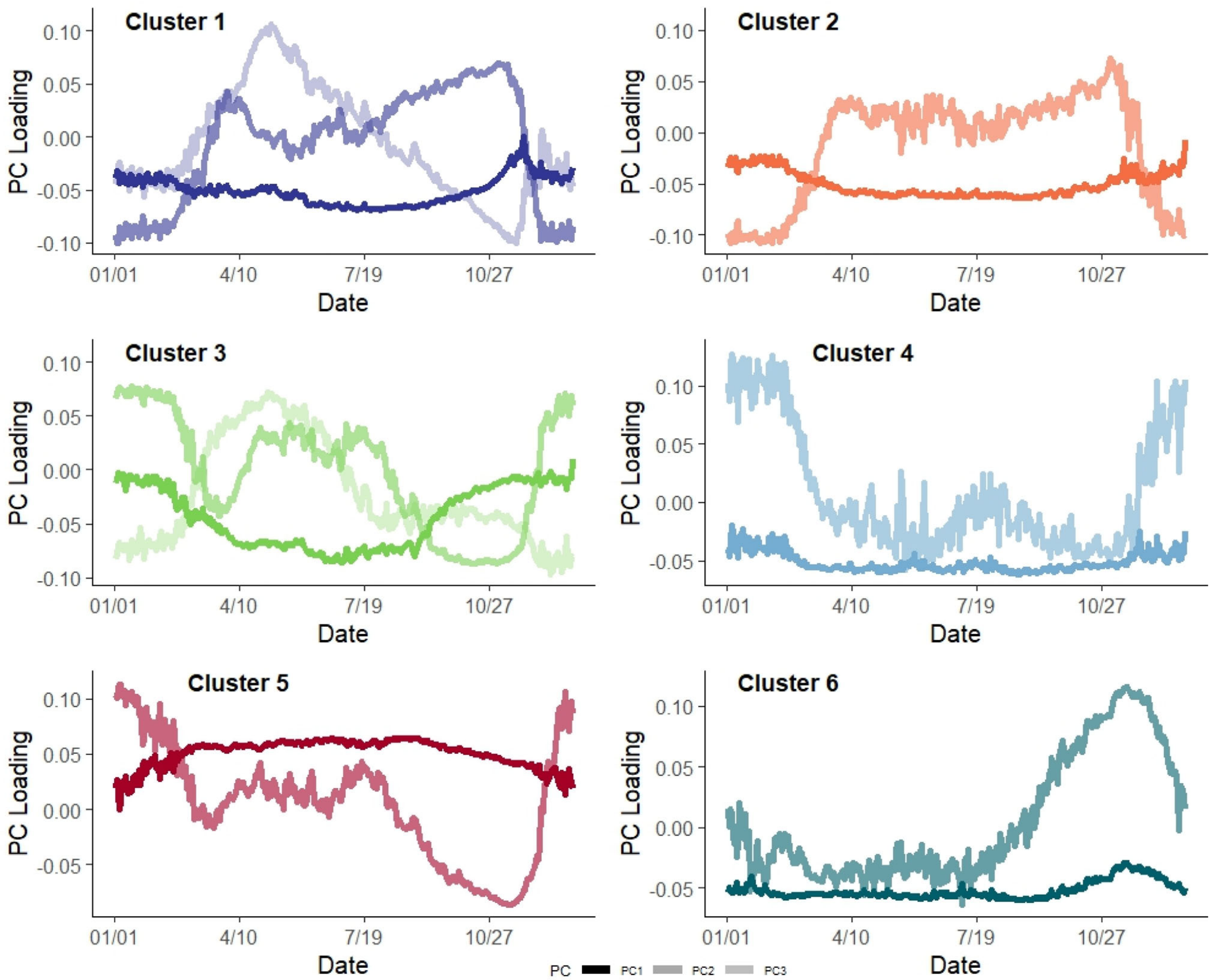

Fig. 3. T-mode PCA results showing times when dominant spatial phases, or the spatial distribution of lake temperatures across the landscape, occurred in annual water temperatures during 1980–2021 at lakes across the Midwest separated by cluster. Map colors correspond to cluster identity from Fig. 2.

