Received: 23 July 2021 | Revised: 10 December 2021 | Accepted: 10 December 2021

DOI: 10.1111/gcb.16079

RESEARCH ARTICLE

Global Change Biology WILEY

Multi-decadal changes in phytoplankton biomass in northern temperate lakes as seen through the prism of landscape properties

Aleksey Paltsev[1] | **Irena F. Creed**[1,2]

[1]Department of Biology, Western University, London, Ontario, Canada

[2]Department of Physical and Environmental Sciences, University of Toronto-Scarborough, Toronto, Ontario, Canada

Correspondence
Irena F. Creed, Department of Physical and Environmental Sciences, University of Toronto-Scarborough, 1065 Military Trail, Toronto, ON, Canada M1C 1A4.
Email: irena.creed@utoronto.ca

Funding information
Natural Sciences and Engineering Research Council of Canada, Grant/Award Number: 06579-2014 and 448172-2014

Abstract

Ecologists collectively predict that climate change will enhance phytoplankton biomass in northern lakes. Yet there are unique variations in the structures and regulating functions of lakes to make this prediction challengeable and, perhaps, inaccurate. We used archived Landsat TM/ETM+ satellite products to estimate epilimnetic chlorophyll-*a* (Chl-*a*) concentration as a proxy for phytoplankton biomass in 281 northern temperate lakes over 28 years. We explored the influence of climate (air temperature, precipitation) and landscape proxies for nutrient sources (proportion of wetlands in a contributing catchment, size of the littoral zone, potential for wind-driven sediment resuspension as estimated by the dynamic ratio) or nutrient sinks (lake volume) in a random forest model to explain heterogeneity in peak Chl-*a*. Lakes with higher Chl-*a* (median Chl-*a* = 2.4 μg L^{-1}, $n = 40$) had smaller volumes ($<44 \times 10^4$ m^3) and were more sensitive to increases in temperature. In contrast, lakes with lower Chl-*a* (median Chl-*a* = 0.6 μg L^{-1}, $n = 241$) had larger volumes ($\geq 44 \times 10^4$ m^3), contributing catchments with smaller proportions of wetlands (<4.5% of catchment area, $n = 70$), smaller littoral zones (<16.4 ha, $n = 137$), minimal wind-driven sediment resuspension (as defined by the dynamic ratio; <0.45, $n = 232$), and were more sensitive to increases in precipitation. Lakes with larger volumes were generally less responsive to climate factors; however, larger volume lakes with a significant proportion of wetlands and larger littoral zones behaved similarly to lakes with smaller volumes. Our finding that lakes with different landscape properties respond differently to climate factors may help predict the susceptibility of lakes to eutrophication under changing climatic conditions.

KEYWORDS
chlorophyll-*a*, climate change, landscape, morphometry, phytoplankton biomass, precipitation, temperature, trophic states

1 | INTRODUCTION

Northern temperate lakes are being affected by global environmental changes (Bedford et al., 2020; Richardson et al., 2018). An increase in temperature and changes in precipitation patterns and atmospheric nitrogen deposition are leading to fundamental alterations in land-aquatic hydrological and biogeochemical linkages (Creed et al., 2018). These environmental changes can be best studied in lakes, as lakes integrate atmospheric, terrestrial, and aquatic processes (Williamson et al., 2009). An important signal of alterations is an increase in the frequency and duration of phytoplankton blooms (Ho et al., 2019; Winter et al., 2011) as well as changes in phytoplankton composition (e.g., toward more cyanobacteria dominated ecosystems; Freeman et al., 2020); these have been observed even in remote northern temperate lakes located far from any confounding local or regional human activities (Winter et al., 2011).

Lake phytoplankton biomass is a product of complex interactions among forces that are external and internal to lakes (Baines et al., 2000; Blenckner, 2005). External forces are broad-scale climate-related variables such as temperature and precipitation (Hollert et al., 2018). Although the direct effect of temperature on phytoplankton biomass has been a major focus of research in recent years, the findings of these studies are contradictory. For example, phytoplankton biomass was found to increase (Jeppesen et al., 2009; Kraemer et al., 2017), decrease (Tadonléké, 2010), or to have no significant change (Kosten et al., 2012; Rasconi et al., 2017) in response to an increase in temperature. However, there is consensus that the growth rates of many cyanobacteria (that constitute over 50% of phytoplankton biomass in temperate lakes; Downing et al., 2001) generally increase with temperature (De Senerpont Domis et al., 2007; O'Neil et al., 2012). Recent studies suggest that although temperature should be considered, precipitation might be more important in influencing lake phytoplankton biomass (Hrycik et al., 2021; Klimaszyk & Rzymski, 2011; Larsen et al., 2020; Sinha et al., 2017) because precipitation-driven runoff influences both nutrient delivery to lakes and nutrient availability in lake catchments via runoff. Given that phytoplankton biomass depends on nutrient availability, even slight changes in precipitation patterns might trigger increases or decreases in phytoplankton biomass (Scheffer et al., 2001; Scheffer & Van Nes, 2007). However, increases or decreases in precipitation do not always imply a subsequent positive correlation with phytoplankton biomass (i.e., low precipitation = lower phytoplankton biomass or vice versa). For instance, a combined effect of decreased precipitation and high temperatures during droughts can cause a drop in lake water level, a longer water residence time, a lower dilution of nutrients in the water column, and, as a result, higher phytoplankton biomass.

Phytoplankton biomass in lakes often does not show synchronous behavior in response to climate factors (Baines et al., 2000; Freeman et al., 2020; Kraemer et al., 2017; Oliver et al., 2017; Paltsev & Creed, 2021) because catchment- and lake-specific properties modify regional climate signals (Blenckner, 2005; Hollert et al., 2018; Palmer et al., 2014). Catchment properties (i.e., catchment size, topography, vegetation and soil type, and the presence of wetlands) affect the source, storage, and transport of water and nutrients (e.g., dissolved organic matter (DOM), nitrogen (N), and phosphorus (P)) to receiving waters (Creed et al., 1996; Creed & Beall, 2009; Kayler et al., 2019; Mengistu et al., 2014; Nõges, 2009; Staehr et al., 2012). Several studies have shown strong relationships between catchment topography and the magnitude and composition of exported nutrients (Kritzberg et al., 2020; Mengistu et al., 2014; Senar et al., 2018). For example, wetlands in lake catchments are sinks of inorganic solutes (e.g., nitrate [NO_3^-]; Enanga et al., 2017) and sources of organic solutes, especially dissolved organic carbon (DOC), dissolved organic nitrogen (DON), and P (Creed & Beall, 2009; Creed et al., 2003, 2008; Enanga et al., 2017), while deciduous forests are generally associated with larger exports of N and P than coniferous forests (Klimaszyk & Rzymski, 2011). Properties of receiving lake basins (e.g., lake area, depth, volume) affect the fates of nutrients within lakes (Read et al., 2015; Richardson et al., 2018; Søndergaard et al., 2001, 2005). Smaller volume and shallower lakes usually have shorter P retention time in sediments than larger volume lakes because P can be easily re-suspended due to wind disturbance or water level fluctuations (Nõges, 2009). Similarly, lakes with well-developed littoral zones (i.e., wide and with established communities of macrophytes) retain more nutrients and organic matter in surface waters than lakes with narrower littoral zones (Kornijów et al., 2016; Vadeboncoeur et al., 2002).

It is difficult to separate the "direct" response of phytoplankton biomass to climate from "indirect" responses modified by landscape properties (Anderson, 2014; Palmer et al., 2014). Phytoplankton biomass is principally determined by processes that affect the availability of nutrients (i.e., growth-limiting nutrients such as P and N, but also micronutrients such as iron; Molot et al., 2010; Sorichetti et al., 2014a, 2014b), the community composition of phytoplankton (e.g., the presence of N-fixing cyanobacteria taxa; Carey et al., 2012; Lürling et al., 2013; Winder & Sommer, 2012), and the presence and abundance of grazing zooplankton (Baines et al., 2000). Therefore, to predict patterns in phytoplankton biomass in lakes, both catchments and receiving lakes should be examined for properties that influence phytoplankton biomass. However, in contrast to many studies where catchments and their lakes are explored as separate units (catchments or receiving lakes; e.g., Magnuson et al., 1990; Palmer et al., 2014; Sharma et al., 2019), there are relatively few studies where the properties of the coupled terrestrial-aquatic system (catchments plus receiving lakes) are studied (e.g., Isles et al., 2020; Senar et al., 2018; Staehr et al., 2012) and even fewer studies where the coupled terrestrial-aquatic systems in a large number of lakes are explored to assess phytoplankton biomass (e.g., Hrycik et al., 2021; Stomp et al., 2011).

Recently, we have shown that phytoplankton biomass is changing in many northern temperate lakes (Paltsev & Creed, 2021). We expected that broad-scale temporal factors (e.g., climate) accounted for most of the variation in phytoplankton biomass and that the lakes responded to climate signals in a uniform manner. However, we found that 79.7% of the variation was due to intrinsic properties of landscape and lake-specific factors (including 35.6% for space and 44.1% for space × time interactions). We also found that some lakes were trending to eutrophication and some lakes to oligotrophication, but that there were no significant trends in either direction in most of the lakes. In this paper, we explore the interactive impact of climate and landscape properties on long-term median chlorophyll-*a* (Chl-*a*) concentration (as a proxy for phytoplankton biomass) in lakes in relatively intact northern temperate forests. We asked two questions. First, is lake Chl-*a* related to climatic conditions? Here, we predicted that Chl-*a* is higher in lakes located in warmer, drier climatic conditions and that Chl-*a* is lower in lakes located in cooler, wetter conditions. Second, is this relationship modified by landscape properties? Here, we predicted that Chl-*a* is higher in small and shallow lakes with enhanced wind-driven sediment resuspension and large proportions of wetlands in their catchments, while Chl-*a* is lower in large and deep lakes with minimal wind-driven sediment resuspension and small proportions of wetlands in their catchments. An improved understanding of these interactive factors influencing nutrient availability in lakes may improve our ability to predict responses of lake phytoplankton biomass to global environmental changes.

