Received: 30 August 2020 | Accepted: 20 April 2021

DOI: 10.1111/gcb.15660

Global Change Biology WILEY

PRIMARY RESEARCH ARTICLE

Tree line advance reduces mixing and oxygen concentrations in arctic–alpine lakes through wind sheltering and organic carbon supply

Marcus Klaus[1,2] | Jan Karlsson[1] | David Seekell[1]

[1]Climate Impacts Research Centre, Department of Ecology and Environmental Science, Umeå University, Umeå, Sweden

[2]Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, Umeå, Sweden

Correspondence and present address
Marcus Klaus, Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, Umeå, Sweden.
Email: marcus.klaus@posteo.net

Funding information
Knut och Alice Wallenbergs Stiftelse, Grant/Award Number: 2016.0083; Svenska Forskningsrådet Formas, Grant/Award Number: 942.2015-723; Vetenskapsrådet, Grant/Award Number: 2016-05275

Abstract

Oxygen depletion in lake bottom waters has adverse impacts on ecosystem health including decreased water quality from release of nutrients and reduced substances from sediments, and the reduction of fish growth and reproduction. Depletion occurs when oxygen is consumed during decomposition of organic matter, and oxygen replenishment is limited by water column stratification. Arctic–alpine lakes are often well mixed and oxygenated, but rapid climate change in these regions is an important driver of shifts in catchment vegetation that could affect the mixing and oxygen dynamics of lakes. Here, we analyze high-resolution time series of dissolved oxygen concentration and temperature profiles in 40 Swedish arctic–alpine lakes across the tree line ecotone. The lakes stratified for 1–125 days, and during stratification, near-bottom dissolved oxygen concentrations changed by −0.20 to +0.15 mg L^{-1} day^{-1}, resulting in final concentrations of 1.1–15.5 mg L^{-1} at the end of the longest stratification period. Structural equation modeling revealed that lakes with taller shoreline vegetation relative to lake area had higher dissolved organic carbon concentrations and oxygen consumption rates, but also lower wind speeds and longer stratification periods, and ultimately, lower near-bottom dissolved oxygen concentrations. We use an index of shoreline canopy height and lake area to predict variations among our study lakes in near-bottom dissolved oxygen concentrations at the end of the longest stratification period (R^2 = 0.41). Upscaling this relationship to 8392 Swedish arctic–alpine lakes revealed that near-bottom dissolved oxygen concentrations drop below 3, 5, and 7 mg L^{-1} in 15%, 32%, and 53% of the lakes and that this proportion is sensitive (5%–22%, 13%–45%, and 29%–69%) to hypothetical tree line shifts observed in the past century or reconstructed for the Holocene (±200 m elevation; ±0.5° latitude). Assuming space-for-time substitution, we predict that tree line advance will decrease near-bottom dissolved oxygen concentrations in many arctic–alpine lakes.

KEYWORDS
dissolved organic carbon, environmental change, forest–tundra ecotone, hypoxia, lake ecosystem, lake stratification, thermal structure, wind speed

See also Commentary on this article by Jane and Rose 27, 4207–4209.

1 | INTRODUCTION

Oxygen is a key driver of the ecological and biogeochemical functioning of lakes (Wetzel, 2001). Dissolved oxygen concentrations (DO) are of vital importance for aerobic biota (Evans, 2007; Vaquer-Sunyer & Duarte, 2008) and regulate the cycling of carbon, nutrients, heavy metals, and greenhouse gases (Davison et al., 1980; Hamilton et al., 1995; Liikanen et al., 2002; Mortimer, 1942) and are therefore a widely used indicator of water quality (Sánchez et al., 2007). In recent decades, DO has declined in many lakes globally as a result of eutrophication and pollution due to human activities (Jenny et al., 2016). Studies on DO depletion have traditionally focused on productive lakes that are under strong human pressures (Charlton, 1980; Edmondson et al., 1956; Foley et al., 2012; Walker, 1979). However, DO frequently depletes also naturally in the hypolimnia of many pristine lakes, many of which are located in the northern forest landscape (Jenny et al., 2016; Nürnberg, 1995). Oxygen depletion has been found in many arctic–alpine lakes during winter (Leppi et al., 2016; Mathias & Barica, 1980) but also in shallow thermokarst and permafrost ponds during summer (Deshpande et al., 2015; Sepulveda-Jauregui et al., 2015). In contrast, tundra lakes, especially in non-permafrost areas, are generally considered well mixed and oxygenated during summer (Karlsson et al., 2004; Vonk et al., 2015). The ongoing climate warming and rising tree lines (Harsch et al., 2009) may turn many tundra lakes into forest lakes. While tree line shifts can cause rapid and strong changes in lake ecosystems (Macdonald et al., 1993) it is uncertain if and how these changes would affect lake DO. Understanding the patterns and drivers of DO in arctic–alpine lakes across tree lines is therefore of vital importance for predictions of their future functioning.

Dissolved oxygen concentrations in lakes are the net result of a complex interaction of biogeochemical and physical sources and sinks (Wetzel, 2001). DO is depleted when more DO is consumed than supplied. DO is supplied mainly through atmospheric invasion and water column mixing, which is usually mainly driven by wind action, but also via gross primary production, which is mainly controlled by light and nutrient conditions. DO is consumed during decomposition of internally produced biomass or organic matter imported from catchment soils (Couture et al., 2015; Nürnberg, 1995). Terrestrial inputs contribute to the pool of dissolved organic carbon (DOC) which often stains the lake color and reduces light penetration. This effect enhances thermal stratification and reduces deep-water ventilation (Caplanne & Laurion, 2008; Read & Rose, 2013; Saros et al., 2016), but also reduces benthic gross primary production (Craig et al., 2015) and promotes net heterotrophy (ecosystem respiration>gross primary production; Ask et al., 2012). Terrestrial organic matter also often provides nutrients which can enhance pelagic gross primary production (Daniels et al., 2015) and further enhance the biomass pool to be decomposed. All these processes can contribute to lower DO in near-bottom waters of stratified lakes with higher DOC, as empirically demonstrated in previous synoptic lake surveys (Lasenby, 1975; Nürnberg, 1995).

Dissolved oxygen dynamics can be expected to vary among lakes in alpine and arctic landscapes where heterogeneous topographic and catchment conditions imprint in a mosaic of biogeochemical and physical lake conditions (Jansson et al., 2008; Moser et al., 2019). A distinct feature of these landscapes is the tree line ecotone, dividing the landscape into forest and tundra. Forest and tundra lakes are fundamentally different in wind exposure and soil conditions. Relative to forest lakes, tundra lakes are characterized by higher wind speeds, lower surface temperatures and hence more intense mixing, and lower terrestrial DOC inputs (Duff et al., 1998; Finstad et al., 2016; Jansson et al., 2008; Rose et al., 2015). These characteristics have potential effects on physical DO renewal and biogeochemical DO demand. However, synoptic surveys along tree line ecotone are rare and have usually not combined DO measurements with other physical and biogeochemical characteristics of lakes and their catchments.

Arctic–alpine lakes are particularly vulnerable to environmental changes because they are typically discontinuous cold polymictic and can easily flip between mixing and stratification regimes (MacIntyre et al., 2009; Michelutti et al., 2016; Saros et al., 2016). They are also often relatively clear, which makes biological DO demand respond particularly strongly to changes in DOC inputs and light conditions (Luoto et al., 2019). There are diverse environmental impacts on mixing and DO dynamics in lakes and these are relatively well studied in temperate or boreal lakes (Foley et al., 2012; Mammarella et al., 2018; Martinsen et al., 2019; Pilla et al., 2018). Yet, relatively little is known about effects in arctic–alpine lakes. An important environmental agent of change in these types of lakes is the shift of the tree line (Moser et al., 2019). Tree line shifts alter local wind speeds and hence lake stratification patterns (Saros et al., 2012; Siver et al., 2018), but also change the terrestrial input of DOC (Fallu et al., 2005; Pienitz et al., 1999). Through these effects, shifting tree lines could potentially alter hypolimnetic DO. The importance of such effects and whether they are primarily driven by changes in wind speed or DOC inputs remains unclear. Yet, this information is essential for accurate mechanistic predictions of tree line effects on mixing and oxygen dynamics in lakes.

Tree line effects can be expected to vary across lakes, because external forces and drivers are moderated by lake-specific characteristics such as morphometry and water color (Ficker et al., 2017; Read & Rose, 2013; Woolway & Merchant, 2019). In particular, lake morphometry can be expected to moderate effects on DO depletion and replenishment through its control on thermal structure and sediment–water interactions (Charlton, 1980; Nürnberg, 1995). This potential diversity in effects is rarely accounted for in studies on environmental impacts on lake mixing and DO dynamics (but see Read et al., 2014), partly because of a lack of high frequency measurements needed to reveal subtle variations in durations and extents of stratification and DO depletion (MacIntyre et al., 2009; Mammarella et al., 2018). This research gap calls for rigorous investigations of mixing and DO dynamics in lakes with diverse morphometries across the tree line ecotone. The Scandinavian arctic–alpine region is of primary interest in this context, because the tree line has locally shifted by up to several hundred meters in the past and similar future shifts are predicted (Bryn & Potthoff, 2018; Kullman, 1995; Moen et al., 2004; Wolf et al., 2008).

Here we study patterns and drivers of mixing and DO among 40 Swedish arctic–alpine lakes located across the tree-line ecotone. We address the question how lake and catchment characteristics correlate with patterns of thermal stratification and DO dynamics near lake bottoms. In particular, we investigate the relative importance of physical and biogeochemical effects of shoreline vegetation on DO dynamics and upscale the net effects across the Swedish arctic–alpine landscape. We use these results to predict future changes for various tree line shift scenarios under the assumption that spatial patterns among lakes are representative of temporal changes within lakes.