Identifying transitional and novel, non-analog temperate lake thermal regimes

Most Midwestern lakes were predicted to shift clusters by the end of the 21st century, and a small number were projected to develop novel, non-analog thermal conditions (Fig. 7; Supporting Information Fig. S13). By 2040–2059, many lakes remained in their original clusters (23.3%) but a large proportion shifted into different clusters, specifically into Cluster 2 (57.4% of all lakes; Table 2; Fig. 7; Supporting Information Fig. S13). Most lakes were classified as Cluster 2 ($n = 5236$; 57.3%), followed by Clusters 4 (1392; 15.2%) and 1 (1348; 14.8%; Table 2; Fig. 7; Supporting Information Fig. S13). Cooler lake types, such as Cluster 1, remained predominant in the northern portions of the Midwest but declined in proportion, whereas southernmost lakes are experiencing pronounced warming and increased variability, exemplified by the expansion of Cluster 4 (Fig. 7). We note the emergence of lakes identified as transitional (318; 3.5%; Fig. 7; Supporting Information Fig. S13), highlighting gradual shifts in thermal regimes in some lakes that do not match contemporary thermal regimes but are not yet non-analogous. Furthermore, we predicted a minority of lakes (184; 2.01%) to have novel, non-analog thermal regimes: 77 lakes were from Cluster 1, 34 from Cluster 3, 32 from Cluster 5, and 11 from Cluster 6 (Fig. 7; Supporting Information Fig. S13). The mean winter water temperature (non-analog variable contribution score = −3.42) and maximum weekly average temperature (− 1.53) negatively contributed to the emergence of non-analogous thermal regimes, while the warming rate of water temperature (6.69) positively contributed, suggesting that extreme, long-term heat events, fast warming rates, and cooler-than-expected winter temperatures are leading to

