Ecological Applications, 0(0), 2019, e01836

Geographic patterns of the climate sensitivity of lakes

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Citation: I. M. McCullough, K. S. Cheruvelil, S. M. Collins, and P. A. Soranno. 2019. Geographic patterns of the climate sensitivity of lakes. Ecological Applications 00(0):e01836. 10.1002/eap.1836

Abstract. Climate change is a well-recognized threat to lake ecosystems and, although there likely exists geographic variation in the sensitivity of lakes to climate, broad-scale, long-term studies are needed to understand this variation. Further, the potential mediating role of local to regional ecological context on these responses is not well documented. In this study, we examined relationships between climate and water clarity in 365 lakes from 1981 to 2010 in two distinct regions in the northeastern and midwestern United States. We asked (1) How do climate–water-clarity relationships vary across watersheds and between two geographic regions? and (2) Do certain characteristics make some lakes more climate sensitive than others? We found strong differences in climate–water-clarity relationships both within and across the two regions. For example, in the northeastern region, water clarity was often negatively correlated with summer precipitation (median correlation = −0.32, n = 160 lakes), but was not correlated with summer average maximum temperature (median correlation = 0.09, n = 205 lakes). In the midwestern region, water clarity was not related to summer precipitation (median correlation = −0.04), but was often negatively correlated with summer average maximum temperature (median correlation = −0.18). There were few strong relationships between local and sub-regional ecological context and a lake's sensitivity to climate. For example, ecological context variables explained just 16–18% of variation in summer precipitation sensitivity, which was most related to total phosphorus, chlorophyll *a*, lake depth, and hydrology in both regions. Sensitivity to summer maximum temperature was even less predictable in both regions, with 4% or less of variation explained using all ecological context variables. Overall, we identified differences in the climate sensitivity of lakes across regions and found that local and sub-regional ecological context weakly influences the sensitivity of lakes to climate. Our findings suggest that local to regional drivers may combine to influence the sensitivity of lake ecosystems to climate change, and that sensitivities among lakes are highly variable within and across regions. This variability suggests that lakes are sensitive to different aspects of climate change (temperature vs. precipitation) and that responses of lakes to climate are heterogeneous and complex.

Key words: climate change; LAGOS-NE; North American lakes; Secchi depth; water clarity; water quality.

Introduction

Climate change is as a major threat to lake ecosystems (Adrian et al. 2009). Understanding how lakes respond to climate variability is important not only to document climate change itself (Magnuson et al. 2000, Winslow et al. 2015), but also to predict how important lake functions may change in the future (Williamson et al. 2009). Although there likely exists geographic variation in the sensitivity of lakes to climate (Adrian et al. 2009), broad-scale, long-term studies are needed to understand this variation.

Manuscript received 11 July 2018; revised 16 October 2018; accepted 13 November 2018. Corresponding Editor: Kevin C. Rose.
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Past broad-scale research has predominantly focused on thermal responses of lakes to climate warming (O'Reilly et al. 2015, Arp et al. 2016, Woolway et al. 2017). Relatively few broad-scale studies have examined lake ecosystem responses to both temperature and precipitation and have often used just one response variable, a relatively homogenous study area, long-term climate averages, or a low number of years. For example, Kraemer et al. (2017) examined metabolic responses of 271 lakes across the globe to four decades of climate warming and found the greatest increases in low latitude/elevation lakes. Rose et al. (2017) examined water clarity responses of 5,002 lakes to precipitation in a wet year vs. a dry year within the state of Wisconsin, USA and found that clarity declines during wet years. Other studies examining either long-term changes in nutrients (Oliver et al. 2017) or water clarity (Lottig et al. 2017) across the northeastern United States used long-term annual climate averages to examine the potential effect of climate on lake responses. Therefore, it is not known how lake ecosystem characteristics respond to inter-annual or sub-annual variability in both temperature and precipitation across broad scales.

In addition to the lack of broad-scale, long-term studies of lake ecosystem responses to climate, it is difficult to predict responses to climate at macroscales (regional to continental) because local to regional ecological context (e.g., lake and watershed morphometry, watershed land use/cover, climate, hydrology) can differ at such broad scales. For example, Rose et al. (2017) found that water clarity, lake morphometry, and watershed climate and land use/cover mediate water clarity responses to precipitation within a single region, but additional research is needed to examine the importance of local to regional ecological context variables across different regions. Data limitations for local to regional ecological context variables as well as lake ecosystem responses have likely played a role in the lack of studies examining their effects on responses of lake ecosystems to climate. Increasingly, however, data sets are being compiled across broad spatial and temporal scales that can be used to conduct these studies.

A mechanistic framework for the effects of climate on lake water clarity

In this study, we examined the climate response of lake water clarity, a common water quality metric that integrates carbon, primary productivity, and turbidity. Previous studies have linked water clarity to precipitation and air temperature, which we synthesized into a single conceptual framework (Fig. 1). For example, precipitation affects water clarity through a variety of linked pathways that influence the main determinants of light in lake water: dissolved organic carbon (DOC), primary productivity, and turbidity.

Dissolved organic carbon is influenced by precipitation through its effect on the volume and timing of runoff and groundwater transport, increasing DOC concentrations in lakes (Schindler et al. 1997, Pace and Cole 2002, Williamson et al. 2014). DOC directly decreases clarity by reducing light penetration, which may limit primary productivity in the short term (Williamson et al. 1999), but DOC may also indirectly reduce clarity in the long term via increases in primary productivity from mineralization of allochthonous DOC in lakes with long hydrologic residence times (Hanson et al. 2011). Precipitation also increases connectivity and DOC transfer among waterbodies (particularly wetlands), which decreases water clarity in downstream waterbodies (Rose et al. 2017).

Alternatively, precipitation-induced increases in runoff and groundwater can increase nutrient concentrations in lakes, increasing primary productivity and reducing water clarity (Fraterrigo and Downing 2008, Jeppesen et al. 2009). Additionally, precipitation (and/or accompanying wind) produces water column turbulence, which

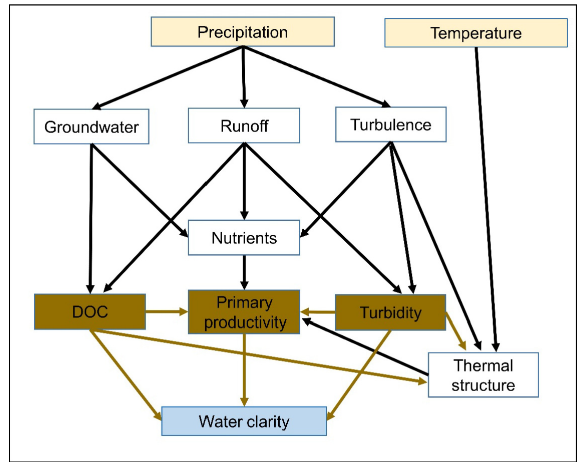

Fig. 1. Mechanisms by which precipitation and air temperatures (driver variables; beige) may affect water clarity (response variable; blue) via dissolved organic carbon (DOC), primary productivity, and turbidity pathways (brown) in lakes, which are assumed to be stratified in summer. Precipitation influences runoff and groundwater volume and timing, increasing concentrations of dissolved organic carbon (DOC), which increases water color and consequently decreases water clarity (DOC pathway). Precipitation also increases connectivity and DOC transfer among waterbodies, decreasing water clarity. Allochthonous DOC can be mineralized and increase productivity. Nutrient concentrations also increase due to precipitation, stimulating productivity and decreasing water clarity (primary productivity pathway). Precipitation also increases water column turbulence, which may lead to internal nutrient loading that increases productivity, decreasing water clarity. Turbulence may also cause sediment resuspension, increasing turbidity (decreasing water clarity) and limiting productivity. Precipitation may also increase turbidity due to sediment concentrations in runoff. Lake thermal structure is closely related to air temperature and regulates light availability and algal growth rates.