2 | MATERIALS AND METHODS

2.1 | Study sites

We studied 40 lakes located in the Scandinavian Mountain range in northwestern Sweden. The lakes are clustered in three regions: Jämtland in the south (63°–64°N) sampled in 2016 and 2017, Ammarnäs in the center (66°N) sampled in 2016, and Abisko in the north (68°N) sampled in 2018 (Figure 1; Table S1). Mean annual air temperatures during 1960–1990 ranged from 0°C in the south to −2°C in the north, and annual precipitation ranged from 300 to 1200 mm depending on orographic exposure. During the sampling periods, air temperatures appeared to be similar across all three study regions and within 0.5°C from the long-term means in Jämtland and Ammarnäs in 2016 and 2017, and 2°C higher in Abisko in 2018. During the study period, autumn precipitation was 50%–100% of long-term averages and summer precipitation was 100%–150% of long-term averages (SMHI, 2020). The sampled lakes are located at elevations between 367 and 998 m above sea level (a.s.l.). The tree line varies from 600–800 m a.s.l. in the south to 400–600 m a.s.l. in the north (Kullman, 1990). The studied catchment areas vary from 8 to 1230 ha. Above the tree line, the catchments are dominated by dry heath and local occurrence of meadows. Below the tree line, the catchments are dominated by birch (*Beluta* spp.) forests and local Norway spruce (*Picea abies*) stands. Accordingly, lakes are hereafter referred to as *tundra* and *forest* lakes. Soils are dominated by washed glacial till on metasedimentary or metavolcanic rocks, with sporadic or discontinuous permafrost above 700–1000 m a.s.l. (Gisnås et al.,

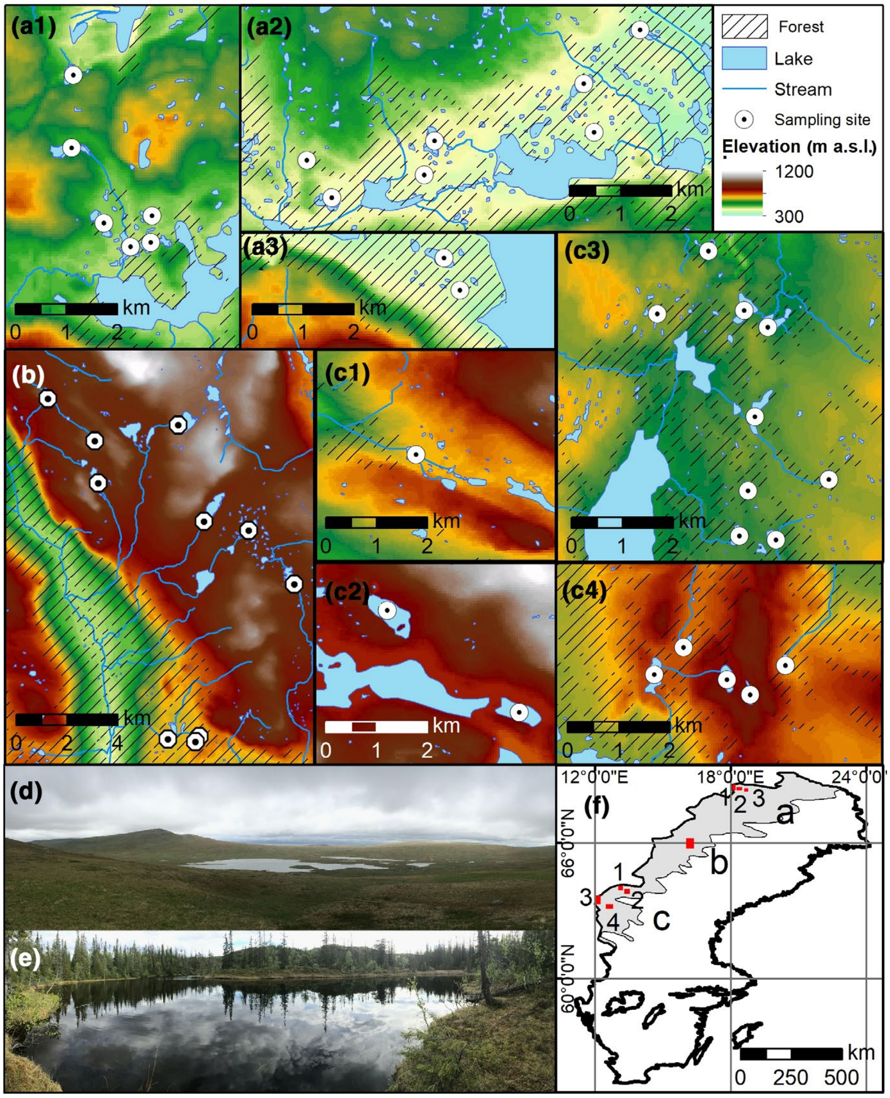

FIGURE 1 Map of terrain, forests, and lakes located in the study areas Abisko (a), Ammarnäs (b) and Jämtland (c). Also shown are photographs taken by Sven Norman of a typical tundra lake (d) and forest lake (e). Location of study areas within the Alpine Bio-geographical region in Sweden (European Environmental Agency, 2016; gray shading; f). Data sources: GSD-vegetation data, © Lantmäteriet (2012); ViVaN lake database (Nisell et al., 2007); watercourses, © SMHI (2012); GSD-elevation data, grid 50+ nh, © Lantmäteriet (2010)

2017). Mires are a minor land cover type in nearly all catchments. The lakes have intermediate surface area (1.7–39.8 ha) and maximum depth (1.9–31.2 m), are relatively clear (light extinction coefficient k_d = 0.2–1.5 m^{-1}) and generally ice-covered from October to June. The lakes in the study region are generally oligotrophic and net heterotrophic (Ask et al., 2012). The study lakes contain Brown Trout (*Salmo trutta*), Arctic Char (*Salvelinus alpinus*), or both. Some lakes also contain Eurasian Minnow (*Phoxinus phoxinus*) and Nine-spined stickleback (*Pungitius pungitius*).

2.2 | Logger deployment

We deployed logger arrays hanging from buoys anchored at the deepest point of each lake between June and September. DO was measured using optical oxygen loggers (MiniDOT; PME) at 10 min intervals at two depths: 0.5 m from the lake surface (hereafter referred to as *near surface*) and 0.7–7 m (mean 2.3 m) from the bottom (hereafter referred to as *near bottom*). The distance of the near-bottom logger was chosen to be larger in deeper lakes that were likely to have deeper hypolimnia. To avoid potential bias caused by possible near-bottom DO gradients, we aimed to place the near-bottom logger in the middle of the hypolimnion (based on mean hypolimnion depth during the open-water season). Water temperature was measured at 10 min intervals using thermistors (HOBO TidbiT V2; Onset Computer Corporation) located at 0.5 m intervals in the upper 3 m and at 1–5 m intervals down to the lake bottom. For more details on oxygen and temperature logger deployment and accuracy assessments, see Text S1. At nine lakes, we deployed weather stations (HOBO U30-NRC) and measured wind speed, wind direction, relative humidity, air temperature, and air pressure every 10 s and logged every 10 min. At 18 of the remaining lakes, we deployed cup anemometers (HOBO S-WSA-M003). All anemometers were installed on islands or the main land within 1–50 m (average 10 m) from the shoreline at 1.9–2.5 m above ground. We did not a priori know the prevalent wind direction for every lake. We therefore placed the anemometers at accessible locations assumed to be representative of the lake centroid and evaluated this assumption a posteriori.

2.3 | Physicochemical analysis

We sampled the lakes at their deepest point approximately every 5 weeks during the ice-free period. During each field visit, we measured depth profiles of photosynthetically active radiation (PAR), water temperature, and DO every 0.5 m (0–3 m) or 1 m (3–10 m) using handheld probes (LI-193 Spherical Quantum Sensor; LI-COR Bioscience; ProDO; YSI). If lakes were stratified, we sampled water at mid-epilimnion and mid-hypolimnion. Lake water was filtered (acid-washed GF/F 0.7 µm; Whatman), acidified with 500 µl of 1.2 M HCl per 50 ml of sample and analyzed for DOC and total dissolved nitrogen (TDN) using a total organic analyzer (IL 500 TOC-TN analyzer; Hach) at the Department of Ecology and Environmental Science (EMG), Umeå University. We calculated the light extinction coefficient (k_d) as the slope of the linear regression between natural logarithm of PAR and depth. DOC was highly correlated with TDN (Pearson correlation, r = 0.91) and k_d (r = 0.96) and hence only DOC is presented in this paper.

2.4 | Lake physics and morphometry

We used thermistor data to calculate the lower boundary of the metalimnion using the function “meta.depths” provided by the “rLakeAnalyzer” package for R (Read et al., 2011). This depth was defined as the lowermost depth with a vertical density gradient of 0.05 kg m^{-3} per meter. We evaluated the sensitivity of this depth to a range of density thresholds of 0.01–0.10 kg m^{-3} m^{-1} commonly used in the literature (Gray et al., 2020). The lakes were considered stratified whenever the density gradient threshold was passed. In four of the study lakes (ZF10, ZF11, ZF13, and ZF21), we missed the onset of the longest stratification period. We assumed the onset to have occurred 10 days before we started monitoring, when regional air temperatures rose consistently above freezing after a major storm event (Figure S1).

We derived lake depth–volume and depth–area relationships from bathymetric data collected using an echo sounder with internal GPS antenna (Lowrance HDS-5 Gen2), interpolated by ordinary kriging (rse = 0.3 m) using the geostatistical analysis package in ArcMap 10.1 (ESRI). Volumes and cross-sectional areas of each 0.5 m stratum were calculated using the 3D analyst surface volume tool in ArcMap.