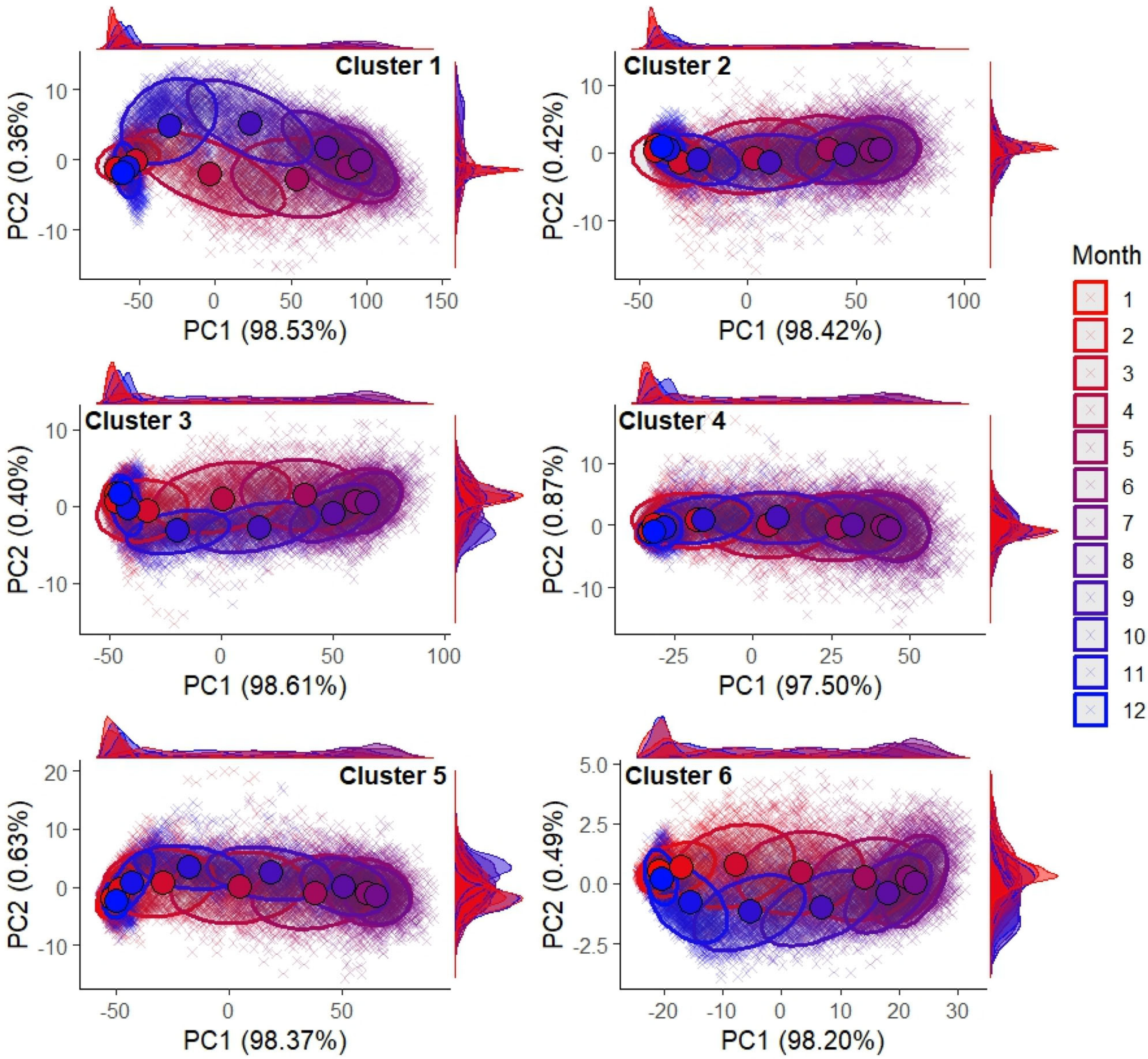

Fig. 4. S-mode PCA results showing principal component scores that describe temporal patterns in mean daily water temperatures during 1980–2021 for lakes across the Midwest separated by cluster and month. Circles represent the center of each monthly ellipse.

non-analogous lake thermal regimes (Supporting Information Table S5).

By 2080–2099, lake thermal regimes are projected to homogenize across the Midwest, with most lakes shifting toward warmer and more variable conditions, while novel and transitional regimes emerge primarily in southern regions (Fig. 7; Supporting Information Fig. S13). Most lakes transition into either Clusters 4 (4567; 50.01%) or 2 (3264; 37.7%); in contrast, other clusters accounted for fewer than 400 lakes each (Table 2; Fig. 7; Supporting Information Fig. S13). Remaining cooler lake types, like Cluster 2, are located only in the northern portions of the Midwest, while the warmer Cluster 4 becomes widespread across the southern and central locations within the Midwest (Fig. 7). We predicted fewer transitional lakes (286; 3.1%) and found that 310 (3.4%) lakes were predicted to have novel, non-analog thermal regimes, totaling 63 from Cluster 1, 42 from Cluster 3, 86 from Cluster 5, and 116 from Cluster 6 (Fig. 7; Supporting Information Fig. S13). Lakes with non-analogous thermal regimes were generally located in southern locations within Indiana and Illinois and in western Michigan (Fig. 7). The 99th percentile in daily water temperature (– 2.18) and maximum weekly average temperature (– 1.74) negatively contributed to the emergence of non-analogous thermal regimes, while the warming rate of water temperature (7.98) and the mean July temperature (6.05) positively contributed, suggesting