2 | STUDY REGION

The 152,231 km^2 study region is located between 44.44°N and 48.38°N within the Great Lakes–St. Lawrence forest region of the temperate forest biome in Canada (Figure 1). Climate in the region is humid continental. Mean annual air temperature for 1984–2011 was +5.1°C, ranging between +7.4°C in the south and +2.6°C in the north, and mean annual precipitation was 960 mm, ranging from 740 mm in the south to 1180 mm in the north (McKenney et al., 2011). Precipitation is influenced by lake effects from the Great Lakes and local orographic effects in areas of relatively high relief (Baldwin et al., 2000). The frost-free period extends from April to November in the warmer and more humid southern parts of the region and from May to September in the colder and less humid northern parts of the region (Baldwin et al., 2000). Peaks in stream discharge happen in March to April (during spring snowmelt) and again from September to November (during autumn storms; Creed et al., 2015). Topography varies from depressions and flats along the shore of the Great Lakes to hills in the Algoma and Madawaska Highlands. Bedrock is the Canadian Shield composed of Precambrian silicate greenstone formed from metamorphosed basalt (Ontario Geological Survey, 2003). Overlying bedrock is a glacio-fluvial outwash consisting of sandy loam ablation till with river and deltaic deposits on top of slit loam basal till (Ontario Geological Survey, 2003). Soils range from brunisols to orthic ferro-humic podzols, with ferric humisols consisting of highly humified organic deposits in wetlands near rivers and lakes (Canada Soil Survey Committee, 1978). Forests in the study region are a mix of deciduous and coniferous tree species, with the latter being more common in the northern areas (Baldwin et al., 2000).

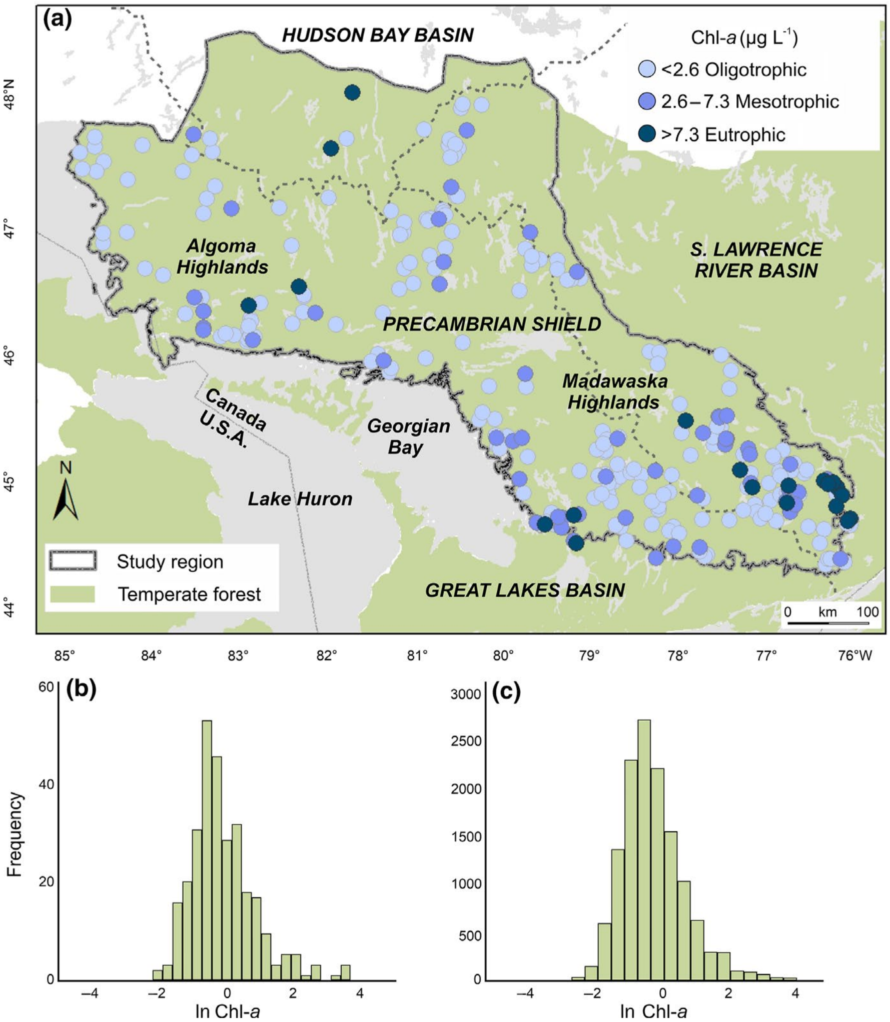

FIGURE 1 (a) Map showing location of the study region and a subset of 281 study lakes; and distribution of ln Chl-*a* in (b) the subset, and (c) all 12,644 lakes [Colour figure can be viewed at wileyonlinelibrary.com]

3 | METHODS

3.1 | Phytoplankton biomass

Chl-*a* was used as a proxy for phytoplankton biomass (Boyer et al., 2009; Freeman et al., 2020; Hrycik et al., 2021). We acknowledge that Chl-*a* may not be a precise measurement of phytoplankton biomass, as the presence of chlorophyll-*a* is species specific, may vary with light and nutrient conditions (Kasprzak et al., 2008; Morel & Bricaud, 1981), or may not (Erratt et al., 2021). However, remote sensing of Chl-*a* remains the only approach for tracking changes in phytoplankton biomass over wide spatial and temporal (decades) domains (Huot et al., 2007) and has been widely used in ecological research (e.g., Ho et al., 2019; Kraemer et al., 2017).

Chl-*a* was modeled for the lakes of the temperate forest biome using remote sensing techniques (for details see Paltsev & Creed, 2021). We acquired 1067 Landsat 4–5 TM and 159 Landsat 7 ETM+ (30-m) images from the United States Geological Survey archives over the study region for the period of August to October for 28 years (1984–2011; Figure 1). The period from August to October is when peak phytoplankton biomass occurs in the study region (Winter et al., 2011). Lake locations and boundaries were determined by reclassifying as water those pixels below the local minimum in the bimodal distribution of Band 5 (shortwave infrared) radiance. Lakes with an area less than 4.5 ha (90 pixels) or high standard deviation of Band 5 radiance values (>median standard deviation of all lakes in an image) were discarded to avoid the problem of mixed reflectance due to adjacency near or along lake shorelines (i.e., areas with shallow water and abundant aquatic vegetation). The remaining lakes were then buffered using a 15-m (0.5-pixel length) buffer inside the lake boundary. A partial atmospheric correction was performed on Bands 1–3 (blue, green, and red) of each image, including subtraction of the Rayleigh scattering radiance from top-of-atmosphere (TOA) radiance (Lobo et al., 2015) followed by the conversion of TOA radiance values to bottom-of-atmosphere (BOA) reflectance values (Chander et al., 2009). The reflectance values in each Band 1–3 were averaged for each lake over all images available for each year (i.e., August–October).

A regression model based on in-situ lake Chl-*a* measurements and average annual BOA reflectance values in Bands 1–3 (expressed as [Band 1–Band 3]/Band 2) was developed to predict natural log-transformed Chl-*a* (ln Chl-*a*) observations in 62 lake samples ($r^2 = .78$, $p < .001$). This regression model was then applied to average annual [Band 1–Band 3]/Band 2 in each lake, resulting in a 28-year (1984–2011) time series of modeled ln Chl-*a* in 12,644 lakes. We used universal space–time kriging to interpolate missing annual ln Chl-*a* where clouds obscured lake pixels. Modeled annual ln Chl-*a* was validated with available in-situ ln Chl-*a* data over both space and time. Median modeled annual Chl-*a* ($\mu g\ L^{-1}$) was calculated for each lake over the 28-year period. Finally, lakes were classified into three trophic states using median modeled annual Chl-*a* according to Carlson and Simpson (1996): oligotrophic (Chl-*a* < 2.6 $\mu g\ L^{-1}$), mesotrophic (Chl-*a* = 2.6–7.3 $\mu g\ L^{-1}$), and eutrophic (Chl-*a* > 7.3 $\mu g\ L^{-1}$; Table 1).

For this study, we selected a subset of 281 lakes using the following criteria: (1) the availability of topographic (digital elevation models (DEMs)) and bathymetric data (lake contour maps) to characterize landscape properties (see Table S1); (2) lake trophic states representing approximately the same distribution of trophic states as in the original dataset of 12,644 lakes (Table 1); (3) Chl-*a* representing the natural range of Chl-*a* in the original dataset (Figure 1; Table 2); and (4) a relatively uniform spatial distribution of these lakes across the study region (Figure 1). Water chemistry samples (e.g., total P) were limited for these remote lakes; therefore, we could not measure the amount and composition of nutrient export to the lakes. Instead, we applied a theoretical approach where the effect of nutrient loading is perceived as "a loading potential" (Table 3).

3.2 | Climate factors

Median monthly maximum air temperature (hereafter: temperature) and total precipitation (hereafter: precipitation) from July to October were determined for each lake and for each year 1984–2011. Temperature and precipitation values were extracted from 60-arcsecond historical monthly air temperature and precipitation grids (see McKenney et al., 2011). The period from July to October was chosen over August to October (i.e., the period for peak Chl-*a* in the study region) to account for a delay in response of phytoplankton biomass to meteorological conditions. One month (i.e., July) is considered a reasonable period for phytoplankton to respond to these conditions over the summer period (Downing et al., 2006).

3.3 | Digital terrain models for landscape factors

Catchment boundaries for each lake were delineated from a hydrologically conditioned 20-m DEM (Ontario Ministry of Natural Resources, 2015) using gridded lake polygons as pour points (Tarboton et al., 1991). Sixty lakes had vector polyline bathymetric data in digital format (Ontario Ministry of Natural Resources, n.d.) and 221 lakes had bathymetric maps in analog format (Western University Map and Data Centre, n.d.); the latter were manually georeferenced and digitized. Digital polylines were interpolated to 20-m grids using the "Topo to Raster" interpolation function in ArcGIS 10.8 (see Hutchinson et al., 2011).

The selected landscape factors extracted from digital elevation or bathymetric data and their hypothesized effects on lake Chl-*a* are summarized in Table 3. We grouped the landscape factors into five categories as follows:

1. Location: latitude, longitude, and altitude values of lake centroids extracted from the DEMs.
2. Nutrient loading potential from contributing catchments: estimated by the ratio of catchment area to lake area and wetland cover (percentage of catchment area excluding lake area that is covered by wetlands; Ontario Ministry of Natural Resources, 2013).