may lead to internal nutrient loading and deepening thermoclines (in stratified lakes) that further increase primary productivity (Soranno et al. 1997, Klug et al. 2012, Kasprzak et al. 2017). Primary productivity-driven decreases in water clarity, however, are also mediated by DOC (Snucins and John 2000 , Read and Rose 2013) and turbidity (Adrian et al. 2009; affecting thermal structure and light availability). In addition, grazing pressure (Carpenter et al. 2001) and hydrologic residence time (particularly in fast-flushing systems; Turner et al. 1983) also influence primary productivity in lakes.

Finally, precipitation influences turbidity through increased runoff, which directly reduces water clarity in lakes due to increased sediment concentrations in runoff and/or sediment resuspension resulting from turbulence (Søndergaard et al. 2003). Turbidity is more likely to influence water clarity in shallow, weakly stratified or glacial-fed lakes (Koenings and Edmundson 1991).

Disentangling the DOC, primary productivity, and turbidity pathways is difficult given that DOC, nutrients, and suspended sediments may enter lakes via similar mechanisms. The three pathways, however, are not mutually exclusive and our framework emphasizes that precipitation affects physical, chemical, and biological properties of lake ecosystems via a set of interacting mechanisms (Fig. 1). Therefore, predicting responses of water clarity to changes in precipitation may be complex and depend on several intertwined processes.

Mechanisms by which air temperatures affect water clarity are generally more straightforward than for precipitation (Fig. 1). Lake thermal structure is closely related to air temperature (Livingstone and Lotter 1998, Boehrer and Schultze 2008) and can influence algal growth rates and the distribution of primary productivity in the water column (Butterwick et al. 2005). Thermal structure, however, can also be mediated by DOC (Snucins and John 2000, Read and Rose 2013), turbidity (Adrian et al. 2009), and water column turbulence (Huisman et al. 2004), each of which can be affected by precipitation and/or wind (Schindler et al. 1996). In summer, deeper lakes are more strongly stratified than shallow lakes and therefore may be more susceptible to deepening thermoclines (via precipitation and/or wind), which may increase primary productivity (from nutrient runoff) and decrease clarity (Klug et al. 2012, Kasprzak et al. 2017). The potential for feedbacks and interactions between changes in temperature and precipitation underscores the need to consider changes in both temperature and precipitation when predicting and conceptualizing effects of climate change on water clarity (Rose et al. 2016).

In this study, we used a recently compiled database with long-term records of water clarity to ask two questions: (1) How do climate-water clarity relationships vary across watersheds and between two geographic regions? (2) Do certain characteristics make some lakes more sensitive to particular climate variables than others?

We expected that lakes in regions and watersheds with large amounts of agriculture and/or wetlands would be sensitive to precipitation, given that agriculture contributes nutrients (Carpenter et al. 1998, Whitehead et al. 2009) and wetlands contribute DOC to lakes at landscape scales (McCullough et al. 2012, Rose et al. 2017). We also hypothesized that precipitation-sensitive lakes would be relatively small, shallow, oligotrophic, and have high watershed area to lake area ratios (i.e., long hydrologic residence times). We expected these low-volume, nutrient-limited lakes with long residence times to experience water clarity declines in response to increases in primary productivity and DOC concentrations, as well as greater possibilities for resuspension of nutrients and sediments that may also reduce water clarity. In contrast to precipitation, we expected that temperature-sensitive lakes would be determined primarily by lake morphometry (small area, shallow) and water quality (eutrophic) rather than regional or sub-regional variables. We hypothesized that these low-volume, nutrient-rich lakes would experience increased primary productivity and reduced water clarity owing to warming water temperatures (Kosten et al. 2012). Additionally, we expected small lakes with extensively forested shorelines to be less temperature-sensitive due to canopy shading.

Methods

Study area and water clarity and ecological context data

We used LAGOS-NE (LAke multi-scaled GeOSpatial and temporal database), a publicly available lake water quality and ecological context database for lakes ≥4 ha in 17 states in the northeastern United States (Soranno et al. 2015, 2017). Water clarity data (measured as Secchi depth, m) and maximum lake depth (m) data came from LAGOS-NE-LIMNO v. 1.087.1 (Soranno and Cheruvelil 2017a). All data were extracted using the LAGOSNE R package v. 1.0.0 (Stachelek and Oliver 2017) and all analyses were performed in R v. 3.4.2 (R Core Team 2017).

We restricted water clarity data to samples collected from 15 June to 15 September to coincide with the summer stratification period. In cases of multiple samples per lake in a given year, we calculated summer means. Balancing the need for relatively long-term water clarity data and a similar set of years across study lakes, we restricted our analysis to lakes with at least 25 yr of data between 1981 and 2010 (365 lakes). Climatologists typically use 30 yr to characterize climate at a given site due to the influence of inter-annual climate variability on the signal to noise ratio (SNR). In general, longer time frames increase SNR, but published analyses of observed and modeled temperatures showed a leveling off of SNR at approximately 25 yr (Santer et al. 2011), suggesting 25–30 yr are sufficient to describe climate at a given site. Were we to include only lakes with 30 yr of data during 1981–2010, our 365-lake data set would become 86 lakes. We performed our analyses with the 25- and 30-yr data sets and found qualitatively similar results; therefore, we chose the 25-yr data set to maintain large sample size in both regions (described in next paragraph).

We divided the data into two regions based on the spatial distribution of study lakes and dominant land use/cover, hydrology, climate, and water quality. The first region (northeastern region) included 160 lakes in the U.S. states of Maine, New York, and Vermont, whereas the second region (midwestern region) included 205 lakes in the U.S. states of Michigan, Minnesota, and Wisconsin. No lakes in other states contained sufficient long-term data for our analysis period. Lake watersheds in the northeastern region were predominantly forested (median forest cover = 85%, median agriculture cover = 8%), whereas lake watersheds in the midwestern region were characterized by a combination of forest (median cover = 43%) and agriculture (median cover = 23%; Table 1). The northeastern region was characterized by greater stream density, runoff, and groundwater compared to the midwestern region. Percent wetland cover was greater in the midwestern region. Total phosphorus (TP) and chlorophyll *a* concentrations (μg/L) were consistently greater in the midwestern region, particularly for TP. In the

TABLE 1. Basic characteristics of lakes (percentiles) by analysis region.