2.5 | Oxygen and temperature analysis

We characterized mixing and oxygen dynamics by the length of the longest stratification period (Strat), the DO recorded by the near-bottom sensor at the end of this period (DO_f), and the rate of change in volumetric DO concentrations (ΔDO) during this period. The ΔDO was linear in our lakes, as in many other lakes (c.f. Couture et al., 2015; Lasenby, 1975) and can be assumed independent of ambient DO in terms of mechanisms (Cornett & Rigler, 1984). We therefore derived ΔDO from linear least-squares regressions following Lasenby (1975), using the “lm” function in the program R 3.6.1 (R Development Core Team, 2019). In some lakes, near-bottom DO reached near-surface levels within a few hours *before* the end of the stratification period due to partial water column mixing. We identified this period by testing for a break point in the regression at which the linear slope changes sign, using the “segment” function in R (Muggeo, 2008), and excluded the period from ΔDO calculations. Mean (±SD) residual standard errors of the regressions were 0.18 ± 0.12 mg L^{-1}, or 15 ± 30% of the total oxygen change during the longest stratification periods. As additional indicators of DO dynamics we also calculated the number of days when DO was below 3, 5, and 7 mg L^{-1}.

2.6 | Computation of wind sheltering

We characterized the effect of wind on lake mixing as a function of lake area and the height of shoreline trees or bluff topography using the sheltering index *W* (Hondzo & Stefan, 1993). *W* denotes the proportion of the lake surface area where wind shear contributes to turbulence and mixing and can theoretically range from 0 (full sheltering) to 1 (full wind access). We estimated *W* following Markfort et al. (2010):

$$W = \frac{D^2/2\cos^{-1}x_t/D - x_t/2\sqrt{D^2 - x_t^2},}{A}$$

where $D = 2\sqrt{\frac{A}{\pi}}$ is the equivalent circular lake diameter and $x_t = ht$ is the shear deficit length, assuming $t = 50$ times the height of the adjacent sheltering feature (h). We computed W_c where $h = h_c$ is the average tree canopy height derived from a 12.5 m resolution gridded tree height dataset (Skogsstyrelsen, 2020). We also computed W_t where $h = h_t$ is the standard deviation of elevation derived from a 2 m resolution digital elevation model (Swedish National Land Survey, 2016). We computed h_c and h_b for 50 m wide buffers around the lake shoreline after evaluating a range of buffer widths (Text S2). The index *W* is valid for relatively round lakes and hence suitable for our study lakes with shoreline development indices ($\text{perimeter}/2\sqrt{\pi A}$) of 1.75 ± 0.40.

We scaled wind speed from anemometer height (z) to standard heights of 10 m above ground using law of the wall scaling, $U_{10} = U_z\left(1 + \frac{C_D^{0.5}}{K}\log\left(\frac{10}{z}\right)\right)$, where $K = 0.4$ is the von Kármán constant, and C_D is the drag coefficient. We computed C_D for nine lakes with full meteorological observations as a function of air and surface water temperature, wind speed, humidity, and anemometer height (Smith, 1988) using an iterative procedure (Hicks, 1975) following MacIntyre et al. (2020). The mean C_D decreased linearly with increasing W_c, indicating lower wind drag in less sheltered lakes as a result of more frequent stable atmospheric conditions (Figure S3). We used this relationship ($C_D = 2.4171 \cdot 10^{-3} – 4.304 \cdot 10^{-4}\ W_c$, $R^2 = 0.50$) to scale C_D across all lakes. W_c was the only significant among a range of tested variables, including Ele, Lat, W_t, DOC, and maximum depth (z_{max}).

2.7 | Statistical analyses

We modeled DO_f as linear least-squares regression functions of *W* using the "lm" function in the statistical program R 3.6.1 (R Development Core Team, 2019). We evaluated three models with predictor variables W_c, W_t, and their linear combination and compared their fits by means of likelihood ratio tests using the "lrtest" function of the R package "lmtest" (Zeileis & Hothorn, 2002). The model with W_c alone yielded the highest goodness of fit (Table S2) and adding W_t to the model did not further improve the fit, indicating that DO_f was predicted by sheltering through trees rather than topography. We therefore limit our further analyses to W_c and call the best model "DO_f model."

We further evaluated potential direct and indirect effects of W_c on DO_f using structural equation modeling (SEM). We chose SEM because of its flexibility in accounting for the expected interactions of the many factors controlling DO_f (Charlton, 1980). We defined plausible causal pathways based on prior theoretical and empirical studies and evaluated the strength and direction of these pathways using our data. This approach is increasingly used in limnology to evaluate hypotheses in complex effect chains (Klaus et al., 2019; Lapierre et al., 2013). We predicted that DO_f correlates with relatively static geographical factors describing the lakes location and morphometry, quasi-static biogeochemical factors characterizing the decomposition of organic matter, and dynamic physical factors including wind speed and stratification. Specifically, we predict:

1. DO_f is lower in lakes with longer stratification periods (Strat) and stronger declines in oxygen concentrations (ΔDO), based on first principles.
2. stratification periods are longer in lakes with lower U_{10} (Wetzel, 2001), in warmer lakes located at lower elevation (Ele) and latitude (Lat) (Read et al., 2014), and in lakes with larger z_{max} (Ficker et al., 2017; Nürnberg, 1995)
3. ΔDO is more negative with higher DOC as a result of higher net heterotrophy (Couture et al., 2015)
4. U_{10} increases with lower tree canopies relative to lake surface area, and hence increases with W_c (Markfort et al., 2010)
5. DOC decreases with W_c because lower tree canopies indicate lower catchment biomass and hence DOC leaching from soils (Jansson et al., 2008), and because a larger proportion of water in larger lakes has passed and been degraded in upstream lakes (Rasmussen et al., 1989)
6. W_c increases with Ele and Lat because tree canopies can be expected to be higher in warmer areas (Simard et al., 2011).

We fitted the SEM using a piecewise approach where linear equations are solved separately and then combined to build a single model, using the "piecewiseSEM" package in R (Lefcheck, 2016). The linear equations were never biased by multicollinearity, as indicated by variance inflation factors always being <2. We evaluated whether the SEM misses important links by Shipley's test of directed separation using Fisher's *C* statistic (Shipley, 2013). A $p > 0.05$ indicates an acceptable model. We fitted two SEM versions to account for missing U_{10} data: one that includes all variables but only the 27 lakes with wind measurements, and one that excludes U_{10} but includes all lakes. We report raw and *z*-normalized path coefficients. We also report the total effect (including all indirect and direct effects) of each explanatory variable on DO_f using the "semEff" package in R (Murphy, 2020). We estimated 95% confidence intervals for total effects using 10 000 bootstrap runs. We removed an outlier lake (BD08) because it sticks out with very high ΔDO relative to its DOC (Figure S7), the smallest z_{max} and the highest TDN but one of the lowest k_d in the dataset (Table S1). We also explored a number of additional alternative model structures but rejected those due to poorer model fit (Text S3).

2.8 | Upscaling and simulations

We used the DO_f model fitted to our 40 study lakes to estimate the general distribution of DO_f in Swedish arctic–alpine lakes listed in the ViVaN lake database (Nisell et al., 2007). To avoid extrapolations, we only selected those 11988 lakes that were similar to our field study lakes in terms of the DO_f model input variables (A = 1.7–39.8 ha, h_c = 0–11 m) and that were located within the Alpine Bio-geographical Region as defined by the European Environmental Agency (2016). We also simulated how hypothetical tree line shifts would translate into DO_f through changing h_c as follows:

First, we modeled mean h_c within the 50 m lake buffers as a function of Ele, Lat, and longitude (Lon). We modeled these relationships using quantile regression forests (QRF) by means of the "quantregForest" package in the statistical program R (Meinshausen, 2017). QRF is a machine learning tool where multiple decision trees are grown as in ordinary random forests, but instead of estimating the conditional mean, QRF estimates the conditional distribution of the response variable. We allowed growing 500 trees with a minimum of five nodes and where one variable was randomly sampled without replacement at each node. This setting generated consistent results with different random seeds selected. We fitted QRF to a training dataset (30% of all lakes) and evaluated prediction accuracy for a validation dataset (70%). QRF can better deal with multicollinearity than SEM, which is why we here also included Lon (correlated with Lat, r = 0.88) to explain potential residual variability by the distance from the warming Atlantic ocean. We quantified the effects of Ele, Lat, and Lon using the variable importance measure, which is calculated by permuting each predictor variable and recording the mean squared prediction error. The larger this measure the more would the predictive accuracy decrease if the predictor variable was excluded from the model.

Second, we used QRF (hereafter referred to as the "h_c model") to simulate canopy heights for hypothetical tree line shifts. We explored scenarios of tree line shifts along elevations of ±50, ±100, and ±200 m and along latitudes of ±0.10°, ±0.25°, and ±0.50°. These scenarios cover the range of tree line shifts that occurred in the Scandinavian mountain range at different time scales of decades to centuries during the Holocene (Table S3).

Third, we used the DO_f model and the modeled h_c to estimate the distribution of DO_f in Swedish arctic–alpine lakes for the different tree line shifts scenarios. We accounted for uncertainties in QRF and DO_f model predictions using a bootstrap approach. For each lake, we randomly sampled 1000 times from the conditional distribution of h_c predicted by the h_c model, and from the normal distribution of DO_f predicted by the DO_f model with means and standard deviations given by the "predict.lm" function in R. For each of the resulting 1000 bootstrap simulations per lake, we calculated DO_f and report the mean and 95% confidence interval among all bootstrap simulations of the proportion of lakes with DO_f <3, 5 and 7 mg L^{-1}.