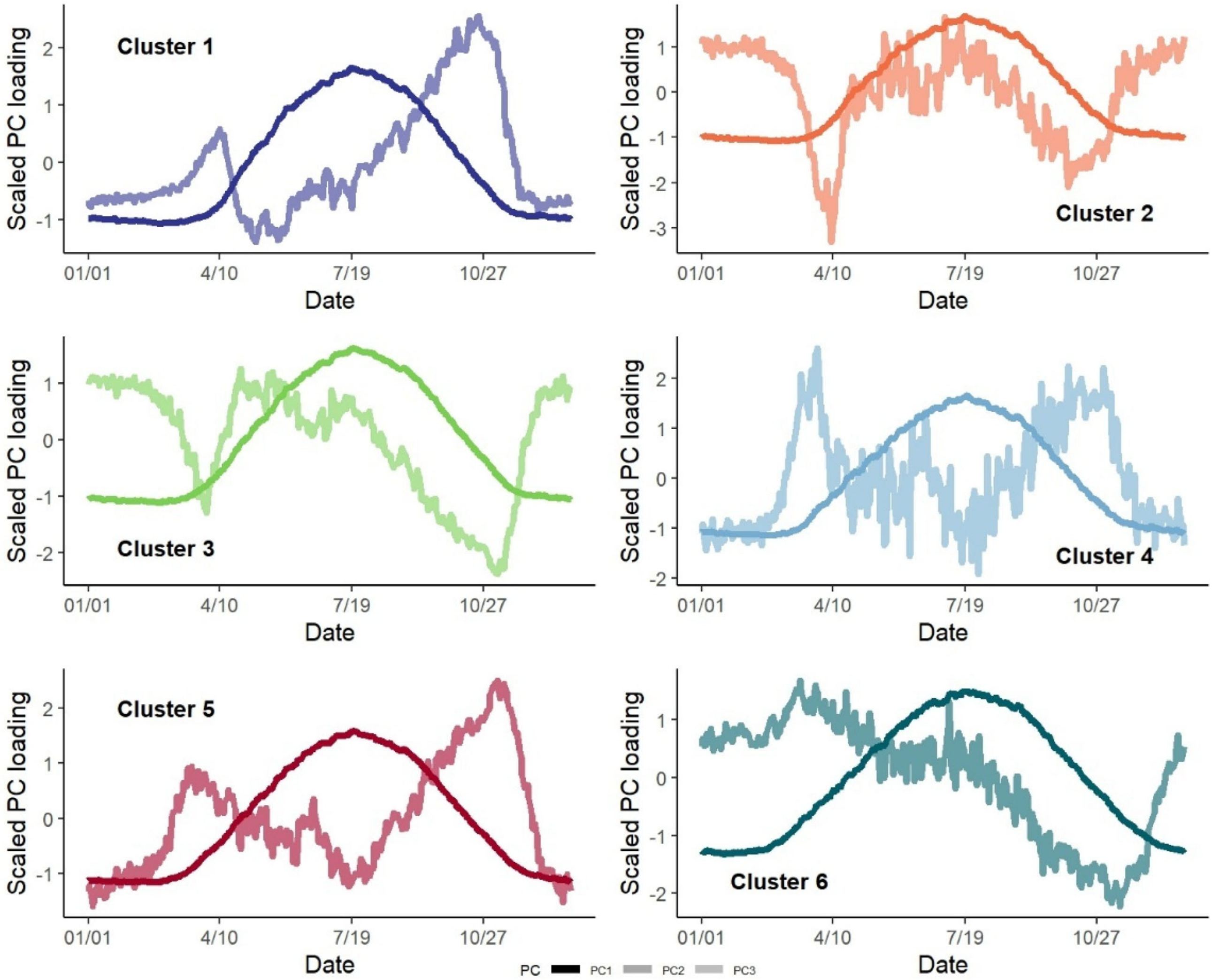

Fig. 5. Annual water temperature timing patterns reconstructed from the S-mode principal components using the scaled eigenvector loading values for PC1 and PC2 averages across years (1980–2021) for lakes across the Midwest separated by cluster.

that summer-specific warming and extreme heat events are dominant drivers of non-analogous regimes by 2080–2099 (Supporting Information Table S5).

Discussion

Our study highlights spatiotemporal variability of thermal regimes across Midwestern lakes, primarily influenced by seasonal temperature dynamics. Lakes across the upper Midwest displayed regionally distinct thermal patterns, where some regimes adhered to annual variation in temperatures while others deviated due to the influence of lake-specific or local-scale characteristics. Process-based simulations driven by climate change projections indicate that as climate patterns shift, lake thermal regimes will respond in non-linear ways. Anticipated changes across cluster types include prolonged growing seasons and increased frequency and duration of hot water temperature days, with some lake clusters predicted to experience greater regime shifts than others. By the end of the 21st century, most lakes will experience greater temperature variability and faster warming rates. This homogenization will result in the loss of lakes characterized by more stable conditions, which currently dominate the cooler and more consistent thermal regimes. Furthermore, our analysis identified a small subset of lakes developing novel, non-analogous thermal regimes, particularly in the southernmost area of our study region, where extreme summer warming and heat events will be more pronounced. Shifting thermal regimes across Midwestern lakes may disrupt ecological baselines, challenging the resilience of temperature-sensitive aquatic organisms or processes, particularly cold-water-dependent species (e.g., Monteith et al. 2007; Hansen et al. 2017, 2022; Bukaveckas et al. 2024) if turbulent mixing of shallow and deep waters occurs (Winslow et al. 2015). As thermal