	Northeastern				Midwestern			
Category and variable	5%	50%	95%	*n*	5%	50%	95%	*n*
Morphometry								
Lake area (ha)	14	234	2,284	157	33	223	2,651	203
Lake maximum depth (m)	7	16	51	157	5	15	40	203
Watershed area (ha) : lake area (ha)	2	6	29	157	1	4	34	203
Terrain								
Watershed mean slope (°)	3	6	12	157	1	3	6	205
Land use/cover								
Watershed forest, 1992 (%)	67	85	95	157	6	43	87	205
Watershed agriculture, 1992 (%)	0	8	25	157	0	23	75	205
Hydrology								
Watershed wetlands, current (%)	1	5	17	157	2	11	34	204
Watershed stream density, current (m/ha)	0	8	24	157	0	2	8	205
Sub-regional mean annual runoff (inches)†,‡	20	25	30	159	4	7	14	204
Sub-regional mean annual groundwater (mm)†	236	339	369	159	52	98	269	204
Climate								
Sub-regional mean annual precipitation (mm)§	1,042	1,178	1,403	160	655	771	892	205
Sub-regional mean annual temperature (°C)§	3	6	7	160	3	5	7	205
Water quality								
Total phosphorus (μg/L)¶	4	9	23	160	6	20	121	166
Chlorophyll *a* (μg/L)¶	2	4	13	152	2	6	53	194

Note: The northeastern region is Maine, New York, and Vermont; the midwestern region is Michigan, Minnesota, and Wisconsin.
†Mean annual 1951–1980.
‡1 inch = 2.54 cm.
§Mean annual 1981–2010.
¶Mean annual 1981–2010 based on available years of data only.

midwestern and northeastern regions, 16% and 64% of lakes were oligotrophic, respectively, and 37% and 3% of lakes were eutrophic, respectively, based on TP thresholds from Dodds et al. (2006). Median annual precipitation was considerably greater in the northeastern region than in the midwestern region (1,178 and 771 mm, respectively), whereas median annual temperatures were similar in both regions (northeastern, 6°C and midwestern, 5°C; Table 1).

We defined ecological context using variables that describe lake morphometry, terrain, land use/cover, freshwater connectivity, hydrology, climate averages, and long-term water quality (Soranno et al. 2017; Table 2). We considered terrain, land use/cover, and freshwater connectivity at the local watershed scale, hydrology at local watershed and sub-regional (12-digit hydrologic unit codes [HUC 12]) scales, and climate at the sub-regional scale. Whereas we used all of these variables to explain precipitation sensitivity, we used lake morphometry, climate, water quality, and percent forest cover within 100 m around lakes to explain temperature sensitivity (Table 2). Most of these data were obtained from LAGOS-NE-GEO v1.05 (Soranno and Cheruvelil 2017b), with the exception of climate averages that we calculated using 1981–2010 data from PRISM (see Climate data). A lake shapefile was obtained from LAGOS-NE-GIS v1.0 (Soranno and Cheruvelil 2017*c*). Long-term water quality means (TP and chlorophyll *a*, μg/L), which have generally not changed in our study regions since 1990 (Oliver et al. 2017), were calculated from all available years of data over 1981–2010. True color was considered, but ultimately excluded due to low data availability (midwestern region, 18 lakes; northeastern region, 63 lakes).

Climate data

We used climate data that were derived from 800-m resolution monthly PRISM climate grids (Daly et al. 2017) and extracted as 1981–2010 means for HUC 12s (Collins et al. 2018). Of the 310 HUC 12s encompassing the study lakes, 88% contained only one lake. Due to inherent multicollinearity among monthly, seasonal, and annual climate variables, we restricted our set of climate variables to annual (water year; previous October to current September) and seasonal averages of mean, maximum, and minimum temperatures, and total precipitation (20 total variables). Seasons were defined as fall, September–November; winter, December–February; spring, March–May; and summer, June-August (Collins et al. 2018).

Table 2. Ecological context variables used to compare to sensitivities of water clarity to climate.

Category	Summer precipitation	Summer maximum temperature
Morphometry	lake area (ha), lake maximum depth (m), watershed area (ha) : lake area (ha)	lake area (ha), lake maximum depth (m)
Terrain	watershed mean slope (°)	
Land use/cover	watershed forest, 1992 (%), watershed agriculture, 1992 (%)	forest within 100-m buffer of lake, 1992 (%)
Freshwater connectivity	watershed wetlands, current (%), watershed stream density, current (m/ha)	
Hydrology	sub-regional mean annual runoff (inches),† sub-regional mean annual groundwater (mm)†	
Climate	sub-regional mean annual summer precipitation (mm)‡	sub-regional mean annual summer maximum temperature (°C)‡
Water quality	total phosphorus (μg/L),§ chlorophyll *a* (μg/L)§	total phosphorus (μg/L),§ chlorophyll *a* (μg/L)§

†Mean annual 1951–1980.
‡Mean annual 1981–2010.
§Mean annual 1981–2010 based on available years of data only.

Data analysis

We mapped climate–water-clarity relationships (climate sensitivities) across the study area using Pearson correlation coefficients (r values) between water clarity and each of the 20 climate variables. We used correlation coefficients rather than slope values to obtain a relative effect of climate across lakes of varying depths. We used random forests in the randomForest R package (Liaw and Wiener 2002) to identify which ecological context variables were the best predictors of the sensitivity of clarity to the top climate predictor of water clarity in the northeastern and midwestern region, respectively (summer precipitation and summer maximum temperature, respectively; see *Results* and Table 2). Variables with negative importance (measured by percent change in mean square error) were discarded and random forests were subsequently rerun. We conducted preliminary analyses with up to 5,000 trees, plotted change in error as a function of number of trees, and selected 500 trees for each random forest because error flattened at about this value (Breiman 2001).

We also calculated univariate correlations between climate sensitivity for summer precipitation and summer maximum temperature and ecological context variables, including those excluded from random forests. The objective of the univariate correlations was to examine the strength and direction of relationships between climate sensitivities and individual ecological context variables, aiding interpretation of random forest results.

Results

Geographic patterns of climate sensitivity

There were differences in climate sensitivities of lakes between the northeastern and midwestern regions. Overall, summer climate variables were the most important predictors of summer water clarity in both regions, but lakes in the northeastern region were more sensitive to precipitation (Fig. 2a, c) and lakes in the midwestern region were more sensitive to temperature (Fig. 2b, d). In both regions, approximately one-third of lakes exhibited no significant correlations between clarity and any climate variable (northeastern, 33%; midwestern, 32%). Although median climate sensitivities were weak (absolute $r < 0.10$) for most climate variables in both regions, a few strong correlations exhibited regional patterns (Table 3).