3 | RESULTS

3.1 | Temporal variability in stratification and DO within lakes

Seasonal patterns in U_{10}, and near-surface and near-bottom water temperature and DO varied strongly among lakes across the forest–tundra ecotone. This is exemplified in Figure 2 for typical forest, tree line, and tundra lakes. Relative to the forest lake, the tundra lake is characterized by higher U_{10}, smaller vertical temperature gradients, shorter stratification periods, and a shift from negative to positive DO trajectories in the near-bottom waters. Whenever the lakes stratified, the near-bottom DO diverged from near-surface DO, with relative drops of up to 6.5 mg L^{-1} below the tree line and increases of up to 1.2 mg L^{-1} above. Lakes differed in how stratification responded to storm events and surface cooling. While the forest lake remained stratified for a prolonged period, despite occasional storm events, the tree line lake shifted more frequently between stratification and mixing and the tundra lake was nearly continuously mixed.

3.2 | Patterns and correlates of DO_f among lakes

The DO observations represented hypolimnia that comprised around 17% (range 1%–64%) of whole-lake volumes, assuming DO being homogenous across the hypolimnia (Figure S4). The *DO* dropped below 7, 5, and 3 mg L^{-1} for 37, 14, and 0 days as a median among the study lakes (range: 4–92, 0–38, and 0–16 days; Figure S5). DO_f ranged from 1.1 to 15.5 mg L^{-1} (Table S1). The near-bottom DO loggers were located well within the hypolimnion in most lakes (Figure S6a). DO_f was not correlated with the distance of the logger relative to the lake bottom and the extent of the hypolimnion, hence there was no systematic pattern in deployment that might bias these results (Figure S6b).

The variability in DO_f was well explained by the SEMs (Fisher's C p > 0.05) shown in Figure 3. All direct effects are shown as biplots in Figure S7 and underlying statistical details are given in Table S4. We here describe in detail the SEM fitted to data from all lakes and after that highlight important differences to the SEM fitted to a subset of lakes with wind measurements. Our originally hypothesized models had a Fisher's C with p = 0.002, and the test of directed separation indicated a missing link between DOC and z_{max} (p = 0.0002). This link likely reflects slower water turnover and/or increased oxidation of DOC in deep lakes (Charlton, 1980; Rasmussen et al., 1989). We therefore included this link in our final SEM. The final SEMs suggested that DO_f decreased significantly with longer Strat and more negative ΔDO. Together, these factors explained 67% of variance in DO_f among lakes, as indicated by the coefficient of determination (R^2) in Figure 3. Strat varied from 1 to 125 days, increased significantly with z_{max} and decreased significantly with W_c (R^2 = 0.72). ΔDO varied from +0.15 to −0.20 mg L^{-1} day^{-1} and became increasingly negative with higher *DOC* (R^2 = 0.30). DOC varied from 0.5 to 7.4 mg L^{-1} and decreased significantly with W_c and z_{max} (R^2 = 0.73). W_c increased significantly with Lat and Ele (R^2 = 0.56). The SEM fitted to

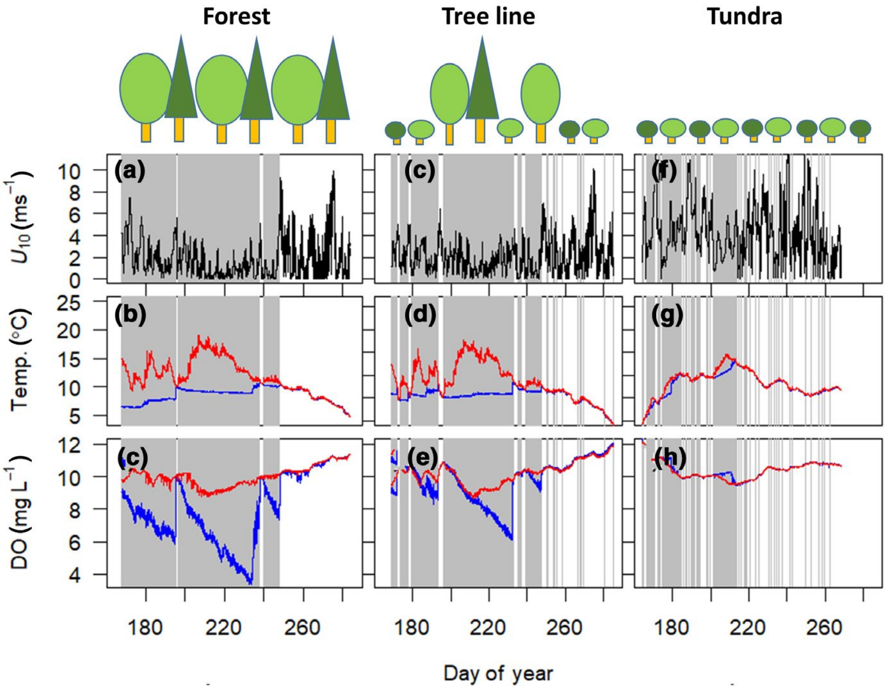

FIGURE 2 Contrasting mixing and dissolved oxygen (DO) dynamics in lakes across the forest–tundra ecotone. Time series of wind speed at 10 m height (U_{10}), and near-surface and near-bottom water temperature (Temp.) and DO concentrations in a forest lake, *Hägglidstjärnarna* (a–c), tree line lake, *Dörrstjärnen* (d–f), and tundra lake, *Krutejaure* (g–i). Gray bars show periods of stratification

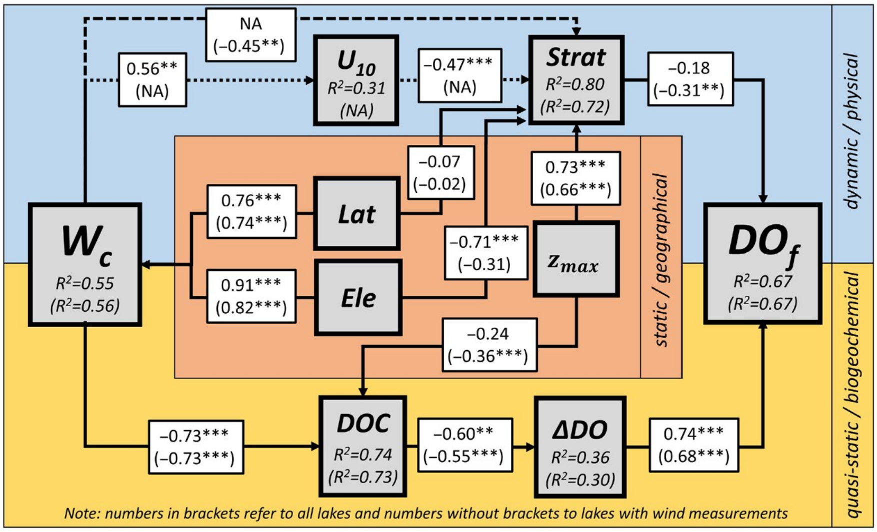

FIGURE 3 Piecewise structural equation model to explain near-bottom dissolved oxygen concentrations at the end of the longest stratification period (DO_f) as functions of static geographical, quasi-static biogeochemical, and dynamic physical characteristics. DO_f is a direct function of the change rate in dissolved oxygen concentrations (ΔDO), and the length of the longest stratification period (Strat), and an indirect function of maximum lake depth (z_{max}), dissolved organic carbon (DOC) concentrations, wind speed at 10 m height (U_{10}), latitude (Lat), elevation (Ele), and the sheltering index (W_c). Numbers in boxes show *z*-normalized path coefficients. The coefficient of determination (R^2) expresses the proportion of variance explained by the paths. Path coefficients and R^2 are given for the full set of lakes that includes the path $W_c \rightarrow$Strat (dashed line, numbers in brackets) and for a subset of lakes with wind measurements that includes the path $W_c \rightarrow U_{10} \rightarrow$Strat (dotted lines, numbers without brackets). Fisher's *C* is 54.2 (p = 0.10) and 39.2 (p = 0.08), respectively. Significance levels: "*" = 0.05, "**" = 0.01, "***" = 0.001. Biplots of all relationships are shown in Figure S7

data from lakes with wind measurements generally revealed similar relationships, but here U_{10} described more explicitly the effect of wind sheltering on stratification. Specifically, U_{10} varied from 1.1 to 5.7 m s^{-1}, increased significantly with W_c (R^2 = 0.31) and had a significant negative effect on Strat. The SEMs were robust against assumptions behind stratification calculations. Path coefficients that include Strat were similar for different hypothetical onsets of stratification in four lakes that were already stratified when we started monitoring (Table S5). Strat, ΔDO, and DO_f were nearly identical for different water density gradient thresholds (0.01–0.10 kg m^{-3} m^{-1}) that define stratified periods, with mean differences (mean relative differences) between the two extreme scenarios of 0.4 days (1.6%), 0.0001 mg L^{-1} day^{-1} (2.5%), and −0.0013 mg L^{-1} (0.01%), respectively.

Considering the total effects that integrate all direct and indirect effects, DO_f was primarily determined by ΔDO (Table 1). In the full dataset, DO_f decreased significantly by 0.66 and 0.30 standard deviations for a decrease in ΔDO and an increase in Strat by one standard deviation, respectively. For the subset of lakes with wind measurements, DO_f was more strongly determined through the DOC pathway compared to the U_{10} pathway. Specifically, DO_f decreased significantly by 0.42 SDs for an increase in DOC by one standard deviation, while the total U_{10} effect was only 0.07 and not significant. The z_{max} did not explain any significant variability in DO_f.