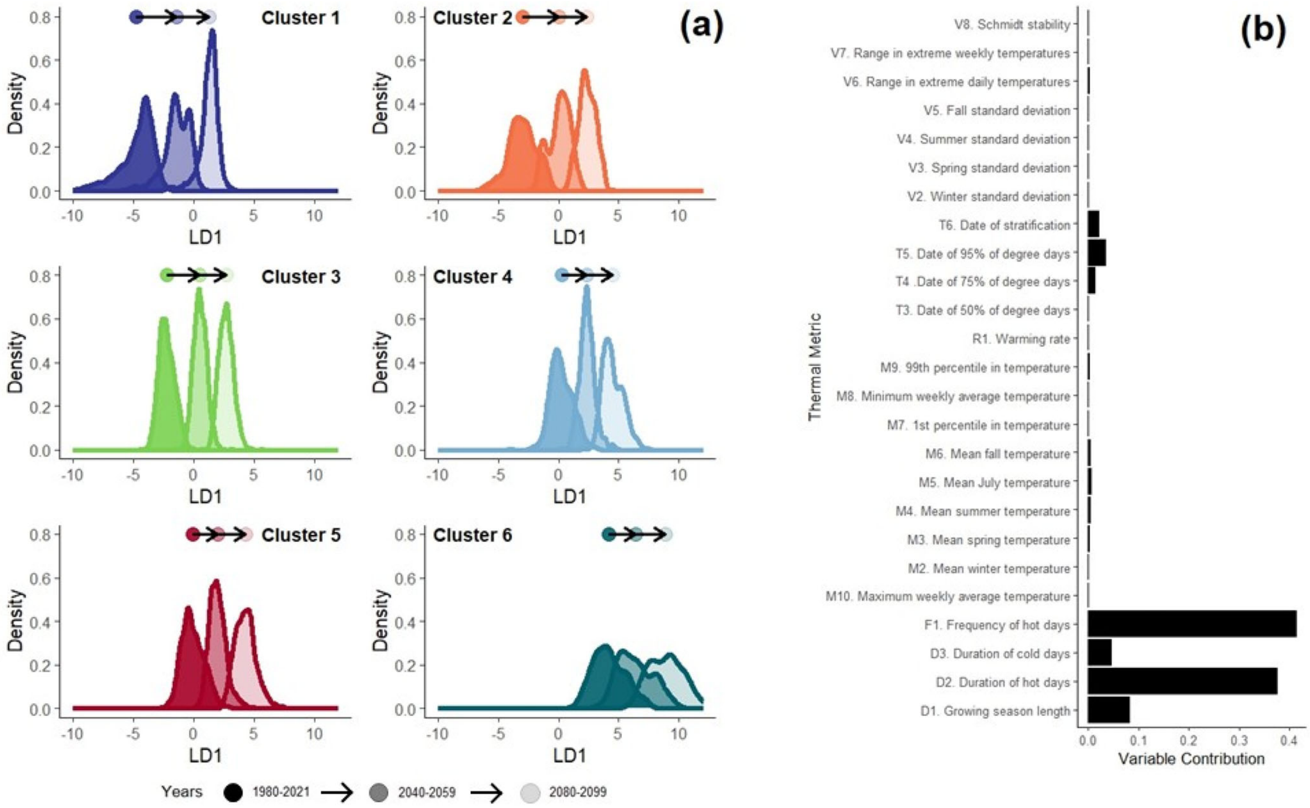

Fig. 6. Density plots of the first DAPC axis examining temperate lake thermal regimes across periods (1980–2021, 2040–2059, 2080–2099) for Midwestern lakes separated by cluster (**a**). Variable contribution values for the thermal metrics included in the DAPC (**b**).

conditions further diverge from historical norms, the ability to detect and characterize shifting or novel thermal regimes is crucial. Integrating these insights into lake conservation frameworks will help predict and mitigate biodiversity loss and ecosystem instability across the densely populated, lake-rich Midwest and lend insights elsewhere.