TABLE 1 Number and proportion of lakes according to the trophic state for all lakes ($n = 12{,}644$) and a subset of lakes ($n = 281$) used in this study

	Oligotrophic lakes (Chl-*a* < 2.6 $\mu g\ L^{-1}$)	Mesotrophic lakes (Chl-*a* = 2.6–7.3 $\mu g\ L^{-1}$)	Eutrophic lakes (Chl-*a* > 7.3 $\mu g\ L^{-1}$)	All lakes
All lakes				
n	8,986	2,700	958	12,644
%	71.1	21.4	7.6	100
Lakes (subset)				
n	203	59	19	281
%	72.2	21.0	6.8	100

TABLE 2 Descriptive statistics for Chl-*a* and climate and landscape factors used in the study (for 281 study lakes)

	Mean	Standard deviation	95% confidence interval (+/−)	Median	Coefficient of dispersion (75th–25th/50th)	Minimum	Maximum
Chl-*a* ($\mu g\ L^{-1}$)	1.9	4.7	0.6	0.7	1.3	0.1	41.3
Monthly median maximum temperature (°C)	19.6	1.1	0.1	19.8	0.1	16.9	21.4
Monthly total precipitation (mm)	90.4	6.1	0.7	90.4	0.1	79.6	104.0
Latitude (°)	45.91	—	—	45.51	—	44.49	48.17
Longitude (°)	−79.68	—	—	−79.40	—	−84.88	−76.21
Altitude (m)	302.1	86.4	10.2	310.2	0.5	120.0	478.9
Wetland cover (%)	6.3	7.2	0.8	4.6	1.3	0.01	64.0
Ratio of catchment area to lake area (catchment/area)	51.0	168.7	19.8	12.1	1.8	1.6	2232.6
Littoral zone (ha)	7.7	17.5	2.1	2.0	3.8	0.1	181.3
Dynamic ratio	0.25	0.33	0.04	0.17	1.12	0.02	3.59
Lake surface area (km^2)	1.1	1.8	0.2	0.5	0.0	0.1	13.9
Lake mean depth (m)	5.4	3.7	0.4	4.6	0.9	0.1	23.8
Lake volume ($10^6\ m^3$)	9.33	26.23	3.08	2.09	0.000003	0.001570	308.90
Fetch distance (m)	2153.7	1724.4	202.5	1599.6	1.2	208.8	10715.7

3. Nutrient resuspension potential from the land–water interface: estimated by the area of the littoral zone, defined as the area adjacent to lakeshore with a depth of ≤2 m and a bathymetric slope ≤2°.
4. Nutrient resuspension potential from the lake sediments: estimated by the dynamic ratio, defined as $DR = \sqrt{A}/D_{\mathrm{mean}}$, where A is lake area in km^2 and D_{mean} is mean lake depth in meters (Hakanson, 2005).
5. Nutrient dilution within the lake: estimated by the lake volume (m^3) and the fetch distance (m).

3.4 | Statistical analysis

Since the overall accuracy of random forest models can be affected by highly correlated variables used in the models (Strobl et al., 2009; Tolosi & Lengauer, 2011), we performed the Pearson correlation test to determine correlations among landscape factors. Landscape factors that did not have correlations with other landscape factors were selected for the regression tree and random forest analyses. Skewed factors were ln-transformed (all but latitude, longitude, dynamic ratio, and wetland cover).

Regression tree analysis was used to identify climate and landscape factors that were related to Chl-*a*. The regression tree was pruned at the branch where the complexity parameter minimized the cross-validation error (De'ath & Fabricius, 2000). Because regression trees may produce unstable models (Breiman, 2001), random forest analysis was also performed where a thousand regression trees (instead of a single tree) were produced and results then aggregated into a single random forest model. These results were presented on a "variable importance plot" that shows the list of factors in increasing order of importance from the bottom to the top of the plot (Strobl et al., 2009). "Importance" was measured by the percent increase in mean squared error of residuals with repetition (*%IncMSE*), a special attribute assigned by random forests (De'ath, 2002; Strobl et al., 2009). The closer *%IncMSE* is

TABLE 3 Hypothesized landscape controls on phytoplankton biomass in the study lakes

Landscape control	Hypothesized effects	Landscape factor
Location and uniqueness of place	Areas with more precipitation lead to more nutrient export from catchments to lakes (Kosten et al., 2012; Nõges, 2009; Pollingher, 1990)	Latitude (°), longitude (°), altitude (m)
Nutrient loading potential from contributing catchments	Higher proportion of wetlands indicates larger input of the nutrients to lakes (e.g., DOC, DON, P; Creed & Band, 1998a; Creed et al., 2008; Mengistu et al., 2014; Verhoeven et al., 2006)	Wetland cover (%) Ratio of catchment area to lake area (unitless)
Nutrient resuspension potential from land–water interface within littoral zone	Wider littoral zones lead to development of rooted aquatic plants increasing the potential for enhanced loading of DOM (Kornijów et al., 2016)	Littoral zone (ha)
Nutrient resuspension potential from lake sediments	Higher dynamic ratios indicate increased probability of wind-driven sediment resuspension, more exposure to the sun/wind (Bachmann et al., 2000; Hakanson, 2005)	Dynamic ratio ($\sqrt{A}/D_{mean}$), where A is the lake surface area (km^2), and D_{mean} is the lake mean depth (m)
Nutrient dilution potential within the water column	Lakes with larger volumes are characterized by higher nutrient dilution in water and enhanced stratification (Nõges, 2009; Staehr et al., 2012)	Lake volume (m^3), Fetch distance (m)

to 0, the less important it is. Climate and landscape factors with the lowest *%IncMSE* were considered "unimportant" (Strobl et al., 2009). We also used partial dependence plots to demonstrate the relationship between Chl-*a* and an individual factor while all other factors were held constant (Friedman, 2001). We evaluated the accuracy of the random forest model by calculating out-of-bag (OOB) errors as a function of the number of trees (see Breiman, 1996). Both regression tree and random forest analyses were performed in R (R Core Team, 2018) using *rpart*, *party*, and *randomForest* (for the random forests) packages.

Median values of climate and landscape factors for each lake trophic state (i.e., oligotrophic, mesotrophic, and eutrophic) were calculated to produce a generalized conceptual model describing climate (i.e., temperature and precipitation) and landscape factors of each trophic state.

4 | RESULTS

The 281 study lakes covered the range of trophic states found in the region; 203 lakes were oligotrophic, 59 lakes were mesotrophic, and 19 lakes were eutrophic (Table 1; Figure 1). Descriptive statistics of the climate factors, landscape factors, and Chl-*a* for these lakes are provided in Table 2.

Pearson correlation analysis revealed that many landscape factors were correlated with each other (Table 4). Only landscape factors that were not correlated with other landscape factors but that were correlated with Chl-*a* were used in the regression tree and random forest analyses. Five landscape factors were selected: latitude, wetland cover, littoral zone, dynamic ratio, and lake volume. Latitude was selected over longitude because of its strong effect on lake phytoplankton abundance and composition (Kosten et al., 2012; Nõges, 2009; Pollingher, 1990).

Regression tree, random forest analysis, and the partial dependence plots revealed complex interactions among climate factors, landscape factors, and Chl-*a* (Figure 2; Figure S1). The OOB error estimation showed that there was no overall decrease in the OOB error after ~800 trees (the lowest OOB error, equal to 0.54, was obtained between 950 and 1000 trees), indicating that there were sufficient trees in the random forest model (Figure S2).

The Chl-*a* in each terminal node of the regression tree showed a systematic increase from the first node (median Chl-*a* = 0.4 μg L^{-1}, $n = 32$) to the last node (median Chl-*a* = 13.7 μg L^{-1}, $n = 7$; Figure 2). Lake volume was the most important predictor of Chl-*a*, making the first split in the tree at 44 × 10^4 m^3, clearly differentiating lakes with larger volumes (≥44 × 10^4 m^3) from lakes with smaller volumes (<44 × 10^4 m^3). Figure 2b shows that after lake volume, precipitation was the second most important predictor of Chl-*a* followed by temperature. However, the regression tree shows a more complex relationship (Figure 2a), where precipitation was the second most important predictor of Chl-*a* in lakes with larger volumes, while temperature was the second most important predictor of Chl-*a* in lakes with smaller volumes (i.e., <44 × 10^4 m^3). Furthermore, temperature was the sole climatic predictor of Chl-*a* only in seven smaller volumes lakes, which were all eutrophic. Dynamic ratio, wetland cover, and littoral zone also contributed to the variation of Chl-*a* but only in larger volume lakes. Latitude did not appear in the tree and was the least important factor reported by the random forest analysis (Figure 2b).

Conceptual models depicting relationships between climate and landscape factors and lake trophic states revealed that each lake trophic state had its "typical" set of climatic conditions (i.e., temperature and precipitation) and landscape properties (Figure 3). Lake volume was largest in oligotrophic lakes (265 × 10^4 m^3), followed by mesotrophic (156 × 10^4 m^3) and eutrophic lakes (34 × 10^4 m^3; Figure 3 but also Figure 2). Precipitation

TABLE 4 Pearson's correlation matrix for Chl-*a* and landscape factors

	Latitude	Longitude	ln Altitude	Wetland cover (%)	ln (Catchment area/ lake area)	ln Littoral zone	Dynamic ratio	ln Lake volume	ln Fetch distance
ln Chl-*a*	**−0.40**	0.23	**−0.28**	**0.31**	0.07	**0.17**	**0.35**	**−0.39**	**−0.18**
Latitude		**−0.75**	**0.49**	−0.13	−0.04	0.01	−0.03	−0.06	−0.02
Longitude			**−0.38**	0.16	0.04	0.01	0.03	−0.07	−0.08
ln Altitude				**−0.43**	−0.13	**−0.19**	**−0.20**	−0.03	−0.11
Wetland cover (%)					0.03	0.14	0.15	0.02	**0.16**
ln (Catchment area/lake area)						**0.66**	0.15	−0.02	0.08
ln Littoral zone							0.15	0.14	**0.64**
Dynamic ratio								−0.04	**0.41**
ln Lake volume									**0.81**

Note: Data are presented as Pearson's *r*. Factor names in boldface indicate factors selected for the regression tree and random forests analyses. Pearson's *r* values in boldface indicate relationship between factors at $p < .05$.

decreased from oligotrophic (92 mm), to mesotrophic (89 mm), to eutrophic (84 mm) lakes. In contrast, temperature increased from oligotrophic (19.5°C), to mesotrophic (20°C), to eutrophic (21°C) lakes. Eutrophic lakes had the highest dynamic ratio (0.50), with the maximum ratio reaching 3.60. Mesotrophic lakes had the second highest dynamic ratio (0.20), followed by oligotrophic lakes (0.15). Wetland cover increased from oligotrophic (4.4%), to mesotrophic (4.8%), to eutrophic (7.1%) lakes. Maximum wetland cover was also found in eutrophic lakes where it reached 64%. Oligotrophic lakes had the smallest median littoral zones (1.8 ha), followed by mesotrophic lakes (2.7 ha) and then eutrophic lakes (3.3 ha).

5 | DISCUSSION

A broad range in long-term median Chl-*a* (our proxy for phytoplankton biomass) exists in thousands of lakes within the relatively intact northern temperate forest (Paltsev & Creed, 2021). Here, we combined climate (i.e., long-term median air temperature and precipitation) and landscape factors for 281 lakes into a single model to understand how landscape properties regulate the response of phytoplankton biomass to climatic conditions. We provide convincing evidence that climate effects are filtered by landscape properties resulting in the heterogeneity of lake Chl-*a* (Figure 2). We found that climate factors were important determinants of Chl-*a*, but that landscape factors that influence nutrient sources, pathways, and fates in lakes were more important determinants. Based on these findings, we developed a simple conceptual model that shows the effects of climate and landscape factors on phytoplankton biomass in northern temperate lakes in a region with minimal human activities (Figure 3).