Among all climate variables, lakes in the northeastern region were most sensitive to summer precipitation (median $r = -0.32$), with 40% of lakes exhibiting significant correlations with water clarity (Fig 2a, Table 3). Water-year precipitation was a weaker predictor (median $r = -0.19$) than summer precipitation and was significantly correlated with water clarity in 23% of lakes. Sensitivities to summer maximum temperature in the northeastern region were generally weaker (median $r = 0.09$) than for lakes in the midwestern region (Fig. 2d, Table 3). In contrast, sensitivities to summer precipitation in the midwestern region were weak (median $r = -0.04$) (Fig. 2c), whereas sensitivities to temperature were greatest for summer maximum temperature (median $r = -0.18$), for which 21% of lakes demonstrated significant correlations (Fig. 2b, Table 3). Summer temperature variables (median $r = -0.18$ to -0.14) were overall stronger predictors than annual temperature variables (median $r = -0.11$ to -0.06) in both regions (Table 3).

In each region, we found both positive and negative correlations between water clarity and all climate variables, indicating intra-regional variability of climate sensitivities (Table 3). For example, correlations between clarity and fall minimum temperatures ranged from -0.35 to 0.48 and -0.40 to 0.51 in the northeastern and midwestern regions, respectively (5th and 95th percentiles). Intra-regional variability occasionally

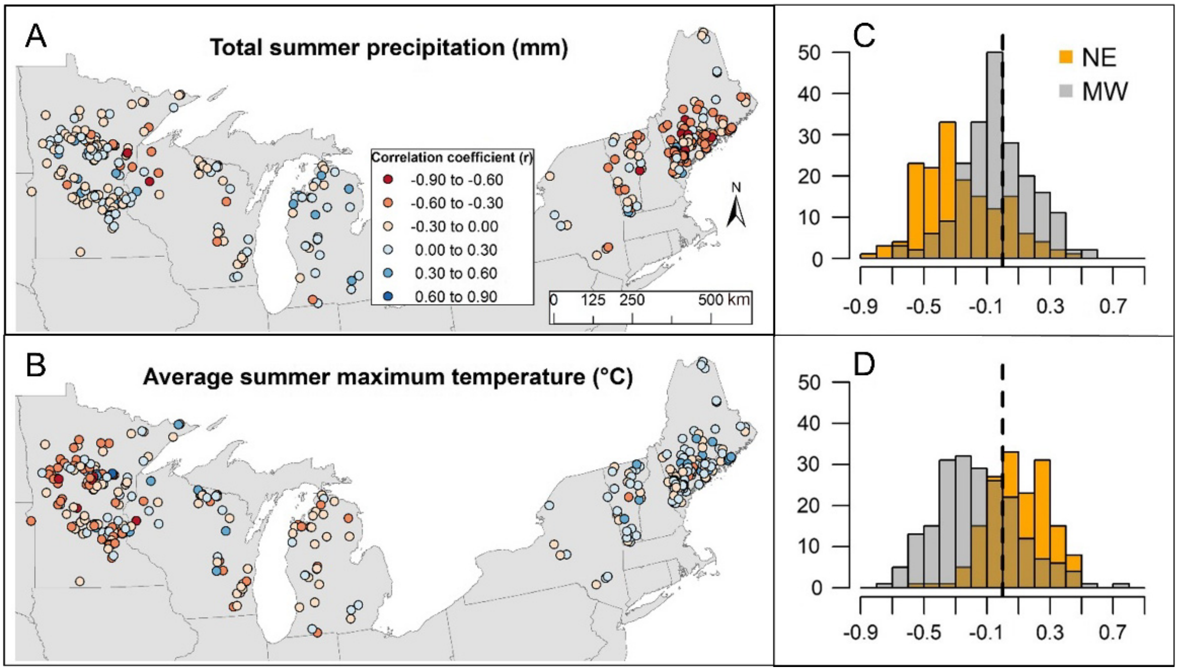

Fig. 2. Mapped climate sensitivities (Pearson correlation coefficients between water clarity and climate) in the northeastern United States for (A) summer (June–August) precipitation (mm) and (B) summer average maximum air temperature (°C). (C–D) Frequency distributions (number of lakes) of climate sensitivities for corresponding climate variables in panels A and B by region (NE, northeastern region [160 lakes; Maine, New York, and Vermont]; MW, midwestern region [205 lakes; Michigan, Minnesota, and Wisconsin]). Vertical dashed lines indicate correlation values of 0. Projection: Albers Equal Area (North American Datum 1983).

Table 3. Sensitivities of water clarity to climate (Pearson correlation coefficients) in the two study regions (1981–2010).

	Northeastern†				Midwestern‡			
Variable	Significant lakes	5%	Median	95%	Significant lakes	5%	Median	95%
Water-year precipitation (mm)	36	−0.52	−0.19	0.25	17	−0.39	−0.02	0.33
Fall precipitation (mm)	6	−0.33	−0.06	0.25	15	−0.38	−0.03	0.31
Winter precipitation (mm)	9	−0.36	−0.07	0.25	17	−0.27	0.07	0.42
Spring precipitation (mm)	5	−0.32	−0.05	0.22	8	−0.34	−0.05	0.27
Summer precipitation (mm)	64	−0.60	−0.32	0.16	18	−0.39	−0.04	0.33
Water-year maximum temperature (°C)	3	−0.26	0.03	0.31	20	−0.42	−0.11	0.31
Fall maximum temperature (°C)	12	−0.26	0.06	0.40	17	−0.35	0.06	0.38
Winter maximum temperature (°C)	3	−0.26	0.02	0.30	6	−0.33	−0.03	0.25
Spring maximum temperature (°C)	8	−0.34	−0.07	0.24	13	−0.38	−0.11	0.26
Summer maximum temperature (°C)	14	−0.20	0.09	0.40	44	−0.56	−0.18	0.32
Water-year minimum temperature (°C)	11	−0.36	0.03	0.31	14	−0.42	−0.06	0.29
Fall minimum temperature (°C)	27	−0.35	0.08	0.48	38	−0.40	0.09	0.51
Winter minimum temperature (°C)	7	−0.31	0.05	0.35	10	−0.35	−0.03	0.30
Spring minimum temperature (°C)	4	−0.32	−0.04	0.21	16	−0.43	−0.08	0.23
Summer minimum temperature (°C)	12	−0.37	−0.03	0.28	26	−0.44	−0.14	0.26
Water-year mean temperature (°C)	5	−0.28	0.03	0.27	15	−0.41	−0.09	0.28
Fall mean temperature (°C)	22	−0.30	0.08	0.44	30	−0.37	0.08	0.43
Winter mean temperature (°C)	7	−0.27	0.05	0.29	10	−0.34	−0.03	0.27
Spring mean temperature (°C)	4	−0.33	−0.06	0.23	11	−0.38	−0.09	0.27
Summer mean temperature (°C)	3	−0.25	0.04	0.30	40	−0.53	−0.17	0.24

Note: Significance based on $P \leq 0.05$.
†Northeastern region is Maine, New York, and Vermont (160 lakes).
‡Midwestern region is Michigan, Minnesota, and Wisconsin (205 lakes).

contrasted with overall regional patterns; we found positive correlations between clarity and summer precipitation in the northeastern region (95th percentile $r = 0.33$) and clarity and summer maximum temperature in the midwestern region (95th percentile $r = 0.32$; Table 3).