3.3 | Tree sheltering effect on DO_f

W_c explained 41% of the variability in DO_f (Figure 4a). DO_f ranged from 1.1 to 15.5 mg L^{-1} and decreased from an average of 8 mg L^{-1} in fully exposed lakes (W_c = 1.00) to 4 mg L^{-1} in fully sheltered lakes (W_c = 0.00). DO_f values resulted from total DO changes during the longest stratification period from −9 to +4 mg L^{-1} (Figure 4b). These extremes in total DO changes were reached in lakes with intermediate Strat but strongly positive or negative ΔDO. Interestingly, there was no lake with long enough stratification and strong enough DO depletion to allow anoxia.

At the sampled lakes, h_c ranged from 0 to 11 m and A from 1.7 to 39.8 ha, which represents 16.1% of all Swedish arctic–alpine lakes (Figure 4c). The sampled lakes fall into a range where W_c responds strongly to changes in h_c for a given A and are therefore particularly suitable to investigate W_c effects on lake conditions.

3.4 | Simulated effect of tree line shifts on DO_f

We upscaled W_c and DO_f to lakes in the whole Swedish arctic–alpine region that are similar to the field study lakes (A = 1.7–39.8 ha, h_c = 0–11 m; Figures 1 and 4c). An important intermediate step in upscaling was to yield canopy height using the h_c model. Canopy height was primarily determined by Ele (variable importance 1023), followed by Lat (906) and Lon (464). This ranking should, however, be regarded with caution because of the high correlation of Lat and Lon (r = 0.88). All predictors included in the h_c model explained together 89% and 69% of the variation in h_c in the training and testing dataset (Figure S8). The good performance suggests that the h_c model is suitable to predict h_c (see predictions in Figure S9) and hence W_c under scenarios of elevational and latitudinal tree line shifts.

For steady state conditions, W_c had a bimodal distribution with peaks around 0 and 1, indicating that most lakes were either fully sheltered or not sheltered at all (Figure 5a). DO_f ranged from 0 to 15 mg L^{-1} and had a wide peak around 6 mg L^{-1} (Figure 5c). The distribution suggests that 14.5, 32.0, and 52.7% of all lakes had modeled DO_f of <3, 5, and 7 mg L^{-1} (Table 2). Tree line advance would enhance the number of lakes with W_c near 0 at the expense of lakes with W_c near 1 (Figure 5a). Consequently, the peak of the DO_f distribution would shift down toward around 5, 4.5, or 4 mg L^{-1} for tree line advances of 50, 100, or 200 m, respectively (Figure 5c). Conversely, tree line retreats of these amounts would shift the peaks to around 7, 8, and 9 mg L^{-1}. The proportion of lakes with DO_f of less than 3, 5, and 7 mg L^{-1} would increase to 21.6%, 45.3%, and 68.5% for a 200 m tree line rise and decrease to 5.1%, 13.4%, and 29.0% for a 200 m tree line descent (Table 2). Latitudinal tree line shifts had only minor effects on the DO_f distribution (Figure 5b,d).

4 | DISCUSSION

4.1 | High between-lake variability in mixing and oxygen dynamics

This study provides evidence for high variability in mixing and DO dynamics among intermediately sized Swedish arctic–alpine lakes. Our study lakes covered the whole range from continuous cold

TABLE 1 Total standardized effects (mean and 95% confidence intervals [CI]) of lake and catchment characteristics on near-bottom oxygen concentrations at the end of the longest stratification period (DO_f). Total effects integrate all direct and indirect effects included in the structural equation model (Figure 3). Effects are given for a subset of lakes with wind measurements, and for the full set of lakes but excluding wind speed

	Total effects					
	Lakes with U_{10} measurement			All lakes		
Predictor	Mean	Lower CI	Upper CI	Mean	Lower CI	Upper CI
ΔDO*	0.69	0.41	0.90	0.66	0.48	0.82
Strat*	−0.17	−0.46	−0.12	−0.30	−0.52	−0.09
DOC*	−0.42	−0.63	−0.20	−0.37	−0.56	−0.20
U_{10}	0.07	−0.02	0.28	NA	NA	NA
W_c*	0.28	0.15	0.42	0.36	0.24	0.49
Ele*	0.28	0.16	0.44	0.30	0.19	0.42
Lat*	0.17	0.06	0.32	0.24	0.12	0.33
z_{max}	−0.02	−0.28	0.18	−0.07	−0.24	0.14

Abbreviations: ΔDO, change rate in near-bottom dissolved oxygen concentrations; DOC, dissolved organic carbon concentrations; Ele, elevation; Lat, latitude; Strat, length of the longest stratification period; U_{10}, wind speed at 10 m height; W_c, sheltering index; z_{max}, maximum lake depth.

*Significant effects ($p < 0.05$).

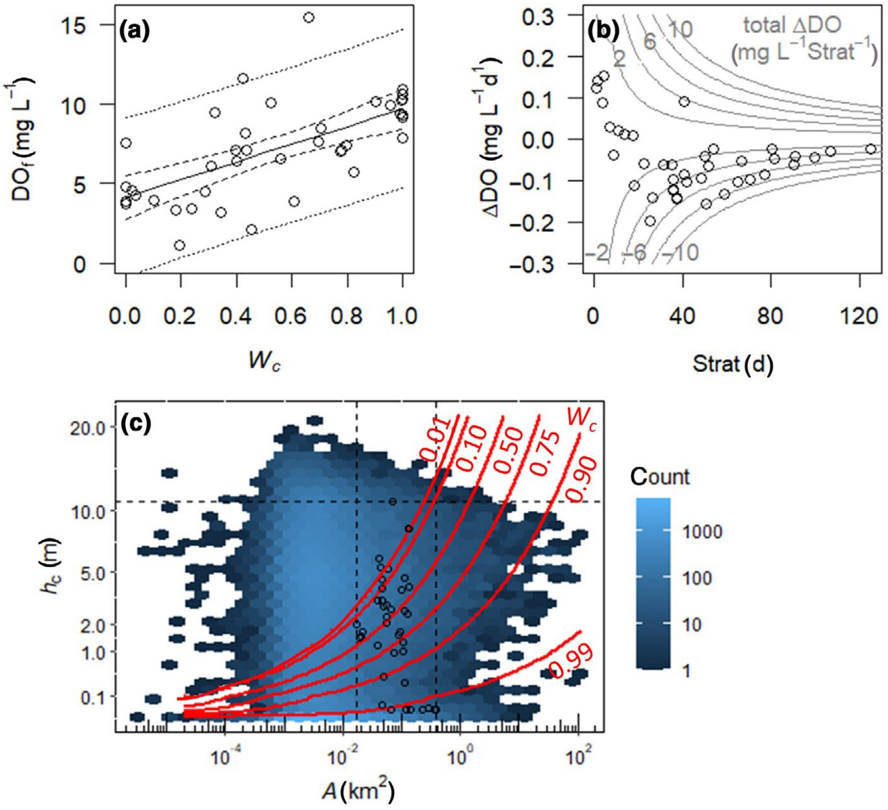

FIGURE 4 Patterns of near-bottom dissolved oxygen dynamics, tree sheltering and stratification among the sampled lakes: dissolved oxygen concentrations at the end of the longest stratification period (DO$_f$) as a function of the sheltering index (W_c; a). The solid line shows the linear regression DO$_f$ = 4.14 (±0.69) + 5.56 (±1.08) W_c, $R^2 = 0.41$, $p < 0.001$. Excluding the observation with DO$_f$ = 15.5 mg L^{-1} would not strongly impact the relationship and yield DO$_f$ = 4.05 (±0.59) + 5.36 (±0.93) W_c, $R^2 = 0.47$, $p < 0.001$. The dashed and dotted lines in a) show 95% confidence and prediction intervals. The total change in dissolved oxygen concentrations is visualized by isolines in (b), as determined by the length of the longest stratification period (Strat) and the rate change of dissolved oxygen concentrations (ΔDO). The dependence of W_c (red solid lines) on tree canopy height (h_c) and lake area (A) is shown in (c). Circles denote the sampled lakes, blue shading denotes the density of Swedish arctic–alpine lakes, dashed lines denote the range of the sampled lakes

polymictic to dimictic types typical for arctic–alpine lakes (Caplanne & Laurion, 2008; MacIntyre et al., 2009; Michelutti et al., 2016; Saros et al., 2016). ΔDO was negative in most of our lakes, which indicates net heterotrophy as shown previously for lakes in the study area (Ask et al., 2012). ΔDO was positive in a few relatively clear and shallow lakes, which indicates net autotrophy common for these types of systems (Mcgowan et al., 2018; Sadro et al., 2011). ΔDO covered nearly the whole range reported for various lakes worldwide (Charlton, 1980; Couture et al., 2015; Müller et al., 2012; Nürnberg, 1995), but was less negative than in thermokarst ponds (Deshpande et al., 2015). Combined, ΔDO and Strat translated into a wide range of DO$_f$ which is a typical feature of arctic–alpine lakes (Eggermont et al., 2007; Leppi et al., 2016).