Lake volume was the most important factor for predicting Chl-*a*. Our finding that Chl-*a* increases with decreasing lake volume is in good agreement with other studies (e.g., Duarte & Kalff, 1989; Kosten et al., 2012; Staehr et al., 2012; Stomp et al., 2011). This inverse correlation between Chl-*a* and lake volume might be explained by lake residence times. Not only do larger volume lakes have more water, but they also have longer water residence times, which result in lower concentrations of nutrients and therefore lower phytoplankton biomass (Cardille et al., 2004; Mosley, 2015; Reckhow, 1988; Staehr et al., 2012).

5.1 | Smaller volume lakes

In smaller volume lakes (<44 × 10^4 m^3), warmer and drier conditions related to higher Chl-*a*. Specifically, temperature was the sole climatic predictor of Chl-*a* in lakes with a temperature above 21°C. These lakes had the smallest volumes (median = 16 × 10^4 m^3), the shallowest depths (median maximum depth = 1.5 m), and the highest temperatures (median = 21.3°C; Table S1). These lakes were also eutrophic with the highest Chl-*a* (>12.0 μg L^{-1}). Direct factors associated with temperature (e.g., heat distribution through the

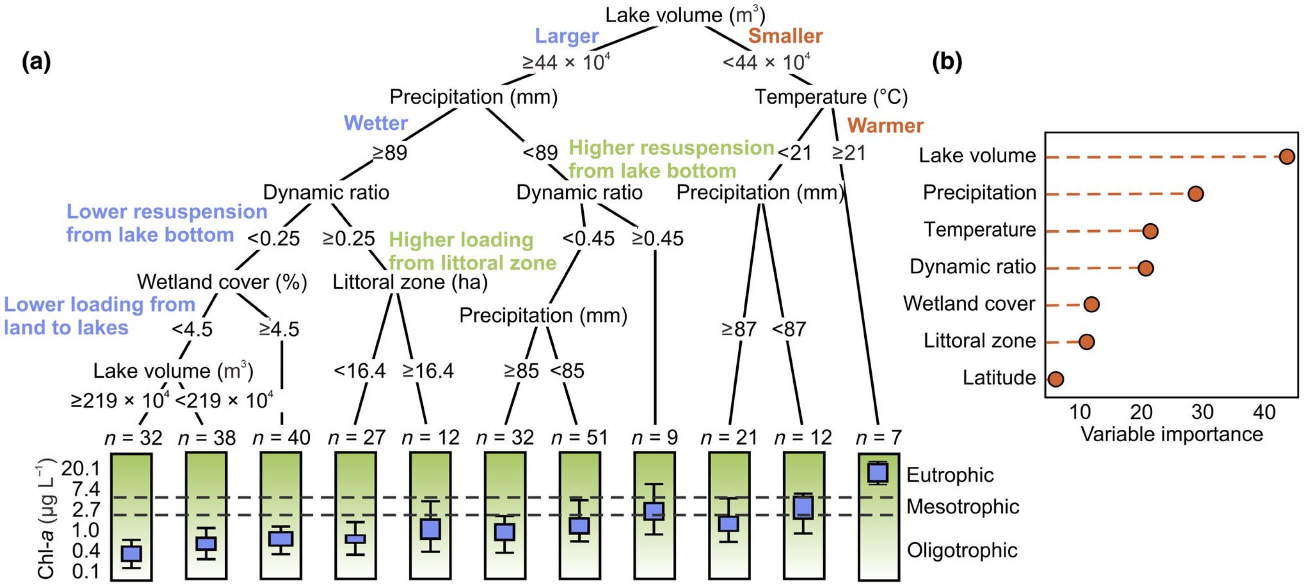

FIGURE 2 (a) Regression tree, and (b) variable importance plot from the random forest model depicting the effect of seven climate and landscape factors on phytoplankton biomass in 281 study lakes, using Chl-*a* as a proxy. Labels for Chl-*a*, lake volume and littoral zone are *back*-transformed from the natural logarithm using the exponential function. Variable importance is measured by the percent increase in mean squared error (*%IncMSE*). Number of trees used in the random forest model is 1000 [Colour figure can be viewed at wileyonlinelibrary.com]

water column) likely played a significant role in determining phytoplankton biomass in these small and shallow lakes. Indeed, the water columns of smaller volume lakes generally warm up faster and deeper (often to the lake bottom) compared to the water columns of larger volume lakes (Johnson et al., 2014; Sharma et al., 2019).

Below the temperature threshold of 21°C, precipitation contributed significantly to Chl-*a*, with lower precipitation correlating with higher Chl-*a*. Lakes in regions of lower precipitation were predominantly mesotrophic and lakes in regions of higher precipitation were predominantly oligotrophic. The interactive effects of higher temperatures accompanied by reduced precipitation or prolonged droughts can lead to longer water residence times (Zwart et al., 2017), lower dilution potential, and increased nutrient levels in the water column (Mosley, 2015)—all of which lead to higher Chl-*a*. These climatic conditions can also cause a significant decrease in the water level of smaller volume lakes, resulting in sediments being in direct contact with the trophogenic layer (the upper photosynthetically active layer of lakes; Nõges, 2009; Søndergaard et al., 2001). In this case, lake sediments (especially in lakes with relatively large surface areas) might be easily disturbed by wind leading to intensified internal nutrient loading.

The idea that temperature is the major driver of phytoplankton biomass has little support in field studies and laboratory experiments. Many studies on the temperature versus phytoplankton biomass relationship show that this relationship is complex and depends upon the rate of temperature increase, changes in precipitation and runoff patterns, nutrient availability in lakes, and the community composition of phytoplankton and zooplankton (Blenckner et al., 2007; Gerten & Adrian, 2002; Ho et al., 2019; Moss et al., 2003; Richardson et al., 2018; Striebel et al., 2016). Here, we found that temperature was the sole predictor of Chl-*a* only in a minority of lakes, which were also the smallest lakes. The positive correlation between temperature and Chl-*a* of small lakes is unlikely to be unique to the lakes of our study region. Kraemer et al. (2017) analyzed phytoplankton biomass in 188 lakes from all continents (except Australia and Antarctica) and found that Chl-*a* in smaller lakes had higher positive correlation coefficients with lake surface temperature than Chl-*a* in larger lakes. The authors also found that an increase in temperature tended to increase Chl-*a* in phytoplankton-rich lakes (i.e., eutrophic lakes) and decrease Chl-*a* in phytoplankton-poor lakes (i.e., oligotrophic lakes).

5.2 | Larger volume lakes

In larger volume lakes (≥44 × 10^4 m^3), precipitation and not temperature was the most important predictor of Chl-*a*. The relationship between precipitation and phytoplankton biomass is also known to be complex. Precipitation affects phytoplankton directly (via the direct contact of precipitation with limnetic and littoral zones of lakes) and indirectly (via run-off and associated nutrient loading from lake catchments; Figure 3; De Senerpont Domis et al., 2013; Hrycik et al., 2021; Larsen et al., 2020; O'Neil et al., 2012; Richardson et al., 2018). For direct effects, increased precipitation is likely to enhance mixing of the water column and diluting of nutrients in lakes, which lead to lower concentrations of nutrients in water and therefore lower phytoplankton biomass (Whitehead et al., 2009). This is especially the case for larger volume lakes with large surfaces that increase direct contact of precipitation with the lakes' open waters (e.g., in