Because there were differences in land use/cover between the two regions, we created two subsets of midwestern lakes to examine whether sensitivities to summer precipitation were similar across regions when controlling for land use. These subsets were determined by median local watershed forest and agricultural cover in the northeastern region (85% and 8%, respectively; Table 1). One subset contained lakes with watersheds with ≥85% forest and ≤8% agriculture ($n = 14$ lakes), mirroring the northeastern region, and the other subset contained all other lakes in the midwestern region ($n = 191$ lakes). Sensitivities to summer precipitation were similar in the two subsets ($P = 0.76$) and were significantly more positive compared to the northeastern region (Fig. 3; pairwise Tukey's honest significant difference tests; $P < 0.001$). This indicates that summer precipitation sensitivities exhibited regional variation that could not be explained by local watershed forest and agricultural cover.

Characteristics of climate-sensitive lakes

Using random forests and all predictor variables, we found that summer precipitation sensitivity was more predictable (16% to 18% variation explained) than summer maximum temperature sensitivity (−4% to 4% variation explained) in both regions. These values, however, indicated that overall predictability of climate sensitivities was relatively weak, particularly for summer maximum temperature. In the northeastern region, chlorophyll *a*, TP, runoff, and lake maximum depth were the strongest predictors of sensitivity to summer precipitation. These respective variables individually explained approximately 14%, 13%, 10%, and 7% of variation in sensitivity to summer precipitation (Table 4). In the midwestern region, sensitivity to summer precipitation was most influenced by summer precipitation (16% variation explained), whereas lake maximum depth, TP, chlorophyll *a*, runoff, and groundwater each explained 9–14%

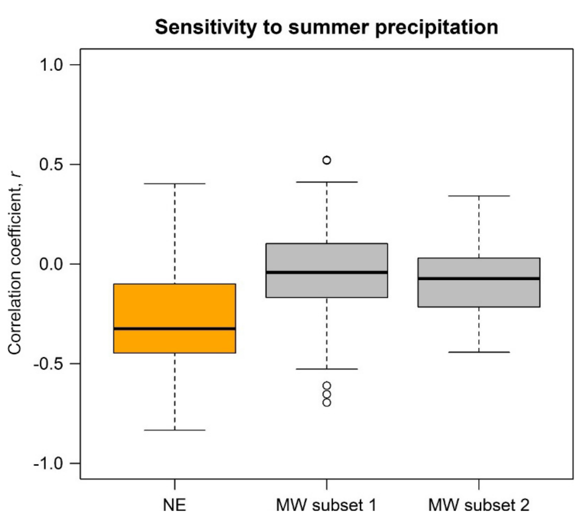

Fig. 3. Sensitivity of water clarity to summer precipitation based on individual lake watershed forest and agricultural cover. The midwestern (MW) region (Michigan, Minnesota, and Wisconsin) was subset according to the median forest (85%) and agricultural (8%) cover in the northeastern (NE) region ($n = 160$ lakes; Maine, New York, and Vermont; Table 1). MW subset 1 contains lake watersheds with <85% forest and >8% agricultural cover ($n = 191$ lakes), whereas MW subset 2 contains lake watersheds with >85% forest and <8% agricultural cover ($n = 14$ lakes). Bold lines represent medians, upper and lower box limits represent interquartile ranges (IQR), whiskers represent IQR ± 1.5 × IQR, and dots represent outliers.

Table 4. Random forest variable importance (percent variation explained) in sensitivities of water clarity to climate.

Variable	Northeastern	Midwestern
Summer precipitation sensitivity variables		
Lake area (ha)	2.45	6.67
Lake maximum depth (m)	7.25	13.52
Watershed area (ha)/lake area (ha) ratio	3.01	2.1
Watershed mean slope (°)	2.69	NA
Watershed forest, 1992 (%)	6.72	5.52
Watershed agriculture, 1992 (%)	2.81	2.42
Watershed wetlands, current (%)	2.32	3.01
Watershed stream density, current (m/ha)	4.79	1.38
Sub-regional mean annual runoff (inches)†	9.59	9.85
Sub-regional mean annual groundwater (mm)†	2.92	9.51
Sub-regional mean annual summer precipitation (mm)‡	0.84	15.91
Total phosphorus (μg/L)§	13.05	10.85
Chlorophyll *a* (μg/L)§	13.79	8.57
Total	17.65	16.08
Summer maximum temperature sensitivity variables		
Lake area (ha)	6.04	4.36
Lake maximum depth (m)	7.29	3.79
Forest within 100-m buffer of lake (%) (1992)	NA	5.22
Sub-regional mean annual summer maximum temperature (°C)‡	7.37	3.72
Total phosphorus (μg/L)§	7.63	10.19
Chlorophyll *a* (μg/L)§	8.31	2.89
Total	4.32	−4.15

Note: Variables with negative percent variation explained were omitted and indicated by NA.
†Mean annual 1951–1980.
‡Mean annual 1981–2010.
§Mean annual 1981–2010 based on available years of data only.

of variation in sensitivity (Table 4). Even though water clarity in the northeastern region was generally more sensitive to summer precipitation than in the midwestern region (Fig. 2, Table 3), random forests indicated that sensitivity to summer precipitation was predictable from some similar local to sub-regional ecological context variables in both regions.

The strength and direction of univariate correlations between precipitation sensitivities and ecological context variables provided additional evidence that precipitation-sensitive lakes in both regions were relatively oligotrophic, deep, and received relatively high amounts of runoff (Table 5, Fig. 4). For lakes in the northeastern region, all of these correlations were significant ($P \le 0.05$) except for runoff (Fig. 4). In addition, precipitation sensitivity in the northeastern region was significantly negatively correlated with watershed percent forest ($r = -0.166$) and mean annual groundwater recharge ($r = -0.163$). Although less influenced by TP ($r = 0.147$) and runoff ($r = 0.031$) than precipitation-sensitive lakes in the northeastern region, precipitation-sensitive lakes in the midwestern region were similarly unproductive and deep. In contrast to the northeastern region, precipitation sensitivity in the midwestern region was significantly negatively correlated with summer precipitation ($r = -0.207$; Table 5).

TP was the top predictor of sensitivity to summer maximum temperature for lakes in the midwestern region, explaining approximately 10% of variation in sensitivity, whereas other variables each explained approximately 5% or less of variation (Table 4). When using all predictors, total variation explained was approximately −4%, indicating that, collectively, all ecological context variables were poor predictors of sensitivity in this region; individual predictors were more useful than the full model. For lakes in the northeastern region, lake area, maximum depth, chlorophyll *a*, TP, and summer maximum temperature each explained approximately 6–8% of variation in sensitivity, but approximately 4% of variation was explained using all predictors (Table 4). Univariate correlations between summer maximum temperature sensitivity and ecological context variables in the midwestern region were overall weak ($r = -0.13$–0.01) and none was significant (Table 6, Fig. 5). In contrast, sensitivity of lakes in the northeastern region to summer maximum temperature was significantly negatively correlated with TP ($r = -0.21$) and chlorophyll *a* ($r = -0.17$), even though only 14 of 160 lakes (9%) in the northeastern region demonstrated significant correlations between clarity and summer maximum temperature and the median correlation was 0.09 (Table 3).