4.2 | The dual shoreline vegetation effect

Figure 6 summarizes conceptually the characteristics that explain variations between lakes in mixing and oxygen dynamics. The figure shows conditions for relatively small and large, and relatively shallow and deep lakes located in the tundra and forest landscape. Relative to tundra lakes, forest lakes are less wind exposed (see also Figure S3b), have higher DOC, and are generally less well mixed and contain less oxygen. We interpret these differences as being a result of taller shoreline vegetation (c.f. Couture et al., 2015; Finstad et al., 2016; Foley et al., 2012; Mcgowan et al., 2018; Pienitz et al., 1997; Reuss et al., 2010). Another important discriminant is lake size. Larger lakes are more wind exposed and therefore more well mixed and hence oxygenated for the same shoreline canopy height (Markfort et al., 2010). Larger lakes also contain less DOC that can be oxidized because a larger proportion of incoming water has passed and been degraded in upstream lakes (Rasmussen et al., 1989). Deeper lakes contain less DOC mainly because of slower water turnover (Rasmussen et al., 1989). However, less DOC does not result in higher DO$_f$ because more of the incoming DOC is oxidized in the hypolimnia being thicker in lakes with larger maximum depth ($r = 0.94$ in our dataset) and less oxygen is replenished because of less intense mixing (Charlton, 1980). Therefore, maximum lake depth had no total effect on lake DO$_f$. All the processes shown in Figure 6 rely on first principles in limnology and should therefore be relevant across

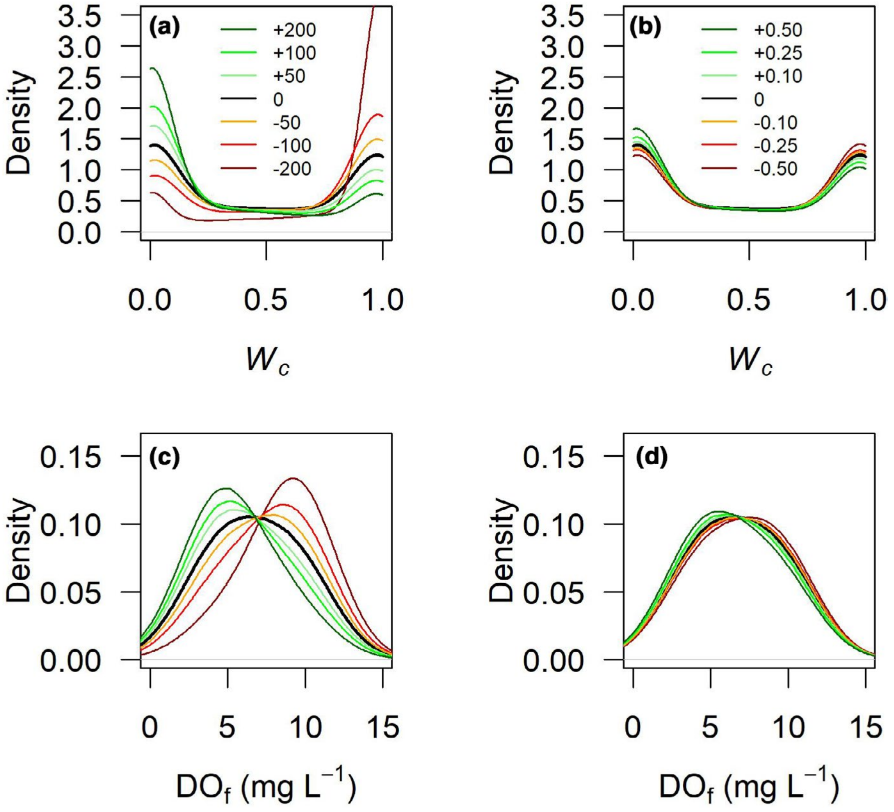

FIGURE 5 Frequency distributions of sheltering and oxygen conditions in Swedish arctic–alpine lakes. Kernel density distributions of the sheltering index (W_c; a, b) and dissolved oxygen concentrations at the end of the longest stratification period (DO_f; c, d) for the steady state (black line) and hypothetical scenarios of tree line shifts along elevations (m; a, c) and latitudes (°; b, d; colored lines). The distribution includes 8392 lakes randomly sampled from lakes that are similar to the field study lakes (A = 1.7–39.8 ha, h_c = 0–11 m). Each lake is bootstrapped 1000 times to account for uncertainty in the DO_f and h_c models

TABLE 2 Modeled proportion of Swedish arctic–alpine lakes with dissolved oxygen concentrations at the end of the longest stratification period of below 3, 5, and 7 mg L^{-1} for different scenarios of elevational and latitudinal tree line shifts. The proportions refer to 8392 lakes randomly sampled from all Swedish arctic–alpine lakes that are similar to the field study lakes (A = 1.7–39.8 ha, h_c = 0–11 m). 95% confidence intervals of means from 1000 bootstrap realizations were always within ±1.0%

	Proportion of lakes (%)		
Scenario	**<3 mg L^{-1}**	**<5 mg L^{-1}**	**<7 mg L^{-1}**
Status quo	14.5	32.0	52.7
Elevational shift (m)			
−200	5.1	13.4	29.0
−100	9.7	22.6	40.9
−50	12.2	27.7	47.5
+50	17.1	36.8	58.5
+100	19.0	40.4	62.7
+200	21.6	45.3	68.5
Latitudinal shift (°)			
−0.50	13.0	29.0	49.0
−0.25	13.8	30.7	51.1
−0.10	14.0	31.1	51.7
+0.10	15.0	33.1	54.0
+0.25	15.5	34.0	55.2
+0.50	16.7	36.2	57.7

the arctic–alpine region, but further studies from outside Sweden are needed to confirm this hypothesis.

Structural equation modeling provided statistical support for the dual effects of shoreline vegetation on lake mixing and oxygen dynamics through wind sheltering and terrestrial inputs of DOC. This is a way forward relative to previous paleolimnological studies which could not fully disentangle these effects due to the lack of reliable and independent proxies and because these studies were limited to only one or a few lakes (Reuss et al., 2010; Saros et al., 2012; Wolfe et al., 1999). Our SEM suggested that W_c effects on DO_f were more strongly mediated through the DOC pathway, relative to the U_{10} pathway. The relatively low importance of the U_{10} pathway may partly be explained by the possibility that our shore-based wind speed measurements may not have fully captured the effects of fetch and canopy height on wind speed at the lake centroid. However, our combined wind speed and wind direction measurements at nine of the study lakes support the assumption that the anemometer locations are representative of lake centroids in terms of the effective fetch (Text S4; Figures S10–S12). Even if we assumed an (unrealistic) 100% correlation between Strat and U_{10}, the U_{10} pathway would still have a slightly lower total effect (0.18) than the DOC pathway (−0.42). This result is in line with our observation that DO_f was not explained by wind sheltering through topographic features (described by W_t), but rather by wind sheltering through trees (described by W_c; Table S2) which stresses the importance of trees primarily as sources of organic matter to lakes, and secondarily as wind shelters.

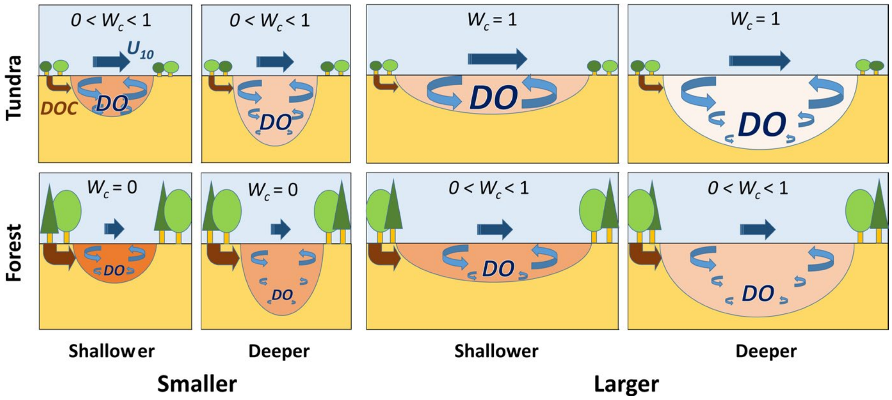

FIGURE 6 Conceptual figure of the dual effect of shoreline vegetation on dissolved oxygen (DO) concentrations near the bottom of arctic–alpine lakes. Shown are conditions for *relatively* small and large (surface area ~2 and ~40 ha), and shallow and deep (maximum depth ~2 and ~30 m) forest and tundra lakes. Shoreline vegetation shelters lakes from wind action and reduces mixing and DO replenishment and increases net DO consumption through enhanced terrestrial inputs of dissolved organic carbon (DOC). Lake size modifies these relationships. Symbol size scales with intensity/size of the process/characteristic. Lake DOC concentrations are visualized by a color gradient from dark to light brown (high to low DOC). W_c is the sheltering index, U_{10} is wind speed at 10 m height

Assuming that spatial and temporal variation are equivalent, this finding may have important implications for the trajectory that U_{10}, DOC, and DO_f would follow in a given lake in response to tree line shifts. The trajectory would depend on the time scales at which influential conditions respond to a stressor (Randsalu-Wendrup et al., 2016). During relatively slow gradual tree line shifts, the decrease in U_{10} and increase in DOC can be expected to occur roughly in synchrony with rising canopy height (Tanentzap et al., 2008). This synchrony, however, is broken by catastrophic or disturbance events such as frost damage, moth defoliation, wildfires, reindeer browsing, or land use change (Cansler et al., 2018; Cudlín et al., 2017; Van Bogaert et al., 2011). While such events would rapidly increase U_{10}, soils would continue to leak DOC for a longer period of time until the buildup of carbon stocks is depleted (Hagedorn et al., 2008). Relatively high DOC levels would then sustain relatively low DO_f levels. The slow response of DOC leakage is supported by observations from southern Swedish lakes where afforestation has likely caused a centennial long rise in lake DOC (Kritzberg, 2017). The existence of such legacy effects of tree line shifts needs to be verified by explicit experimental tests or long-term monitoring of arctic–alpine lakes around the tree line ecotone.

4.3 | Landscape level sensitivity of lake oxygen to tree line shifts

Upscaling results from the study lakes demonstrate a strong sensitivity of DO_f in Swedish arctic–alpine lakes to realistic tree line shift scenarios. Our upscaling predicts widespread oxygen depletion in Swedish arctic–alpine lakes for the scenario that tree line advance continues the 20th century trends found in many locations in Fennoscandia (Table S3). Such a trajectory is within projections for 21st century climate change scenarios (Moen et al., 2004; Pearson et al., 2013; Wolf et al., 2008). The resulting DO predictions should, however, be considered with caution, because temporal trajectories may differ from spatial patterns. Moreover, tree line advance may in reality not keep up with predicted warming rates (Hofgaard et al., 2013; Rees et al., 2020) and can vary locally or be masked by other important drivers of tree line dynamics such as land use legacy, grazing etc. (Cudlín et al., 2017; Kullman & Öberg, 2009; Van Bogaert et al., 2011).