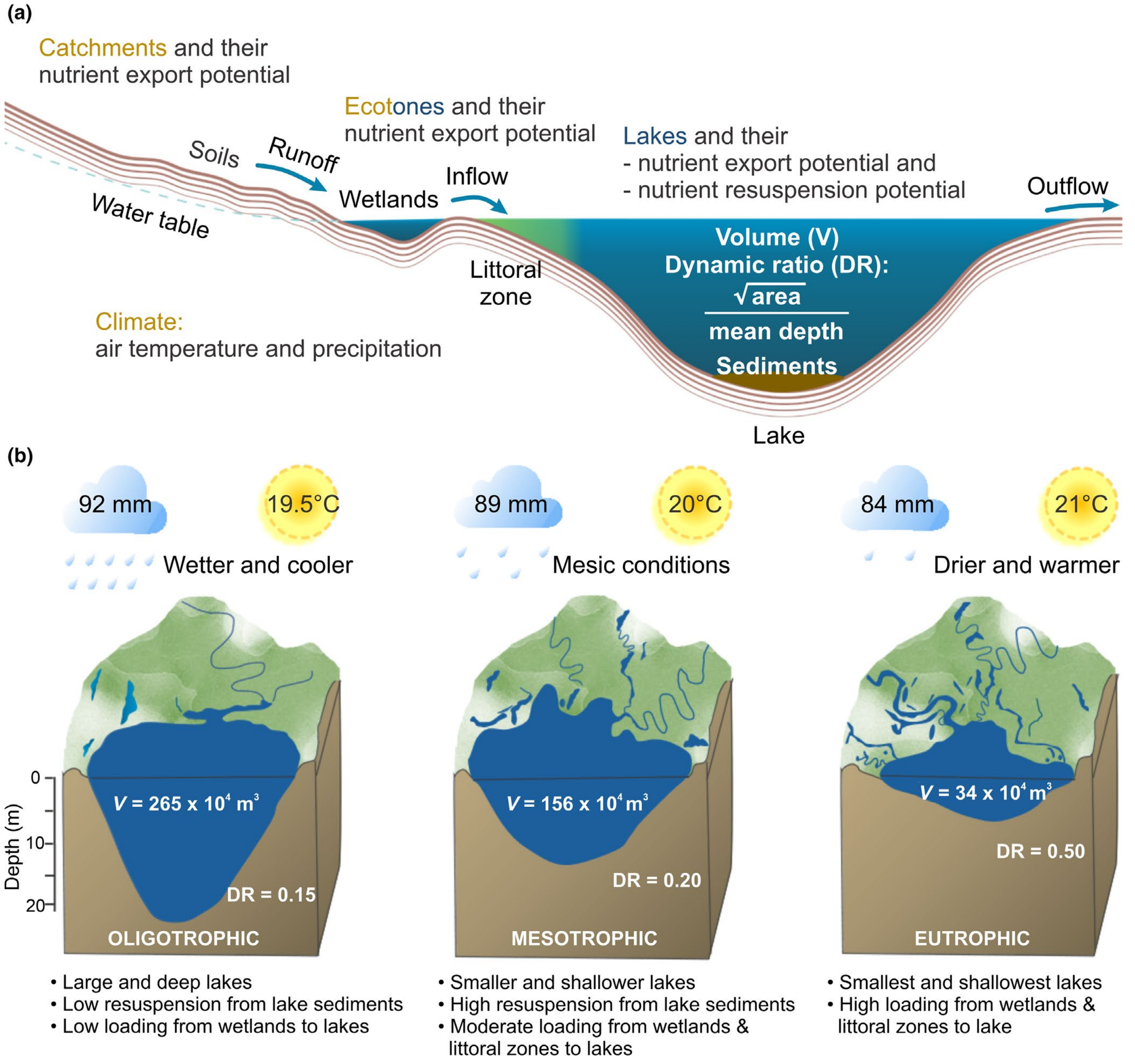

FIGURE 3 Conceptual models depicting hypothesized effects of climate and landscape factors on phytoplankton biomass in (a) all study lakes (generalized model), and (b) lakes within each lake trophic state. The factors are median values (except for maximum depth, which is mean value). Oligotrophic lakes (low Chl-*a*; range: 0.1–2.6 μg L^{-1}) receive the highest precipitation and, as one might expect, higher runoff. However, small proportions of wetlands in their catchments indicates that the runoff is likely to have relatively low nutrient concentration. Further, since these lakes also have the largest volume and they are the deepest, they are prone to nutrient dilution. Finally, small littoral zones and small dynamic ratios indicate that these lakes are not susceptible to wind-driven sediment resuspension (i.e., sediments are unlikely to be disturbed by wind as indicated by the dynamic ratio). Mesotrophic lakes (moderate Chl-*a*; range: 2.6–7.3 μg L^{-1}) receive less precipitation but are characterized by higher external (i.e., they have more wetlands in their catchments) and internal (i.e., they have higher dynamic ratios) nutrient loading than oligotrophic lakes. Further, since mesotrophic lakes have smaller volume, the process of nutrient dilution is less pronounced there. Eutrophic lakes (high Chl-*a*; range: 7.3–41.3 μg L^{-1}) receive the least precipitation and have the higher temperature than oligotrophic and mesotrophic lakes. Reduced water inflow makes water "stay longer" in the lakes, therefore extending the residence time. Further, because of the combined effect of higher temperature and shallow depth, the water column of eutrophic lakes might warm down to the bottom, leading to reduced concentration of dissolved oxygen and enhanced internal nutrients loading from sediments. Very high dynamic ratio means eutrophic lakes are susceptible to wind disturbance. Finally, these lakes have high loading of external (allochthonous) material because of extensive wetland cover [Colour figure can be viewed at wileyonlinelibrary.com]

our study, lakes with the largest volumes (>219 × 10^4 m^3) also had the largest surface areas (median = 0.9 km^2). For indirect effects, increased precipitation is likely to inundate high-nutrient areas (e.g., wetlands) within the lake catchment (Creed et al., 1996) resulting in the mobilization of nutrient-enriched waters to lakes (e.g., Creed & Band, 1998a; Mengistu et al., 2014; Sinha et al., 2017; Weyhenmeyer et al., 2016; Zwart et al., 2017), and therefore higher phytoplankton biomass (Sorichetti et al., 2014b). However, we found that larger volume lakes with more precipitation (≥89 mm from July to October) typically had lower Chl-*a* than larger volume lakes with less precipitation (<89 mm). This suggests that larger volume lakes with more precipitation were more dependent on external nutrient loading potentials while the larger volume lakes with less precipitation were more dependent on internal nutrient loading potential (Figure 2).

In larger volume lakes with more precipitation, we found that catchments with low external nutrient loading potential from wetlands had low Chl-*a* and, vice versa, catchments with higher external nutrient loading potential from wetlands or higher internal nutrient loading potential from the littoral zone had higher Chl-*a*. A lake's external nutrient loading potential might be explained by the soil types within the lake catchments. In our study region, catchments dominated with mineral soils are experiencing decreasing trends in the export of P (Eimers et al., 2009; Mengistu et al., 2013) and N (Geddes & Martin, 2017; Mengistu et al., 2013) for at least the last 20 years. These mineral soils are known to have naturally low P concentrations (Jeffries & Snyder, 1983). However, leaching rates of P might be further lowered due to soil acidification and associated enhanced absorption of P to soil mineral surfaces (Eimers et al., 2009). Thus, it is unlikely that more precipitation and associated runoff from mineral soils contributes substantially to the increased nutrient flux (P and N) and, by extension, phytoplankton biomass in larger volume lakes.

In contrast, catchments dominated with organic soils (i.e., wetlands) are experiencing variable trends in the export of nutrients depending on climatic conditions (Senar et al., 2018). Wetlands typically cover a small portion of catchments (in the study region, the median wetland cover in catchments of oligotrophic lakes was only 4.4%). Despite this, the contribution of wetlands to the external nutrient loading to lakes and streams of the study region has been found to be significant (Creed et al., 2008; Mengistu et al., 2014). Wetlands are often located in topographic flats or depressions near lakes and, therefore, catchment discharge waters pass through them on their way to receiving waters (Creed & Beall, 2009). Wetlands are known sources of P and organic solutes such as DOC and DON (Creed & Beall, 2009; Creed et al., 2003, 2008; Enanga et al., 2017; Mengistu et al., 2014) and, therefore, more wetlands indicate larger exports of these nutrients to lakes (Creed & Band, 1998a, 1998b; Verhoeven et al., 2006). Furthermore, often adjacent to wetlands, littoral zones along the shorelines of lakes serve as points of entry for nutrients released from these wetlands (Kornijów et al., 2016). Large littoral zones indicate extensive shallow areas within lakes—areas that are often occupied by communities of rooted macrophytes. These communities act as a filter for external material where nutrients are retained and accumulated, being taken up by the macrophytes and attached algae, and are finally released into the sediments and the water column in the same or transformed (and often more accessible for phytoplankton) forms (Kornijów et al., 2016; Orihel et al., 2017). Therefore, a larger littoral zone reflects a higher potential for enhanced nutrient loading (Vadeboncoeur et al., 2002; Zhu et al., 2015) and, as a result, higher Chl-*a*.

In larger volume lakes with less precipitation, we found that catchments with higher nutrient-resuspension potentials from the lake sediments had higher Chl-*a*. Lake sediments often contain high concentrations of N, P, and micronutrients such as iron that control phytoplankton growth (Molot et al., 2010; Sorichetti et al., 2014b). The dynamic ratio indicates the relative area of lake bottom influenced by wind-driven resuspension; a higher dynamic ratio represents a higher risk of wind-induced sediment resuspension events (Bachmann et al., 2000; Hakanson, 2005; Qin et al., 2004; Zhu et al., 2015) and, therefore, internal loading of nutrients from sediments that promote phytoplankton growth (Søndergaard et al., 2001). The intensified internal nutrient loading can also happen without disturbing lake sediments. In relatively deep lakes, when warmer temperatures and reduced precipitation lengthen the period of thermal stratification (Winder & Sommer, 2012), a low dissolved oxygen layer forms leading to the release of P from lake sediments into the waters below the thermocline that winds can then bring to the surface waters (Dittrich et al., 2013; Nürnberg & LaZerte, 2004).

We found that landscape factors are more important in regulating Chl-*a* in oligotrophic and mesotrophic lakes (Chl-*a* $< 7.3\ \mu g\ L^{-1}$) than eutrophic lakes (Figures 2 and 3). This suggest that oligotrophic lakes are likely to be more sensitive to precipitation-driven biogeochemical changes occurring within coupled catchment-lake systems than eutrophic lakes (Reinl et al., 2021).

This study region is projected to become warmer (Zhou et al., 2018). While projections of precipitation are less clear, the general trend is that winter precipitation will increase while summer precipitation will decrease (Yeung et al., 2018; Zhou et al., 2018). The seasonal changes in precipitation will likely result in larger relative discharges of water and nutrients from catchments to lakes during spring runoff. The elevated discharges combined with the increasing temperature might increase phytoplankton biomass in medium- to small-sized lakes with lower dilution potential and many wetlands in the catchments. Weather events are also predicted to be more unstable. Extreme events, ranging from drought conditions to floods, are projected to occur more frequently and last longer (Zhou et al., 2018). Changes at this scale will likely interrupt hydrologic cycles within catchment-lake system (Senar et al., 2018; Zwart et al., 2017) and, consequently, alter the magnitude and composition of nutrient export into lakes (Creed et al., 2018). In this case, wetlands and littoral zones might play a major role in regulating nutrient export because they serve as either sinks or sources of nutrients depending on current climatic conditions (e.g., a prolonged period of hydrologic dysconnectivity between a wetland and a lake during droughts interrupted by intensive hydrologic connectivity during floods; Senar et al., 2018).

6 | CONCLUSION

Interactions of climate and landscape factors influence phytoplankton biomass in northern temperate lakes. We conclude that lake volume, which regulates mixing of the water column and dilution of nutrients, was the dominant factor influencing phytoplankton biomass. In lakes with the smallest volumes, temperature was the sole climate predictor of phytoplankton biomass (i.e., higher temperatures = higher Chl-*a*). In larger volume lakes, temperature effects were overridden by both the direct and indirect effects of precipitation on phytoplankton biomass. In these larger volume lakes, precipitation-driven alterations in nutrient export from lake catchments with a higher potential for nutrient loading from wetlands and a higher potential for nutrient loading from resuspension of nutrients in lake sediments increased nutrient availability and, thereby, supported a larger phytoplankton biomass. Climate change predictions for the northern temperate region are warmer conditions with less precipitation in summer but more precipitation in winter. Our conclusions indicate that the response of phytoplankton biomass in the lakes of this region will depend on landscape factors, with smaller and shallower lakes with many wetlands experiencing the largest increases in phytoplankton biomass. Larger lakes with high external or internal nutrient loading potentials will be particularly vulnerable to climate driven shifts from oligotrophic to eutrophic trophic states.

ACKNOWLEDGMENTS

This study was funded by a Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grant 06579-2014 NSERC Collaborative Research to IFC and a Training Experience (CREATE) Grant 448172-2014 to IFC that funded AP. The authors are grateful to Cindy Chu (Ontario Ministry of Natural Resources and Forestry) for sharing vector polyline bathymetric data (in a digital format) for many of study lakes. The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad at https://doi.org/10.5061/dryad.2fqz612qn.