Our multivariate classification of Midwestern lake thermal regimes reveals six distinct clusters, primarily defined by long-term warming rates and summer temperature dynamics, with secondary influences from extreme temperature events and seasonal variability. Unlike traditional classifications based on mixing regimes (e.g., dimictic, monomictic, polymictic; Lewis Jr 1983), the clusters identified herein reflect broader thermal patterns that integrate warming rates, seasonal variability, and temperature extremes. While these clusters do not directly correspond to traditional classifications, they provide a complementary framework that accounts for both physical and ecologically relevant responses to warming. Lakes with warmer summer temperatures and extended growing seasons are likely to support higher productivity and be warm-water species dominant, while lakes with shorter growing seasons and stable winter temperatures may allow for cold-water-adapted species persistence. For instance, prolonged growing seasons and summer heat waves can increase the frequency of algal blooms and dissolved oxygen fluctuations, impacting food web stability and habitat availability (e.g., Monteith et al. 2007; Heathcote et al. 2015; Brehob et al. 2024; Bukaveckas et al. 2024). Seasonal temperature variation further influences lake phenology, influencing primary productivity, food availability, and species composition across trophic levels (e.g., Yang et al. 2018; Jane et al. 2023). Schmidt stability—a defining metric in some clusters—further shapes nutrient cycling and dissolved oxygen levels (Heiskanen et al. 2015; Farrell et al. 2024; Jane et al. 2023), with implications for the survival of oxythermal-sensitive species. For instance, lakes with prolonged stratification often develop hypoxic conditions below the thermocline, restricting habitat for cold-water fish like cisco *Coregonus artedi*, whereas more frequent mixing can moderate oxygen levels across depths (Hansen et al. 2022). By classifying Midwestern lakes based on seasonal and annual thermal variability, our approach builds on traditional frameworks and provides a foundation for future conservation efforts targeting climate-sensitive systems.

Temperate lake thermal regimes exhibit substantial heterogeneity across the landscape from 1980 to 2021, even across geographically proximate lakes or those at similar latitudes. Thermal regime variability across the landscape resulted from the complex interplay of lake-specific characteristics,