Our upscaling was representative of a large proportion of arctic–alpine lakes in terms of DOC concentrations because 72% of global arctic–alpine lakes fall into the range of 0.5–7.4 mg DOC L^{-1} (Sobek et al., 2007). However, upscaling was limited to intermediately sized lakes. While lakes larger than our study lakes ($A > 39.8$ ha) are rare in the arctic–alpine region in Sweden (1.7%), smaller lakes ($A < 1.7$ ha) are common (81.8%). Similar patterns exist globally (<1% and 95%) according to equations by Downing et al. (2006) and assuming the minimum A is 0.1 ha. Such ponds can be expected to be well sheltered if they are located at or below the tree line (Figure 4c). Our upscaling (Figure 5) may therefore underestimate the proportion of lakes with low oxygen concentrations for tree line rise scenarios. To test this hypothesis and for a full understanding of landscape scale consequences of tree line shifts, we urge further studies on oxygen dynamics in ponds across the tree line ecotone.

4.4 | Can arctic–alpine lakes turn anoxic? The potential role of warming

Anoxia would result from a combination of sufficiently long stratification and sufficiently large DO depletion rates, for example, $\Delta DO < 0.2$ mg L^{-1} day^{-1} and Strat > 50 days. We did not observe such conditions (Figure 4b) and therefore predict that tree line uplift is unlikely to cause anoxia in lakes similar to the study lakes if all other conditions remained constant (Figure 5). However, alternative stressors, in addition to tree line uplift, may indeed drive arctic–alpine lakes toward anoxia. Importantly, tree line shifts are often driven by climatic changes (Harsch et al., 2009; Cudlín et al., 2017) and interact with these changes in their impact on lake DO. For example, climate warming and enhanced precipitation would further enhance DOC inputs to lakes (de Wit et al., 2016; Weyhenmeyer & Karlsson, 2009). Warming air may translate into warming of lake surface waters relative to bottom waters (Bartosiewicz et al., 2019; Reilly et al., 2015), which prolongs and intensifies thermal stratification (MacIntyre et al., 2009; Michelutti et al., 2016; Saros et al., 2016) and hence aggravates DO depletion (Bartosiewicz et al., 2019; Ficker et al., 2017; Wilhelm & Adrian, 2008). Warming could become the main driver of hypoxia once other factors have shifted the lakes toward reduced DO (Foley et al., 2012; Jenny et al., 2016; North et al., 2014). Clearly, the complex interactions of climate and catchment effects on lake DO deserve further attention.

5 | CONCLUSIONS

This study shows that Swedish arctic–alpine lakes with taller shoreline vegetation relative to lake surface area stratify more strongly and have lower near-bottom oxygen concentrations primarily because of higher DOC concentrations and secondarily because of lower wind speeds. Based on this finding, we predict tree line shifts to cause widespread changes in lake mixing and oxygen dynamics at the landscape level. Our results underpin the tight coupling between catchment vegetation and gas dynamics in lakes (Jansson et al., 2008; Maberly et al., 2013) and highlight important indirect consequences of terrestrial greening and subsequent aquatic browning (Finstad et al., 2016; Kritzberg, 2017) for aquatic biota and biogeochemical cycling (Solomon et al., 2015). For example, stronger thermal stratification and DO depletion decrease available fish habitat and may reduce growth and reproduction of cold-water fish (Anttila et al., 2015; Coutant, 1985; Schindler et al., 1996). Hypoxia will further affect the cycling of carbon, nutrients, heavy metals and greenhouse gases (Bartosiewicz et al., 2019; Davison et al., 1980; Hamilton et al., 1995; Liikanen et al., 2002; Mortimer, 1942) and stratification affects air-water gas exchange (Åberg et al., 2010; Macintyre et al., 2020). The centrality of stratification and oxygen to key functions of lake ecosystems implies that tree line shifts and subsequent changes in stratification and oxygen status stand to have far-reaching impacts on the biological, chemical and physical patterns and processes of arctic and alpine lakes.

ACKNOWLEDGEMENTS

We thank Dirk Verheijen, Karl Heuchel, Bror Holmgren, Sven Norman and the county board Jämtland for fieldwork, and Anders Jonsson and the Biogeochemical Analytical Facility, a KBC infrastructure at Umeå University, for water chemical analysis. Important ideas for this paper were sparked by discussions with Dominic Vachon on wind sheltering effects on lake gas dynamics. We thank the Swedish Infrastructure for Ecosystem Science (SITES) for providing data for lake Almberga (BD15). This study was financed by Formas (dnr: 942.2015-723), the Swedish Research Council (dnr: 2016-05275) and Knut and Alice Wallenberg Foundation (dnr: 2016.0083).

AUTHOR CONTRIBUTION

Jan Karlsson designed the field study with contributions from David Seekell and Marcus Klaus. Marcus Klaus designed the analytical framework with contributions from Jan Karlsson and David Seekell. Marcus Klaus compiled all data, performed all analyses and drafted the manuscript. Jan Karlsson and David Seekell reviewed the manuscript critically and contributed with important edits. Marcus Klaus finalized the manuscript. All co-authors have seen and approved the submitted manuscript.

DATA AVAILABILITY STATEMENT

All original data shown in Figures 3 and 4 are available in Table S1. Raw data are available through the corresponding author upon request.

ORCID

Marcus Klaus https://orcid.org/0000-0003-0747-3524

REFERENCES

Åberg, J., Jansson, M., & Jonsson, A. (2010). Importance of water temperature and thermal stratification dynamics for temporal variation of surface water CO_2 in a boreal lake. *Journal of Geophysical Research*, *115*(G2), G02024. https://doi.org/10.1029/2009JG001085

Andrew J., T., Norman D., Y., Keller, B., Girard, R., Heneberry, J., Gunn, J. M., Hamilton, D. P., & Taylor, P. A. (2008). Cooling lakes while the world warms: Effects of forest regrowth and increased dissolved organic matter on the thermal regime of a temperate, urban lake. *Limnology and Oceanography*, *53*(1), 404–410. https://doi.org/10.4319/lo.2008.53.1.0404

Anttila, K., Lewis, M., Prokkola, J. M., Kanerva, M., Seppanen, E., Kolari, I., & Nikinmaa, M. (2015). Warm acclimation and oxygen depletion induce species-specific responses in salmonids. *Journal of Experimental Biology*, *218*(10), 1471–1477. https://doi.org/10.1242/jeb.119115

Ask, J., Karlsson, J., & Jansson, M. (2012). Net ecosystem production in clear-water and brown-water lakes. *Global Biogeochemical Cycles*, *26*(1), 1–7. https://doi.org/10.1029/2010GB003951

Bartosiewicz, M., Przytulska, A., Lapierre, J., Laurion, I., Lehmann, M. F., & Maranger, R. (2019). Hot tops, cold bottoms: Synergistic climate warming and shielding effects increase carbon burial in lakes. *Limnology and Oceanography Letters*, *4*(5), 132–144. https://doi.org/10.1002/lol2.10117

Bryn, A., & Potthoff, K. (2018). Elevational treeline and forest line dynamics in Norwegian mountain areas – A review. *Landscape Ecology*, *33*(8), 1225–1245. https://doi.org/10.1007/s10980-018-0670-8

Cansler, C. A., McKenzie, D., & Halpern, C. B. (2018). Fire enhances the complexity of forest structure in alpine treeline ecotones. *Ecosphere*, *9*(2), e02091. https://doi.org/10.1002/ecs2.2091

Caplanne, S., & Laurion, I. (2008). Effect of chromophoric dissolved organic matter on epilimnetic stratification in lakes. *Aquatic Sciences*, *70*(2), 123–133. https://doi.org/10.1007/s00027-007-7006-0

Charlton, M. N. (1980). Hypolimnion oxygen consumption in lakes: Discussion of productivity and morphometry effects. *Canadian*

Journal of Fisheries and Aquatic Sciences, *37*(10), 1531–1539. https://doi.org/10.1139/f80-198

Cornett, R. J., & Rigler, F. H. (1984). Dependence of hypolimnetic oxygen consumption on ambient oxygen concentration: Fact or artifact? *Water Resources Research*, *20*(7), 823–830. https://doi.org/10.1029/WR020i007p00823

Coutant, C. C. (1985). Striped bass, temperature, and dissolved oxygen: A speculative hypothesis for environmental risk. *Transactions of the American Fisheries Society*, *114*, 31–61. https://doi.org/10.1577/1548-8659(1985)114

Couture, R. M., De Wit, H. A., Tominaga, K., Kiuru, P., & Markelov, I. (2015). Oxygen dynamics in a boreal lake responds to long-term changes in climate, ice phenology, and DOC inputs. *Journal of Geophysical Research: Biogeosciences*, *120*(11), 2441–2456. https://doi.org/10.1002/2015JG003065

Craig, N., Jones, S. E., Weidel, B. C., & Solomon, C. T. (2015). Habitat, not resource availability, limits consumer production in lake ecosystems. *Limnology and Oceanography*, *60*(6), 2079–2089. https://doi.org/10.1002/lno.10153