Discussion

We demonstrated that climate sensitivity of lakes for an important ecosystem-level characteristic, water clarity, varies both within and between the two study regions, and that some aspects of local to sub-regional ecological

Table 5. Correlations between sensitivities of water clarity to summer precipitation and ecological context variables (Table 1) by region.

Category and variable	Northeastern	Midwestern	n
Morphometry			
Lake area (ha)	−0.064	0.078	157, 203
Lake maximum depth (m)	**−0.209**	**−0.175**	157, 202
Watershed area (ha) : lake area (ha)	0.043	0.104	157, 203
Terrain			
Watershed mean slope (°)	−0.018	0.029	157, 205
Land use/cover			
Watershed forest, 1992 (%)	**−0.166**	−0.061	157, 205
Watershed agriculture, 1992 (%)	0.101	0.08	157, 205
Freshwater connectivity			
Watershed wetlands, current (%)	0.032	−0.134	157, 204
Watershed stream density, current (m/ha)	0.153	0.076	157, 205
Hydrology			
Sub-regional mean annual runoff (inches)†	−0.124	0.031	159, 204
Sub-regional mean annual groundwater (mm)†	**−0.163**	0.130	159, 204
Climate			
Sub-regional mean annual summer precipitation (mm)‡	0.053	**−0.207**	160, 205
Water quality			
Total phosphorus (μg/L)§	**0.385**	0.147	160, 166
Chlorophyll *a* (μg/L)§	**0.342**	**0.191**	152, 194

Notes: Values in boldface type represent significant correlations ($P \le 0.05$). For n, the first number is the northeastern region and the second number is the midwestern region.

†Mean annual 1951–1980.

‡Mean annual 1981–2010.

§Mean annual 1981–2010 based on available years of data only.

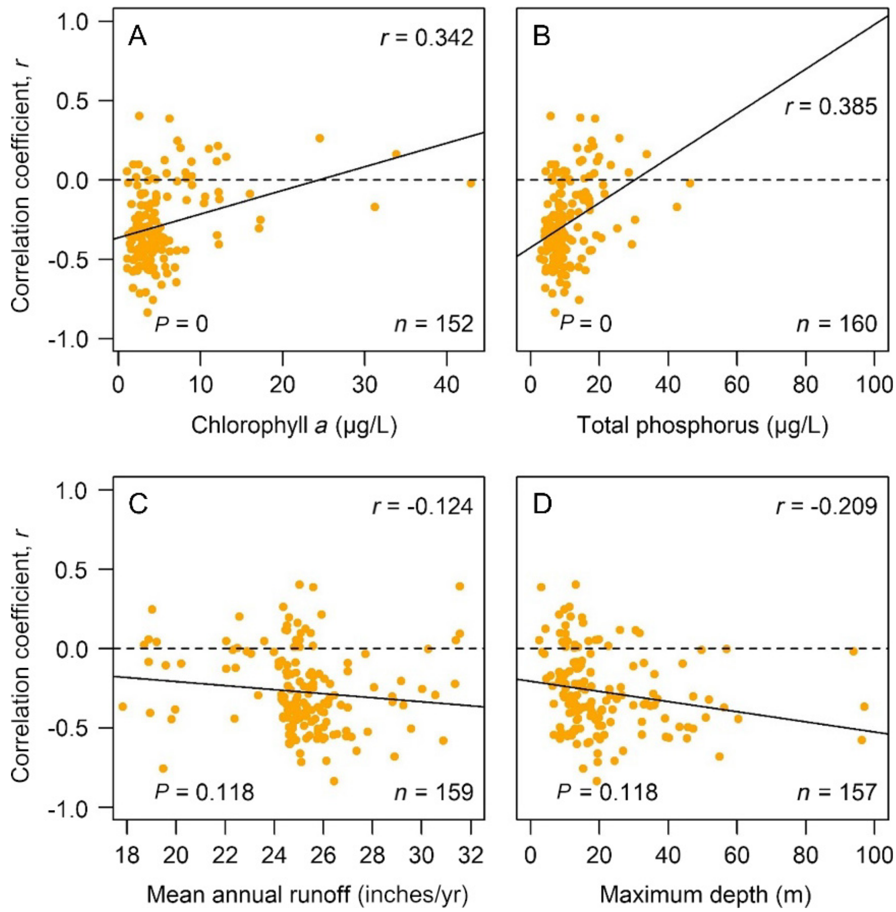

FIG. 4. Univariate relationships between sensitivity of water clarity to total summer precipitation (Pearson coefficients, *r*) and the top four most important predictors of sensitivity identified using random forest in northeastern region lakes (Table 4): (A) chlorophyll *a*, (B) total phosphorus, (C) mean annual runoff (1 inch = 2.54 cm), and (D) maximum lake depth. Northeastern region is Maine, New York, and Vermont.

context weakly influence climate sensitivity. Specifically, northeastern lakes were generally most sensitive to summer precipitation, but correlations ranged from −0.60 to 0.16 (5th and 95th percentiles) and only 40% were significant (Table 3). Midwestern lakes were generally most sensitive to summer maximum temperature, but correlations ranged from −0.56 to 0.32 (5th and 95th percentiles) and only 21% were significant. Further, clarity in 33% of lakes in both regions was not significantly correlated with any climate variable. Ecological context variables explained approximately 18% or less and 4% or less of variability in sensitivity to summer precipitation and maximum temperature, respectively, in both regions (Table 4). Large differences in climate sensitivities between the two regions and weak effects of local to sub-regional ecological context suggest that regional variables (e.g., climate) exert some control on the climate sensitivities of lakes, but also sensitivities within regions to the same climate variables are highly heterogeneous. An important implication of our study is that it will be important to account for the factors that regulate water clarity to understand and extrapolate patterns or trends observed from studies of one region to another, or in response to different aspects of climate change. Our results are consistent with prior work demonstrating that local to regional drivers combine to influence water clarity in North American lakes (Rose et al. 2017, Vogt et al. 2017), and that water clarity trends do not have a strong regional signal (Lottig et al. 2017). Water clarity and many of the ecological context variables we examined are less spatially autocorrelated than measures of climate (Lapierre et al. 2018), and these differences in the extent of spatial autocorrelation likely lead to weak relationships among ecological context variables and climate sensitivities. This underlying heterogeneity may explain variable climate sensitivities over short distances, including divergences from regional patterns.

Interpreting climate sensitivities and the role of local to regional ecological context

The most important factors that mediated the sensitivity of lakes in the northeastern region to summer precipitation were chlorophyll *a*, nutrients, runoff, and depth

Table 6. Correlations between sensitivities of water clarity to summer maximum temperature and ecological context variables (Table 1) by region.