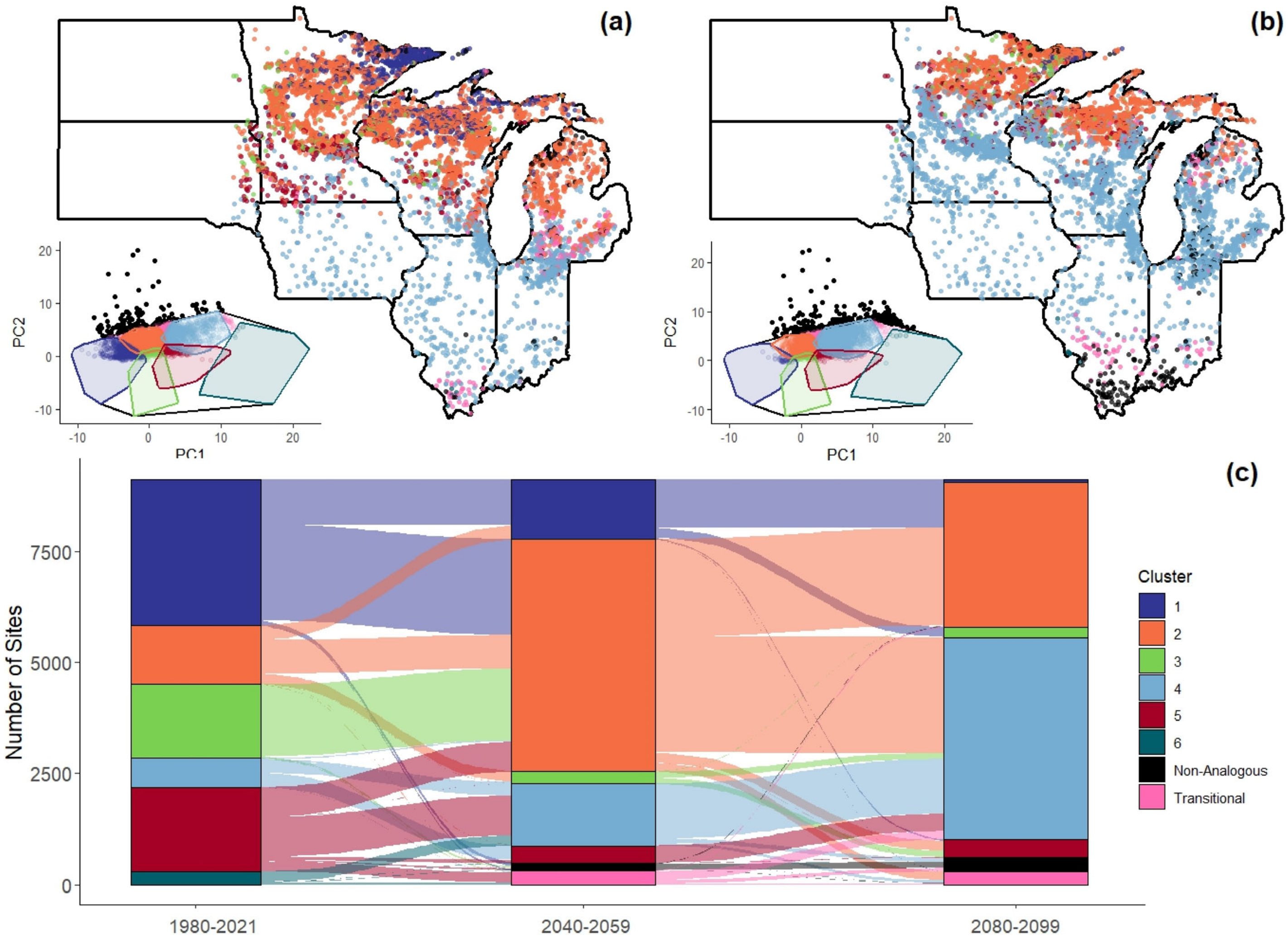

Fig. 7. Maps and ordination plots depicting cluster identity, as well as transitional and non-analog future thermal regimes, across Midwestern lakes during 2040–2059 (**a**) and 2080–2099 (**b**). The convex hull represents the boundaries defined by the PCs defined by the PCA of water temperature data from 1980 to 2021; the black convex hull represents the boundary for all lakes, not separated by cluster. Transparent points represent lakes with future thermal regimes that have current analogs or are transitional, whereas solid points outside of the boundaries represent lakes with novel, non-analog thermal regimes. Sankey plot depicting the number of lakes per cluster under current (1980–2021) and both future (2040–2059 and 2080–2099) conditions (**c**). Colored lines show movement among lake clusters and the line width is proportional to the number of lakes moving between cluster types.

including lake size and morphology (Toffolon et al. 2014; Kraemer et al. 2015; Calamita et al. 2021), water clarity (Heiskanen et al. 2015; Rose et al. 2016), and surrounding land cover (e.g., Schiesari 2006), all of which modulate annual temperature dynamics. Lake depth and morphology can affect thermal stratification, distribution, and circulation patterns (e.g., Verburg et al. 2011; Winslow et al. 2015; Yang et al. 2018), while water clarity and landscape cover (e.g., overstory vegetation) regulate solar radiation absorption and thermal energy transfer (e.g., LeBlanc et al. 1997; Torma and Wu 2019). Small variations in a lake's elevation can also interact with lake morphology and surrounding land cover to affect micro-climatic patterns, including air temperature, humidity, and wind patterns, which in turn shape seasonal warming and cooling dynamics (e.g., O'Reilly et al. 2015). Landscape-scale thermal heterogeneity has historically supported diverse aquatic species with varying thermal tolerances across the Midwest by providing thermal refugia that buffer against extreme distributional shifts. These thermal "refugia" enhance ecological resilience and sustain complex community interactions, even as climate change intensifies (Heino et al. 2009; Comte et al. 2013).