ORCID

Irena F. Creed https://orcid.org/0000-0001-8199-1472

REFERENCES

Anderson, N. J. (2014). Landscape disturbance and lake response: Temporal and spatial perspectives. *Freshwater Reviews*, *7*, 77–120. https://doi.org/10.1608/FRJ-7.2.811

Bachmann, R. W., Hoyer, M. V., & Canfield, D. E. (2000). The potential for wave disturbance in shallow Florida Lakes. *Lake and Reservoir Management*, *16*, 281–291. https://doi.org/10.1080/07438140009354236

Baines, S. B., Webster, K. E., Kratz, T. K., Stephen, R., Ecology, S., & Mar, N. (2000). Synchronous behavior of temperature, calcium, and chlorophyll in lakes of Northern Wisconsin. *Ecology*, *81*, 815–825.

Baldwin, D. J. B., Desloges, J. R., & Band, L. E. (2000). Physical geography of Ontario. In A. Perera, D. Euler, & I. D. Thompson (Eds.), *Ecology of a managed terrestrial landscape: Patterns and processes of forest landscapes in Ontario* (pp. 141–162). University of British Columbia Press.

Bedford, J., Ostle, C., Johns, D. G., Atkinson, A., Best, M., Bresnan, E., & McQuatters-Gollop, A. (2020). Lifeform indicators reveal large-scale shifts in plankton across the North-West European shelf. *Global Change Biology*, *26*, 3482–3497. https://doi.org/10.1111/gcb.15066

Blenckner, T. (2005). A conceptual model of climate-related effects on lake ecosystems. *Hydrobiologia*, *533*, 1–14. https://doi.org/10.1007/s10750-004-1463-4

Blenckner, T., Adrian, R., Livingstone, D. M., Jennings, E., Weyhenmeyer, G. S., George, D. G., Jankowski, T., Jarvinen, M., Aonghusa, C. N., Nõges, T., Straile, D., & Teubner, K. (2007). Large-scale climatic signatures in lakes across Europe: A meta-analysis. *Global Change Biology*, *13*, 1314–1326. https://doi.org/10.1111/j.1365-2486.2007.01364.x

Boyer, J. N., Kelble, C. R., Ortner, P. B., & Rudnick, D. T. (2009). Phytoplankton bloom status: Chlorophyll-*a* biomass as an indicator of water quality condition in the southern estuaries of Florida, USA. *Ecological Indicators*, *9*, S56–S67. https://doi.org/10.1016/j.ecolind.2008.11.013

Breiman, L. (1996). *Out-of-bag estimation*. Technical report, Department of Statistics. University of California.

Breiman, L. (2001). Random forests. *Machine Learning*, *45*, 5–32. https://doi.org/10.1023/A:1010933404324

Canada Soil Survey Committee. (1978). *Proceedings of the eighth meeting of the Canada Soil Survey Committee of Canada*. Mimeographed report of the Canada Department of Agriculture, 354 p.

Cardille, J., Coe, M. T., & Vano, J. (2004). Impacts of climate variation and catchment area on water balance and lake hydrologic type in groundwater-dominated systems: A generic lake model. *Earth Interactions*, *8*, 1–24.

Carey, C. C., Ibelings, B. W., Hoffmann, E. P., Hamilton, D. P., & Brookes, J. D. (2012). Eco-physiological adaptations that favour freshwater cyanobacteria in a changing climate. *Water Research*, *46*(5), 1394–1407. https://doi.org/10.1016/j.watres.2011.12.016

Carlson, R. E., & Simpson, J. (1996). *A Coordinator's guide to volunteer lake monitoring methods*. North American Lake Management Society, 96 p.

Chander, G., Markham, B., & Helder, D. (2009). Summary of current radiometric calibration coefficients for Landsat MSS, TM, ETM+, and EO-1 ALI sensors. *Remote Sensing of Environment*, *113*, 893–903. https://doi.org/10.1016/j.rse.2009.01.007

Creed, I. F., & Band, L. E. (1998a). Export of nitrogen from catchments within a temperate forest: Evidence for a unifying mechanism regulated by variable source area dynamics. *Water Resources Research*, *34*, 3105–3120. https://doi.org/10.1029/98WR01924

Creed, I. F., & Band, L. E. (1998b). Exploring functional similarity in the export of nitrate-N from forested catchments: A mechanistic modeling approach. *Water Resources Research*, *34*, 3079–3093. https://doi.org/10.1029/98WR02102

Creed, I. F., Band, L. E., Foster, N. W., Morrison, I. K., Nicolson, J. A., Semkin, R. S., & Jeffries, D. S. (1996). Regulation of nitrate-N release from temperate forests: A test of the N flushing hypothesis. *Water Resources Research*, *32*, 3337–3354. https://doi.org/10.1029/96WR02399

Creed, I. F., & Beall, F. D. (2009). Distributed topographic indicators for predicting nitrogen export from headwater catchments. *Water Resources Research*, *45*, W10407. https://doi.org/10.1029/2008WR007285

Creed, I. F., Beall, F. D., Clair, T. A., Dillon, P. J., & Hesslein, R. H. (2008). Predicting export of dissolved organic carbon from forested catchments in glaciated landscapes with shallow soils. *Global Biogeochemical Cycles*, *22*(GB4024). https://doi.org/10.1029/2008GB003294

Creed, I. F., Bergström, A.-K., Trick, C. G., Grimm, N. B., Hessen, D. O., Karlsson, J., Kidd, K. A., Kritzberg, E., McKnight, D. M., Freeman, E. C., Senar, O. E., Andersson, A., Ask, J., Berggren, M., Cherif, M., Giesler, R., Hotchkiss, E. R., Kortelainen, P., Palta, M. M., … Weyhenmeyer, G. A. (2018). Global change-driven effects on dissolved organic matter composition: Implications for food webs of northern lakes. *Global Change Biology*, *24*, 3692–3714. https://doi.org/10.1111/gcb.14129

Creed, I. F., Lutz, B., Hwang, T., & Way, D. A. (2015). Climate warming causes intensification of the hydrological cycle in northern forests. *Hydrological Processes*, *29*, 3519–3534. https://doi.org/10.1002/hyp.10450

Creed, I. F., Sanford, D. E., Beall, F. D., Molot, L. A., & Dillon, P. J. (2003). Cryptic wetlands: Integrating hidden wetlands in regression models of the export of dissolved organic carbon from forested landscapes. *Hydrological Processes*, *17*, 3629–3648. https://doi.org/10.1002/hyp.1357

De Senerpont Domis, L. N., Elser, J. J., Gsell, A. S., Huszar, V. L. M., Ibelings, B. W., Jeppesen, E., Kosten, S., Mooij, W. M., Roland, F., Sommer, U., Van Donk, E., Winder, M., & Lürling, M. (2013). Plankton dynamics under different climatic conditions in space and time. *Freshwater Biology*, *58*, 463–482. https://doi.org/10.1111/fwb.12053

De Senerpont Domis, L. N., Mooij, W. M., & Huisman, J. (2007). Climate-induced shifts in an experimental phytoplankton community: A mechanistic approach. In R. D. Gulati, E. Lammens, N. De Pauw, & E. Van Donk (Eds.), *Shallow lakes in a changing world* (pp. 403–413). Springer.

De'ath, G. (2002). Multivariate regression trees: a new technique for modeling species–environment relationships. *Ecology*, *83*, 1105–1117.

De'ath, G., & Fabricius, K. E. (2000). Classification and regression trees: A powerful yet simple technique for ecological data. *Ecology*, *81*, 3178–3192.

Dittrich, M., Chesnyuk, A., Gudimov, A., McCulloch, J., Quazi, S., Young, J., Winter, J., Stainsby, E., & Arhonditsis, G. (2013). Phosphorus retention in a mesotrophic lake under transient loading conditions: Insights from a sediment phosphorus binding form study. *Water Research*, *47*, 1433–1447. https://doi.org/10.1016/j.watres.2012.12.006

Downing, J. A., Prairie, Y. T., Cole, J. J., Duarte, C. M., Tranvik, L. J., Striegl, R. G., McDowell, W. H., Kortelainen, P., Caraco, N. F., Melack, J. M., & Middelburg, J. J. (2006). The global abundance and size distribution of lakes, ponds, and impoundments. *Limnology and Oceanography*, *51*(5), 2388–2397. https://doi.org/10.4319/lo.2006.51.5.2388

Downing, J. A., Watson, S., & McCauley, E. (2001). Predicting cyanobacteria dominance in lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, *58*, 1905–1908. https://doi.org/10.1139/f01-143

Duarte, C. M., & Kalff, J. (1989). The influence of catchment geology and lake depth on phytoplankton biomass. *Archiv für Hydrobiology*, *115*, 27–40.

Eimers, M. C., Watmough, S. A., Paterson, A. M., Dillon, P. J., & Yao, H. (2009). Long-term declines in phosphorus export from forested catchments in south-central Ontario. *Canadian Journal of Fisheries and Aquatic Sciences*, *66*(10), 1682–1692. https://doi.org/10.1139/F09-101

Enanga, E. M., Casson, N. J., Fairweather, T. A., & Creed, I. F. (2017). Nitrous oxide and dinitrogen: The missing flux in nitrogen budgets of forested catchments? *Environmental Science & Technology*, *51*, 6036–6043. https://doi.org/10.1021/acs.est.6b03728

Erratt, K. J., Creed, I. F., Chemali, C., Ferrara, A. J., Tai, V., & Trick, C. G. (2021). Performance and competitiveness of red vs. green phenotypes of a cyanobacterium grown under artificial lake browning. *Algae*, *36*, 1–12. https://doi.org/10.4490/algae.2021.36.7.19

Freeman, E. C., Creed, I. F., Jones, B., & Bergstrom, A.-K. (2020). Global changes may be promoting a rise in select cyanobacteria in nutrient-poor northern lakes. *Global Change Biology*, *26*, 4966–4987. https://doi.org/10.1111/gcb.15189

Friedman, J. H. (2001). Greedy function approximation: A gradient boosting machine. *The Annals of Statistics*, *29*(5), 1189–1232. https://doi.org/10.1214/aos/1013203451

Geddes, J. A., & Martin, R. V. (2017). Global deposition of total reactive nitrogen oxides from 1996 to 2014 constrained with satellite observations of NO_2 columns. *Atmospheric Chemistry and Physics*, *17*(16), 10071–10091. https://doi.org/10.5194/acp-17-10071-2017

Gerten, D., & Adrian, R. (2002). Effects of climate warming, North Atlantic Oscillation, and El Niño-Southern Oscillation on Thermal conditions and plankton dynamics in northern hemispheric lakes. *The Scientific World Journal*, *2*, 586–606. https://doi.org/10.1100/tsw.2002.141

Hakanson, L. (2005). The importance of lake morphometry and catchment characteristics in limnology–ranking based on statistical analyses. *Hydrobiologia*, *541*, 117–137. https://doi.org/10.1007/s10750-004-5032-7