Category and variable	Northeastern	Midwestern	n
Morphometry			
Lake area (ha)	0.070	−0.134	157, 203
Lake maximum depth (m)	0.079	0.007	157, 202
Land use/cover			
Forest within 100-m buffer of lake, 1992 (%)	0.037	0.111	160, 205
Climate			
Sub-regional mean annual summer maximum temperature (°C)†	−0.060	−0.090	160, 205
Water quality			
Total phosphorus (μg/L)‡	**−0.209**	−0.082	160, 166
Chlorophyll *a* (μg/L)‡	**−0.173**	−0.094	152, 194

Notes: Values in boldface type represent significant correlations ($P \leq 0.05$). For n, the first number is the northeastern region and the second number is the midwestern region.
†Mean annual 1981–2010.
‡Mean annual 1981–2010 based on available years of data only.

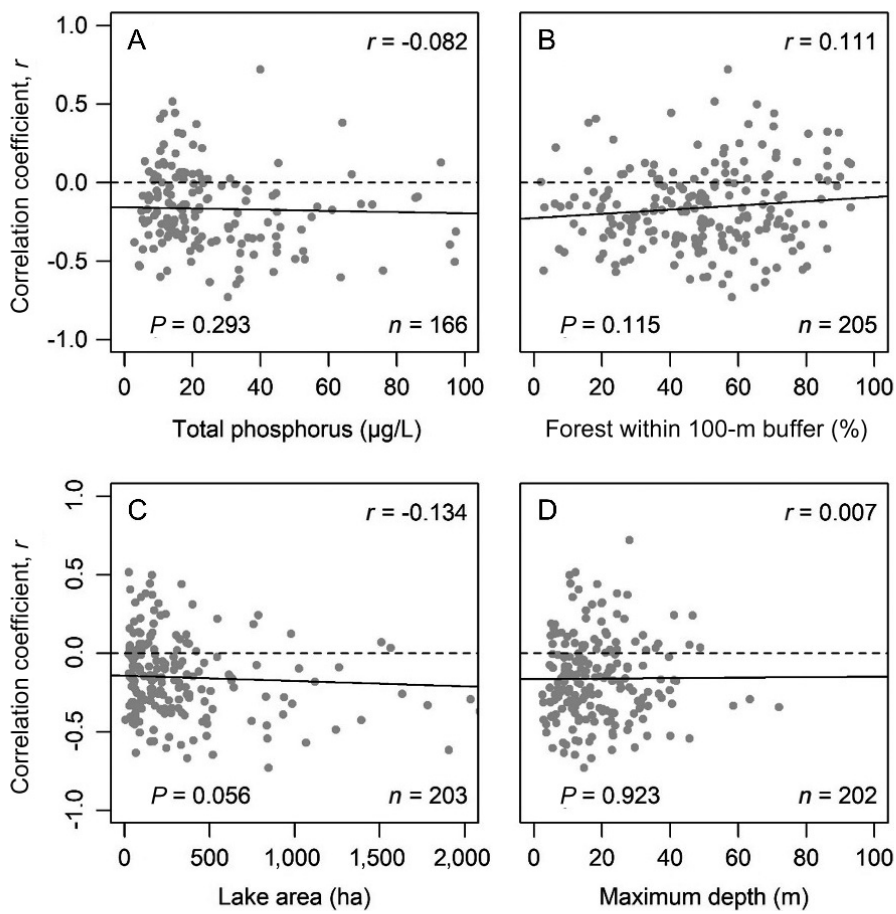

Fig. 5. Univariate relationships between sensitivity of water clarity to average summer maximum temperature (°C) (Pearson coefficients; r) and the top four most important predictors of sensitivity identified using random forest in midwestern region lakes (Table 4). (A) Total phosphorus, (B) percent forest within a 100-m buffer around lake shorelines, (C) lake area, (D) maximum lake depth. Midwestern region is Michigan, Minnesota, and Wisconsin. The x-axes were trimmed for panels A and C to enhance visualization of relationships. Panel A contains 11 lakes with total phosphorus > 100 μg/L and panel C contains 2 lakes with area >2,000 ha.

(Table 4). Although most lakes in the midwestern region were not sensitive to summer precipitation, these ecological context variables generally also explained variation in sensitivity for the midwestern region, suggesting that some aspects of local to sub-regional ecological context are important across regions even if regional climate sensitivities are different. Although our study contained only two regions, large differences in local to sub-regional ecological context (i.e., climate, hydrology, and lake water quality) across the two regions likely help broadly explain regional differences in the sensitivity of lakes to precipitation.

Contrary to expectations, differences in local watershed land use/cover across the two regions did not influence the sensitivity of lakes to precipitation. Despite the prevalence of agriculture in the midwestern region, lakes in the northeastern region were considerably more precipitation-sensitive than lakes in the midwestern region. Given the lack of agriculture in the northeastern region, precipitation sensitivity in this region can most likely be explained by the DOC pathway (Fig. 1). Northeastern region lakes are predominantly oligotrophic (Table 1), suggesting DOC rather than phytoplankton control on water clarity (Webster et al. 2008). Similar to the midwestern region, greater hydrologic connectivity in the northeastern region would deliver DOC to lakes following precipitation (Rose et al. 2017), and our estimates of wetland cover, which were obtained from aerial photo interpretation, may be underestimated in this region due to widespread forest cover (Ozesmi and Bauer 2002). Although we would therefore expect the primary productivity pathway (Fig. 1) to predominate in agricultural watersheds and regions, contrary to expectations, percent agriculture explained <3% of variation in precipitation sensitivity in both regions (Table 4). Further, the lack of increased precipitation sensitivity of lakes in heavily forested vs. agricultural midwestern watersheds (Fig. 3) suggests that water clarity declines in these lakes are likely attributable to DOC rather than primary productivity.

Our expectation that small, shallow, oligotrophic lakes with high watershed to lake area ratios would be precipitation sensitive was only partly true. Whereas we found no effect of lake area or the watershed to lake area ratio in either region, we found that deep, oligotrophic lakes were sensitive to precipitation in both regions (Table 5). These results suggest that nutrient-induced increases in primary productivity may decrease water clarity in these lakes, but precipitation-induced declines in water clarity, particularly for clear lakes, may also be due to DOC (Rose et al. 2017). Although these lakes are nutrient-poor, clarity in clear lakes is more sensitive to increased DOC than in colored lakes (Read and Rose 2013), and oligotrophic lakes in the northeastern region tend to be deep and clear (Webster et al. 2008). The increased precipitation sensitivity of deep, oligotrophic lakes reflects that clarity in these lakes, unlike in shallow or productive lakes, is more sensitive to DOC than primary productivity.