However, our findings indicate that thermal heterogeneity across Midwestern lakes is at risk of climate-driven homogenization. While the contemporary landscape supports a broad diversity of lake types, projected warming will shift most lakes into just two dominant clusters by the late 21st century. Lakes with stable, cooler thermal regimes will become increasingly rare, while lakes with warmer, more variable conditions will expand across the Midwest. This shift could weaken ecological buffering capacity, impacting aquatic biodiversity, nutrient cycling, and habitat availability for temperature-sensitive species (Hansen et al. 2017; Farrell et al. 2024). Furthermore, a small but notable subset of lakes ($n = 310$; 3.4%) will develop novel, non-analog regimes, predominantly in the southern portions of the Midwest and western Michigan. These lakes will experience extreme heat events, rapid warming rates, and altered seasonal dynamics that diverge from historical precedents, posing potential adaptation challenges for aquatic species and ecosystem processes (e.g., Custer et al. 2024). As lakes lose their historically stable thermal characteristics, species that rely on predictable seasonal transitions—such as cold-water fish, invertebrates, and planktonic communities—may face increased physiological stress and habitat loss (Heino et al. 2009; Comte et al. 2013). The loss of thermal diversity and the emergence of novel regimes could accelerate biotic homogenization across the landscape, favoring more generalist species (e.g., Kirk et al. 2020). Such changes will require resource managers to rethink conservation priorities, emphasizing adaptive strategies that maintain both thermal and ecological diversity in lakes (e.g., riparian restoration, reducing nutrient loading, fish community augmentation; Magee et al. 2019).

Our results are influenced by several sources of uncertainty inherent in both classification methods and climate projections. Corson-Dosch et al. (2023) relied on a high-emissions scenario (RCP8.5; Notaro et al. 2015) and used six GCMs to project future water temperatures, establishing an upper bound on potential warming effects. High-emission scenarios provide a useful worst-case framework that allows for conservation efforts to prepare for extreme outcomes, and averaging water temperature projections across GCMs could introduce variability because each model represents different hypotheses about climate system dynamics. Furthermore, our reliance on previously validated GLM simulations ensures that the broad-scale thermal patterns we describe are robust, even though they do not explicitly resolve lateral temperature gradients or partial ice cover but remain effective for broadly capturing vertical thermal dynamics and seasonal trends in large-scale studies of lake thermal regimes. Additionally, multivariate analyses, such as PCA and DAPC, inherently reduce data dimensionality, potentially oversimplifying or overgeneralizing complex ecological patterns by condensing diverse temperature metrics. While multivariate approaches help to organize complex datasets, they may obscure ecologically significant details, especially for low-variance metrics that nonetheless hold biological importance. To mitigate this, we sought a comprehensive set of scaled temperature metrics, yet we recognize the limitations of any classification scheme in capturing thermal complexity. Finally, our study was spatially constrained to the upper Midwest in the north-central United States, meaning that "transitional" and "novel" classifications should be interpreted within this geographic scope.

In a century increasingly defined by global warming and climatic shifts, temperate lake thermal regimes are shifting in ways that pose challenges for ecological management and adaptation (e.g., Stefan et al. 1998; Kraemer et al. 2015; Richardson et al. 2017; Martinsen et al. 2019; Jane et al. 2023; Piccolroaz et al. 2023). Local decision-makers must balance conservation efforts with the increasing complexity of climate-induced thermal regime changes (e.g., Feiner et al. 2022). Leveraging large simulated temperature datasets, like those from Corson-Dosch et al. (2023), enables ecologists to examine multiple facets of thermal regime—as well as variability, magnitude, and timing—across broad landscapes. This approach provides insights beyond monolithic metrics, capturing complex temperature dynamics across lakes while preserving the granularity necessary for local application. Furthermore, our landscape-scale analysis identifies lake clusters and key thermal metrics that are directly relevant for conservation. For example, regional insights into the expansion of summer heat waves and prolonged growing seasons inform strategies for preserving habitat for temperature-sensitive species, while resilience indicators help prioritize conservation resources (e.g., Hansen et al. 2022). Ultimately, integrating broad-scale thermal data into local management efforts will enhance climate resilience strategies, equipping practitioners to address both present conditions and future challenges, thereby safeguarding freshwater ecosystems under accelerating climate pressures.

Author Contributions

Christopher J. Sullivan designed the analysis, performed the analysis, and wrote the paper. Gretchen J. A. Hansen conceived the investigation, secured funding, and wrote the paper, and Jordan S. Read conceived of the investigation, edited the paper, and provided technical expertise.

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Conflicts of Interest

None declared.

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Supporting Information

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

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