Ho, J. C., Michalak, A. M., & Pahlevan, N. (2019). Widespread global increase in intense lake phytoplankton blooms since the 1980s. *Nature*, *574*(7780), 667–670. https://doi.org/10.1038/s41586-019-1648-7

Hollert, H., Crawford, S. E., Brack, W., Brinkmann, M., Fischer, E., Hartmann, K., Keiter, S., Ottermanns, R., Ouellet, J. D., Rinke, K., Rösch, M., Roß-Nickoll, M., Schäffer, A., Schüth, C., Schulze, T., Schwarz, A., Seiler, T.-B., Wessels, M., Hinderer, M., & Schwalb, A. (2018). Looking back–looking forward: A novel multi-time slice weight-of-evidence approach for defining reference conditions to assess the impact of human activities on lake systems. *Science of the Total Environment*, *626*, 1036–1046. https://doi.org/10.1016/j.envint.2010.06.009

Hrycik, A. R., Isles, P. D. F., Adrian, R., Albright, M., Bacon, L. C., Berger, S. A., & Pierson, D. C. (2021). Earlier winter/spring runoff and snowmelt during warmer winters lead to lower summer chlorophyll-*a* in north temperate lakes. *Global Change Biology*, *7*, 4615–4629. https://doi.org/10.1111/gcb.15797

Huot, Y., Babin, M., Bruyant, F., Grob, C., Twardowski, M. S., & Claustre, H. (2007). Does chlorophyll a provide the best index of phytoplankton biomass for primary productivity studies? *Biogeosciences Discussions*, *4*, 707–745. https://doi.org/10.5194/BGD-4-707-2007

Hutchinson, M. F., Xu, T., & Stein, J. A. (2011). Recent Progress in the ANUDEM elevation gridding procedure. In T. Hengel, I. S. Evans, J. P. Wilson, & M. Gould (Eds.), *Geomorphometry* (pp. 19–22). University of Redlands.

Isles, P. D. F., Jonsson, A., Creed, I. F., & Bergström, A.-K. (2020). Does browning affect the identity of limiting nutrients in lakes? *Aquatic Sciences*, *82*(2), 1–14. https://doi.org/10.1007/s00027-020-00718-y

Jeffries, D. S., & Snyder, W. R. (1983). *Geology and geochemistry of the Muskoka-Haliburton study area*. Ontario Ministry of Environment Data Report, 102 p.

Jeppesen, E., Kronvang, B., Meerhoff, M., Søndergaard, M., Hansen, K. M., Andersen, H. E., Lauridsen, T. L., Liboriussen, L., Beklioglu, M., Özen, A., & Olesen, J. E. (2009). Climate change effects on runoff, catchment phosphorus loading and lake ecological state, and potential adaptations. *Journal of Environment Quality*, *38*(5), 1930–1941. https://doi.org/10.2134/jeq2008.0113

Johnson, M. F., Wilby, R. L., & Toone, J. A. (2014). Inferring air-water temperature relationships from river and catchment properties. *Hydrological Processes*, *28*, 2912–2928. https://doi.org/10.1002/hyp.9842

Kasprzak, P., Padisák, J., Koschel, R., Krienitz, L., & Gervais, F. (2008). Chlorophyll a concentration across a trophic gradient of lakes: An estimator of phytoplankton biomass? *Limnologica*, *38*, 327–338. https://doi.org/10.1016/j.limno.2008.07.002

Kayler, Z. E., Premke, K., Gessler, A., Gessner, M. O., Griebler, C., Hilt, S., Klemedtsson, L., Kuzyakov, Y., Reichstein, M., Siemens, J., Totsche, K.-U., Tranvik, L., Wagner, A., Weitere, M., & Grossart, H.-P. (2019). Integrating aquatic and terrestrial perspectives to improve insights into organic matter cycling at the landscape scale. *Frontiers in Earth Science*, *7*, 2296–6463. https://doi.org/10.3389/feart.2019.00127

Klimaszyk, P., & Rzymski, P. (2011). Surface runoff as a factor determining trophic state of midforest lake. *Polish Journal of Environmental Studies*, *20*, 1203–1210.

Kornijów, R., Measey, G. J., & Moss, B. (2016). The structure of the littoral: effects of waterlily density and perch predation on sediment and plant-associated macroinvertebrate communities. *Freshwater Biology*, *61*, 32–50. https://doi.org/10.1111/fwb.12674

Kosten, S., Huszar, V. L. M., Bécares, E., Costa, L. S., Donk, E., Hansson, L.-A., Jeppesen, E., Kruk, C., Lacerot, G., Mazzeo, N., Meester, L., Moss, B., Lürling, M., Nõges, T., Romo, S., & Scheffer, M. (2012). Warmer climates boost cyanobacterial dominance in shallow lakes. *Global Change Biology*, *18*, 118–126. https://doi.org/10.1111/j.1365-2486.2011.02488.x

Kraemer, B. M., Mehner, T., & Adrian, R. (2017). Reconciling the opposing effects of warming on phytoplankton biomass in 188 large lakes. *Scientific Reports*, *7*, 1–7. https://doi.org/10.1038/s41598-017-11167-3

Kritzberg, E. S., Hasselquist, E. M., Škerlep, M., Löfgren, S., Olsson, O., Stadmark, J., Valinia, S., Hansson, L.-A., & Laudon, H. (2020). Browning of freshwaters: Consequences to ecosystem services, underlying drivers, and potential mitigation measures. *Ambio*, *49*, 375–390. https://doi.org/10.1007/s13280-019-01227-5

Larsen, M. L., Baulch, H. M., Schiff, S. L., Simon, D. F., Sauvé, S., & Venkiteswaran, J. J. (2020). Extreme rainfall drives early onset cyanobacterial bloom. *FACETS*, *5*, 899–920. https://doi.org/10.1139/facets-2020-0022

Lobo, F. L., Costa, M. P. F., & Novo, E. M. L. M. (2015). Time-series analysis of Landsat-MSS/TM/OLI images over Amazonian waters impacted by gold mining activities. *Remote Sensing of Environment*, *157*, 170–184. https://doi.org/10.1016/j.rse.2014.04.030

Lürling, M., Eshetu, F., Faassen, E. J., Kosten, S., & Huszar, V. L. M. (2013). Comparison of cyanobacterial and green algal growth rates at different temperatures. *Freshwater Biology*, *58*, 552–559. https://doi.org/10.1111/j.1365-2427.2012.02866.x

Magnuson, J. J., Benson, B. J., & Kratz, T. K. (1990). Temporar coherence in the limnology of a suite of lakes in Wiskonsin, U.S.A. *Freshwater Biology*, *23*, 145–159.

McKenney, D. W., Hutchiinson, M. F., Papadopol, P., Lawrence, K., Pedlar, J., Campbell, K., Milewska, E., Hopkinson, R. F., Price, D., Owen, T. (2011). Customized spatial climate models for North America. *Bulletin of the American Meteorological Society*, *92*, 1611–1622. https://doi.org/10.1175/BAMS-D-10-3132.1

Mengistu, S. G., Creed, I. F., Webster, K. L., Enanga, E., & Beall, F. D. (2014). Searching for similarity in topographic controls on carbon, nitrogen and phosphorus export from forested headwater catchments. *Hydrological Processes*, *28*, 3201–3216. https://doi.org/10.1002/hyp.9862

Mengistu, S. G., Quick, C. G., & Creed, I. F. (2013). Nutrient export from catchments on forested landscapes reveals complex nonstationary and stationary climate signals. *Water Resource Research*, *49*, 3863–3880. https://doi.org/10.1002/wrcr.20302

Molot, L. A., Li, G., Findlay, D. L., & Watson, S. B. (2010). Iron-mediated suppression of bloom-forming cyanobacteria by oxine in a eutrophic lake. *Freshwater Biology*, *55*, 1102–1117. https://doi.org/10.1111/j.1365-2427.2009.02384.x

Morel, A., & Bricaud, A. (1981). Theoretical results concerning light absorption in a discrete medium, and application to specific absorption of phytoplankton. *Deep Sea Research*, *1*(28A), 1375–1393. https://doi.org/10.1016/0198-0149(81)90039-X

Mosley, L. M. (2015). Drought impacts on the water quality of freshwater systems; review and integration. *Earth-Science Reviews*, *140*, 203–214. https://doi.org/10.1016/j.earscirev.2014.11.010

Moss, B., Mckee, D., Atkinson, D., Collings, S. E., Eaton, J. W., Gill, A. B., Harvey, I., Hatton, K., Heyes, T., & Wilson, D. (2003). How important is climate? Effects of warming, nutrient addition and fish on phytoplankton in shallow lake microcosms. *Journal of Applied Ecology*, *40*, 782–792. https://doi.org/10.1046/j.1365-2664.2003.00839.x

Nõges, T. (2009). Relationships between morphometry, geographic location and water quality parameters of European lakes. *Hydrobiologia*, *633*(1), 33–43. https://doi.org/10.1007/s10750-009-9874-x

Nürnberg, G. K., & LaZerte, B. D. (2004). Modeling the effect of development on internal phosphorus load in nutrient-poor lakes. *Water Resources Research*, *40*, 1–9. https://doi.org/10.1029/2003WR002410

O'Neil, J. M., Davis, T. W., Burford, M. A., & Gobler, C. J. (2012). The rise of harmful cyanobacteria blooms: The potential roles of eutrophication and climate change. *Harmful Algae*, *14*, 313–334. https://doi.org/10.1016/j.hal.2011.10.027

Oliver, S. K., Collins, S. M., Soranno, P. A., Wagner, T., Stanley, E. H., Jones, J. R., Stow, C. A., & Lottig, N. R. (2017). Unexpected stasis in a changing world: Lake nutrient and chlorophyll trends since 1990. *Global Change Biology*, *23*, 5455–5467. https://doi.org/10.1111/gcb.13810

Ontario Geological Survey. (2003). *Surficial geology of southern Ontario*. Misc. Release-Data 128, Toronto, ON, Canada. 52 p.

Ontario Ministry of Natural Resources (n.d.). Metadata record for historic bathymetry maps. https://geohub.lio.gov.on.ca/datasets

Ontario Ministry of Natural Resources. (2013). *Ontario wetland inventory database*. https://data.ontario.ca/dataset/wetlands

Ontario Ministry of Natural Resources. (2015). *Provincial digital elevation model* (Version 3.0). http://geo1.scholarsportal.info

Orihel, D. M., Parsons, C. T., Venkiteswaran, J. J., Casson, N. J., Seckar, D. C. M., Baulch, H. M., & Venkiteswaran, J. J. (2017). Internal phosphorus loading in Canadian fresh waters: A critical review and data analysis. *Canadian Journal of Fisheries and Aquatic Sciences*, *74*, 2005–2029. https://doi.org/10.1139/cjfas-2016-0500

Palmer, M. E., Yan, N. D., & Somers, K. M. (2014). Climate change drives coherent trends in physics and oxygen content in North American lakes. *Climatic Change*, *124*, 285–299. https://doi.org/10.1007/s10584-014-1085-4

Paltsev, A., & Creed, I. F. (2021). Are northern lakes in relatively intact temperate forests showing signs of increasing phytoplankton biomass? *Ecosystems*. https://doi.org/10.1007/s10021-021-00684-y

Pollingher, U. (1990). Effects of latitude on phytoplankton composition and abundance in large lakes. In M. M. Tilzer & C. Serruya (Eds.), *Large lakes. Ecological structure and function* (pp. 368–402). Springer Verlag.