The low variation explained in summer maximum temperature sensitivity indicated that local to sub-regional ecological context variables are weak predictors of temperature sensitivity in both the northeastern and midwestern regions (Table 4, 6). In the northeastern region, however, the significant, negative correlations between temperature sensitivity and TP and chlorophyll *a* (Table 6) suggest that the relatively nutrient-poor, unproductive lakes in this region may be sensitive to future climate warming in addition to precipitation changes. As these energy- and nutrient-limited systems experience warmer temperatures, productivity might be expected to increase; however, lake water temperatures respond heterogeneously to widespread air temperature increases (O'Reilly et al. 2015). Further, increases in DOC associated with precipitation increases may buffer water clarity from the effects of warming by reducing light penetration (Rose et al. 2016).

Our study identified that lakes in different regions may respond more strongly to precipitation than temperature (or vice versa), but mechanistic linkages between effects of precipitation and temperature on lake clarity suggest that future lake ecosystem responses to climate change may reflect the combined effects of changes in precipitation and temperature. In particular, DOC mediates effects of precipitation and temperature on water clarity, and more widespread DOC or color data than what were available for this study could aid prediction and interpretation of the climate sensitivity of lakes. In addition, more accurate hydrologic residence times or knowledge of food web dynamics (e.g., dominance of piscivorous vs. planktivorous fish) may also account for at least some of the unexplained variation in the climate sensitivity of lakes. We were unable to account for potential measurement error or inconsistencies in observation techniques across different monitoring programs and the hundreds of professional and citizen scientists who collected data used in our study, but monitoring programs increasingly use standard protocols to ensure data reliability across observers (e.g., Maine Volunteer Lake Monitoring Program Secchi certification). It is also important to note that we only examined predictors of climate sensitivity for lakes in the northeastern and upper midwestern United States, mostly in the temperate deciduous forest biome. Additional studies of lakes spanning wider ecological gradients, particularly temperature (which varied little between our two regions), would be necessary to identify broader scale patterns of water clarity responses to climate change.

Importance of temporal scale in climate sensitivity

We identified geographic patterns in the sensitivity of lakes to seasonal climate variables. Because we used monthly climate data, however, we were not able to resolve finer-scaled weather events and their effects on summer water clarity. Whereas we found that summer climate was often correlated with summer average water clarity, other studies have found that weather events can have a strong effect on water clarity through effects on DOC and stratification. For example, Jennings et al. (2012) found that lake DOC concentrations after extreme precipitation events could take up to a year to return to pre-event levels, demonstrating that short, infrequent weather events may disproportionately affect water clarity. In addition, Klug et al. (2012) found that the severity and persistence of effects from extreme precipitation events were greater for lakes with long water residence times and large watershed area to lake volume ratios. This was primarily due to effects of terrestrially derived carbon (DOC and particulate OC) inputs rather than disruptions to thermal structure, which typically recovered to approximately 80% of pre-storm stability within one week (Klug et al. 2012). Carbon inputs may decrease water clarity both directly (i.e., turbidity, color) and indirectly via ecosystem impacts (i.e., primary productivity). In addition, extreme winds (which may occur with or without precipitation) can also cause rapid water clarity declines that last weeks as a result of thermocline deepening and subsequent increases in primary productivity (Kasprzak et al. 2017). These various mechanisms help explain the significant negative relationship that we observed between summer precipitation and water clarity in 40% of the lakes in the northeastern region.

These studies of lake responses to weather demonstrate that short-term precipitation and/or wind events may decrease water clarity by disrupting lake thermal structure and increasing allochthonous OC loads, but that increasing OC loads generally cause greater and more persistent effects on water clarity than changes in thermal structure. A high seasonal value for precipitation indicates either a single large storm, many smaller storms, or some combination, which could indicate reduced thermal stability and increased OC loads overall. Short, extreme precipitation events are expected to intensify during the 21st century in our study regions (Villarini et al. 2013, Swain and Hayhoe 2015) and therefore may exert increasing control over water clarity compared to long-term climate variability.

The fine-scale studies mentioned above are complementary to our results and suggest that to understand climate effects on lakes fully, we must examine this problem not only at multiple spatial scales, as we have done here (i.e., local to regional), but also at multiple temporal scales. Our results show that seasonal climate matters, and there are regional differences in climate sensitivities of lakes; however, studies conducted at finer temporal scales also show the importance of weather events on summer lake ecosystem properties. A future challenge will be to find the data sets or modeling frameworks to examine this problem at the multiple necessary spatial and temporal scales.

Conclusions

The sensitivity of lake ecosystems to climate change depends on a combination of patterns and processes that operate at multiple spatial and temporal scales, including regional climate and local lake characteristics. Our findings suggest that water clarity declines may be associated with warmer summers in the midwestern region and wetter summers in the northeastern region, but that future responses of lakes to climate change will be spatially heterogeneous across and within regions. Although we cannot predict water clarity responses to emerging novel climate regimes, historical coupling of climate and water clarity across two to three decades provides some basis for qualitatively predicting future water clarity responses to climate change. Ultimately, predicting the vulnerability of lake ecosystems to climate change will depend on integrating patterns of climate sensitivity, as done in this study, with patterns of climate change exposure (i.e., future climate projections).

Lakes are widely regarded as sentinels of climate change. The sentinel concept provides a motivating framework and a compelling backdrop for studying the effects of climate change on lakes, but should not be interpreted to mean that all lakes are necessarily sensitive to climate change. Using long-term data from 365 lakes, we found that water clarity was strongly correlated with summer precipitation or temperature in some lakes, but not in the majority of lakes, and that water clarity was not correlated with any of 20 climate variables in 33% of lakes. Furthermore, local and sub-regional ecological context (e.g., lake morphometry, water quality, watershed land use/cover) generally explained little variation in the climate sensitivity of lakes. One possible explanation is that non-climatic stressors may overwhelm or confound climate signals in some lakes, particularly in highly disturbed watersheds. This idea suggests that the sentinel concept is most useful when applied within the context of particular response variables and climate-related stressors (Adrian et al. 2009). As such, we emphasize that many lakes may not be effective climate change sentinels because the climate sensitivity of lakes is highly variable, scale-dependent, and not easily predictable based on ecological context.

Acknowledgments

This work was supported by the U.S. National Science Foundation Macrosystems Biology program (EF #1638679, #1638554, #1065786, #1065818, and #1065649). P. A. Soranno was supported by the USDA National Institute of Food and Agriculture, Hatch Project 1013544. S. M. Collins was supported by a U.S. National Science Foundation Postdoctoral Research Fellowship in Biology (DBI-1401954). We thank our collaborators associated with the Continental Limnology and CSI-Limnology teams for assembling these data sets and contributing to discussions that helped lead to this paper. We appreciate two anonymous peer reviewers and the subject matter editor, Kevin Rose, whose suggestions improved the manuscript. Author contribution: I. M. McCullough conceived of the research questions, wrote analysis scripts, and produced tables and figures. S. M. Collins provided early results that identified the major climate variables to analyze. All authors helped to frame the research questions and contributed to manuscript writing.

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Data Availability

Analysis scripts are available on GitHub/Zenodo: https://doi.org/10.5281/zenodo.1488201.