Qin, B., Weiping, H., Guang, G., Liancong, L., & Jinshan, Z. (2004). Dynamics of sediment resuspension and the conceptual schema of nutrient release in the large shallow Lake Taihu, China. *Chinese Science Bulletin*, *49*, 54–64. https://doi.org/10.1007/BF02901743

R Core Team. (2018). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Rasconi, S., Winter, K., & Kainz, M. J. (2017). Temperature increase and fluctuation induce phytoplankton biodiversity loss–evidence from a multi-seasonal mesocosm experiment. *Ecology and Evolution*, *7*, 2936–2946. https://doi.org/10.1002/ece3.2889

Read, E. K., Patil, V. P., Oliver, S. K., Hetherington, A. L., Brentrup, J. A., Zwart, J. A., Winters, K. M., Corman, J. R., Nodine, E. R., Woolway, R. I., Dugan, H. A., Jaimes, A., Santoso, A. B., Hong, G. S., Winslow, L. A., Hanson, P. C., & Weathers, K. C. (2015). The importance of lake-specific characteristics for water quality across the continental United States. *Ecological Applications*, *25*, 943–955. https://doi.org/10.1890/14-0935.1

Reckhow, H. K. (1988). Empirical models for trophic state in southeastern U.S lakes and reservoirs. *Water Resources Bulletin*, *24*(4), 723–734. https://doi.org/10.1111/j.1752-1688.1988.tb00923.x

Reinl, K. L., Brookes, J. D., Carey, C. C., Harris, T. D., Ibelings, B. W., Morales-Williams, A. M., De Senerpont Domis, L. N., Atkins, K. S., Isles, P. D. F., Mesman, J. P., North, R. L., Rudstam, L. G., Stelzer, J. A. A., Venkiteswaran, J. J., Yokota, K., & Zhan, Q. (2021). Cyanobacterial blooms in oligotrophic lakes: Shifting the high-nutrient paradigm. *Freshwater Biology*, *66*, 1846–1859. https://doi.org/10.1111/fwb.13791

Richardson, J., Miller, C., Maberly, S. C., Taylor, P., Globevnik, L., Hunter, P., Jeppesen, E., Mischke, U., Moe, S. J., Pasztaleniec, A., Søndergaard, M., & Carvalho, L. (2018). Effects of multiple stressors on cyanobacteria abundance vary with lake type. *Global Change Biology*, *24*, 5044–5055. https://doi.org/10.1111/gcb.14396

Scheffer, M., Carpenter, S., Foley, J. A., Folke, C., & Walker, B. (2001). Catastrophic shifts in ecosystems. *Nature*, *413*, 591–596. https://doi.org/10.1038/35098000

Scheffer, M., & Van Nes, E. H. (2007). Shallow lakes theory revisited: various alternative regimes driven by climate, nutrients, depth and lake size. *Hydrobiologia*, *584*, 455–466. https://doi.org/10.1007/s10750-007-0616-7

Senar, O. E., Creed, I. F., & Webster, K. L. (2018). Catchment-scale shifts in the magnitude and partitioning of carbon export in response to changing hydrologic connectivity in a northern hardwood forest. *Journal of Geophysical Research: Biogeosciences*, *123*, 2337–2352. https://doi.org/10.1029/2018JG004468

Sharma, S., Blagrave, K., Magnuson, J. J., O'Reilly, C. M., Oliver, S., Batt, R. D., Magee, M. R., Straile, D., Weyhenmeyer, G. A., Winslow, L., & Woolway, R. I. (2019). Widespread loss of lake ice around the Northern Hemisphere in a warming world. *Nature Climate Change*, *9*, 227–231. https://doi.org/10.1038/s41558-018-0393-5

Sinha, E., Michalak, A. M., & Balaji, V. (2017). Eutrophication will increase during the 21st century as a result of precipitation changes. *Science*, *357*, 405–408. https://doi.org/10.1126/science.aan2409

Søndergaard, M., Jensen, P. J., & Jeppesen, E. (2001). Retention and internal loading of phosphorus in shallow, eutrophic lakes. *The Scientific World Journal*, *1*, 427–429. https://doi.org/10.1100/tsw.2001.72

Søndergaard, M., Jeppesen, E., Jensen, J., & Peder (2005). Pond or lake: Does it make any difference? *Archiv für Hydrobiologie*, *162*, 143–165. https://doi.org/10.1127/0003-9136/2005/0162-0143

Sorichetti, R. J., Creed, I. F., & Trick, C. G. (2014a). Evidence for iron-regulated cyanobacterial predominance in oligotrophic lakes. *Freshwater Biology*, *59*, 679–691. https://doi.org/10.1111/fwb.12295

Sorichetti, R. J., Creed, I. F., & Trick, C. G. (2014b). The influence of iron, siderophores and refractory DOM on cyanobacterial biomass in oligotrophic lakes. *Freshwater Biology*, *59*, 1423–1436. https://doi.org/10.1111/fwb.12355

Staehr, P. A., Baastrup-Spohr, L., Sand-Jensen, K., & Stedmon, C. (2012). Lake metabolism scales with lake morphometry and catchment conditions. *Aquatic Sciences*, *74*, 155–169. https://doi.org/10.1007/s00027-011-0207-6

Stomp, M., Huisman, J., Mittelbach, G. G., Litchman, E., & Klausmeier, C. A. (2011). Large-scale biodiversity patterns in freshwater phytoplankton. *Ecology*, *92*(11), 2096–2107. https://doi.org/10.2307/23034942

Striebel, M., Schabhüttl, S., Hodapp, D., Hingsamer, P., & Hillebrand, H. (2016). Phytoplankton responses to temperature increases are constrained by abiotic conditions and community composition. *Oecologia*, *182*, 815–827. https://doi.org/10.1007/s00442-016-3693-3

Strobl, C., Malley, J., & Tutz, G. (2009). An introduction to recursive partitioning: Rationale, application, and characteristics of classification and regression trees, bagging, and random forests. *Psychological Methods*, *14*, 323–348. https://doi.org/10.1037/a0016973

Tadonléké, R. D. (2010). Evidence of warming effects on phytoplankton productivity rates and their dependence on eutrophication status. *Limnology and Oceanography*, *55*, 973–982. https://doi.org/10.4319/lo.2010.55.3.0973

Tarboton, D. G., Bras, R. L., & Rodriguez-Iturbe, I. (1991). On the extraction of channel networks from digital elevation data. *Hydrological Processes*, *5*, 81–100. https://doi.org/10.1002/hyp.3360050107

Tolosi, L., & Lengauer, T. (2011). Classification with correlated features: Unreliability of feature ranking and solutions. *Bioinformatics*, *27*, 1986–1994. https://doi.org/10.1093/bioinformatics/btr300

Vadeboncoeur, Y., Zanger, M. J., & Lodge, D. M. (2002). Putting the lake back together: Reintegrating benthic pathways into lake food web models. *BioScience*, *52*, 44.

Verhoeven, J. T. A., Arheimer, B., Yin, C., & Hefting, M. M. (2006). Regional and global concerns over wetlands and water quality. *Trends in Ecology & Evolution*, *21*, 96–103. https://doi.org/10.1016/j.tree.2005.11.015

Western University Map and Data Centre (n.d.). Maps and atlases: Topographic maps collection. www.lib.uwo.ca/madgic

Weyhenmeyer, G. A., Müller, R. A., Norman, M., & Tranvik, L. J. (2016). Sensitivity of freshwaters to browning in response to future climate change. *Climatic Change*, *134*(1–2), 225–239. https://doi.org/10.1007/s10584-015-1514-z

Whitehead, P. G., Wilby, R. L., Battarbee, R. W., Kernan, M., & Wade, A. J. (2009). A review of the potential impacts of climate change on surface water quality. *Hydrological Sciences Journal*, *54*, 101–121. https://doi.org/10.1623/hysj.54.1.101

Williamson, C. E., Saros, J. E., & Schindler, D. W. (2009). Sentinels of change: Lakes and reservoirs provide key insights into the effects and mechanisms of climate change. *Science*, *323*, 887–888. https://doi.org/10.1126/science.1169443

Winder, M., & Sommer, U. (2012). Phytoplankton response to a changing climate. *Hydrobiologia*, *698*, 5–16. https://doi.org/10.1007/s10750-012-1149-2

Winter, J. G., DeSellas, A. M., Fletcher, R., Heintsch, L., Morley, A., Nakamoto, L., & Utsumi, K. (2011). Algal blooms in Ontario, Canada: Increases in reports since 1994. *Lake and Reservoir Management*, *27*, 107–114. https://doi.org/10.1080/07438141.2011.557765

Yeung, A. C. Y., Paltsev, A., Daigle, A., Duinker, P. N., & Creed, I. F. (2018). Atmospheric change as a driver of change in the Canadian boreal zone. *Environmental Reviews*, 1–31. https://doi.org/10.1139/er-2018-0055

Zhou, X., Huang, G., Baetz, B. W., Wang, X., & Cheng, G. (2018). PRECIS-projected increases in temperature and precipitation over Canada. *Quarterly Journal of the Royal Meteorological Society*, *144*(711), 588–603. https://doi.org/10.1002/qj.3231

Zhu, M., Zhu, G., Nurminen, L., Wu, T., Deng, J., Zhang, Y., Qin, B., & Ventelä, A.-M. (2015). The influence of macrophytes on sediment resuspension and the effect of associated nutrients in a shallow and Large Lake (Lake Taihu, China). *PLoS One*, *10*, 1–20. https://doi.org/10.1371/journal.pone.0127915

Zwart, J. A., Sebestyen, S. D., Solomon, C. T., & Jones, S. E. (2017). The Influence of hydrologic residence time on lake carbon cycling dynamics following extreme precipitation events. *Ecosystems*, *20*, 1000–1014. https://doi.org/10.1007/s10021-016-0088-6

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Paltsev, A., & Creed, I. F. (2022). Multi-decadal changes in phytoplankton biomass in northern temperate lakes as seen through the prism of landscape properties. *Global Change Biology*, 28, 2272–2285. https://doi.org/10.1111/gcb.16079