Cudlín, P., Cudlín, P., Cudlín, P., Tognetti, R., Malis, F., Alados, C. L., Bebi, P., Grunewald, K., Zhiyanski, M., Andonowski, V., La Porta, N., Bratanova-Doncheva, S., Kachaunova, E., Edwards-Jonášová, M., Ninot, J. M., Rigling, A., Hofgaard, A., Hlásny, T., Skalák, P., & Wielgolaski, F. E. (2017). Drivers of treeline shift in different European mountains. *Climate Research*, *73*, 135–150. https://doi.org/10.3354/cr01465

Daniels, W. C., Kling, G. W., & Giblin, A. E. (2015). Benthic community metabolism in deep and shallow Arctic lakes during 13 years of whole-lake fertilization. *Limnology and Oceanography*, *60*(5), 1604–1618. https://doi.org/10.1002/lno.10120

Davison, W., Heaney, S. I., Talling, J. F., & Rigg, E. (1980). Seasonal transformations and movements of iron in a productive English lake with deep-water anoxia. *Schweizerische Zeitschrift Für Hydrologie*, *42*(2), 196–224. https://doi.org/10.1007/BF02502434

de Wit, H. A., Valinia, S., Weyhenmeyer, G. A., Futter, M. N., Kortelainen, P., Austnes, K., Hessen, D. O., Räike, A., Laudon, H., & Vuorenmaa, J. (2016). Current browning of surface waters will be further promoted by wetter climate. *Environmental Sciences and Technology Letters*, *3*(12), 430–435. https://doi.org/10.1021/acs.estlett.6b00396

Deshpande, B. N., Macintyre, S., Matveev, A., & Vincent, W. F. (2015). Oxygen dynamics in permafrost thaw lakes: Anaerobic bioreactors in the Canadian subarctic. *Limnology and Oceanography*, *60*, 1656–1670. https://doi.org/10.1002/lno.10126

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). Abundance and size distribution of lakes, ponds and impoundments. *Limnology and Oceanography*, *51*(5), 2388–2397. https://doi.org/10.1016/B978-0-12-409548-9.03867-7

Duff, K. E., Laing, T. E., Smol, J. P., & Lean, D. R. S. (1998). Limnological characteristics of lakes located across Arctic treeline in northern Russia. *Hydrobiologia*, *391*, 205–222. https://doi.org/10.1023/A:1003542322519

Edmondson, W. T., Anderson, G. C., & Peterson, D. R. (1956). Articial eutrophication of Lake Washington. *Limnology and Oceanography*, *1*(1), 47–53. https://doi.org/10.4319/lo.1956.1.1.0047

Eggermont, H., Russell, J. M., Schettler, G., Van Damme, K., Bessems, I., & Verschuren, D. (2007). Physical and chemical limnology of alpine lakes and pools in the Rwenzori Mountains (Uganda-DR Congo). *Hydrobiologia*, *592*(1), 151–173. https://doi.org/10.1007/s10750-007-0741-3

European Environmental Agency. (2016). Biogeographical regions dataset. Available at https://www.eea.europa.eu/data-and-maps/data/biogeographical-regions-europe-3

Evans, D. O. (2007). Effects of hypoxia on scope-for-activity and power capacity of lake trout (*Salvelinus namaycush*). *Canadian Journal of Fisheries and Aquatic Sciences*, *361*, 345–361. https://doi.org/10.1139/F07-007

Fallu, M. A., Pienitz, R., Walker, I. R., & Lavoie, M. (2005). Paleolimnology of a shrub-tundra lake and response of aquatic and terrestrial indicators to climatic change in Arctic Québec, Canada. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *215*(3–4), 183–203. https://doi.org/10.1016/j.palaeo.2004.07.006

Ficker, H., Luger, M., & Gassner, H. (2017). From dimictic to monomictic: Empirical evidence of thermal regime transitions in three deep alpine lakes in Austria induced by climate change. *Freshwater Biology*, *62*(8), 1335–1345. https://doi.org/10.1111/fwb.12946

Finstad, A. G., Andersen, T., Larsen, S., Tominaga, K., Blumentrath, S., de Wit, H. A., Tømmervik, H., & Hessen, D. O. (2016). From greening to browning: Catchment vegetation development and reduced S-deposition promote organic carbon load on decadal time scales in Nordic lakes. *Scientific Reports*, *6*(1), 1–8. https://doi.org/10.1038/srep31944

Foley, B., Jones, I. D., Maberly, S. C., & Rippey, B. (2012). Long-term changes in oxygen depletion in a small temperate lake: Effects of climate change and eutrophication. *Freshwater Biology*, *57*(2), 278–289. https://doi.org/10.1111/j.1365-2427.2011.02662.x

Gisnås, K., Etzelmüller, B., Lussana, C., Hjort, J., Sannel, A. B. K., Isaksen, K., Westermann, S., Kuhry, P., Christiansen, H. H., Frampton, A., & Åkerman, J. (2017). Permafrost map for Norway, Sweden and Finland. *Permafrost and Periglacial Processes*, *28*, 359–378. https://doi.org/10.1002/ppp.1922

Gray, E., Mackay, E. B., Elliott, J. A., Folkard, A. M., & Jones, I. D. (2020). Wide-spread inconsistency in estimation of lake mixed depth impacts interpretation of limnological processes. *Water Research*, *168*, 115136. https://doi.org/10.1016/j.watres.2019.115136

Hagedorn, F., Van Hees, P. A. W., & Handa, I. T. (2008). Elevated atmospheric CO_2 fuels leaching of old dissolved organic matter at the alpine treeline. *Global Biogeochemical Cycles*, *22*, 1–11. https://doi.org/10.1029/2007GB003026

Hamilton, S. K., Sippel, S. J., & Melack, J. M. (1995). Oxygen depletion and carbon dioxide and methane production in waters of the Pantanal wetland of Brazil. *Biogeochemistry*, *30*(2), 115–141. https://doi.org/10.1007/BF00002727

Harsch, M. A., Hulme, P. E., McGlone, M. S., & Duncan, R. P. (2009). Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecology Letters*, *12*(10), 1040–1049. https://doi.org/10.1111/j.1461-0248.2009.01355.x

Hicks, B. B. (1975). A procedure for the formulation of bulk transfer coefficients over water. *Boundary-Layer Meteorology*, *8*(3–4), 515–524. https://doi.org/10.1007/BF02153568

Hofgaard, A., Tømmervik, H., Rees, G., & Hanssen, F. (2013). Latitudinal forest advance in northernmost Norway since the early 20th century. *Journal of Biogeography*, *40*(5), 938–949. https://doi.org/10.1111/jbi.12053

Hondzo, M., & Stefan, H. G. (1993). Lake water temperature simulation model. *Journal of Hydraulic Engineering*, *119*(11), 1251–1273. https://doi.org/10.1061/(ASCE)0733-9429(1993)119:11(1251

Jansson, M., Hickler, T., Jonsson, A., & Karlsson, J. (2008). Links between terrestrial primary production and bacterial production and respiration in lakes in a climate gradient in subarctic Sweden. *Ecosystems*, *11*(3), 367–376. https://doi.org/10.1007/s10021-008-9127-2

Jenny, J.-P., Francus, P., Normandeau, A., Lapointe, F., Perga, M.-E., Ojala, A., Schimmelmann, A., & Zolitschka, B. (2016). Global spread of hypoxia in freshwater ecosystems during the last three centuries is caused by rising local human pressure. *Global Change Biology*, *22*(4), 1481–1489. https://doi.org/10.1111/gcb.13193

Karlsson, J., Jonsson, A., Meili, M., & Jansson, M. (2004). $\delta^{15}N$ of zooplankton species in subarctic lakes in northern Sweden: Effects of diet and trophic fractionation. *Freshwater Biology*, *49*(5), 526–534. https://doi.org/10.1111/j.1365-2427.2004.01208.x

Klaus, M., Seekell, D. A., Lidberg, W., & Karlsson, J. (2019). Evaluations of climate and land management effects on lake carbon cycling need to account for temporal variability in CO_2 concentrations. *Global Biogeochemical Cycles*, *33*, 243–265. https://doi.org/10.1029/2018GB005979

Kritzberg, E. S. (2017). Centennial-long trends of lake browning show major effect of afforestation. *Limnology and Oceanography Letters*, *2*(4), 105–112. https://doi.org/10.1002/lol2.10041

Kullman, L. (1990). Dynamics of altitudinal tree-limits in Sweden: A review. *Norwegian Journal of Geography*, *44*(2), 103–116. https://doi.org/10.1080/00291959008552248

Kullman, L. (1995). Holocene tree-limit and climate history from the Scandes Mountains. *Sweden. Ecology*, *76*(8), 2490–2502. https://doi.org/10.2307/2265823

Kullman, L., & Öberg, L. (2009). Post-Little Ice Age tree line rise and climate warming in the Swedish Scandes: A landscape ecological perspective. *Journal of Ecology*, *97*(3), 415–429. https://doi.org/10.1111/j.1365-2745.2009.01488.x

Lantmäteriet. (2010). GSD-höjddata, grid 50+ (GSD-elevation data, grid 50+ nh). https://www.lantmateriet.se/sv/Kartor-och-geografisk-information/geodataprodukter/produktlista/hojddata-grid-50/

Lantmäteriet. (2012). GSD-Vegetationsdata (GSD vegetation data). https://zeus.slu.se/get

Lapierre, J.-F., Guillemette, F., Berggren, M., & del Giorgio, P. A. (2013). Increases in terrestrially derived carbon stimulate organic carbon processing and CO_2 emissions in boreal aquatic ecosystems. *Nature Communications*, *4*, 2972. https://doi.org/10.1038/ncomms3972

Lasenby, D. C. (1975). Development of oxygen deficits in 14 southern Ontario lakes. *Limnology and Oceanography*, *20*(6), 993–999. https://doi.org/10.1016/B978-0-12-409751-3.50010-4

Lefcheck, J. S. (2016). PIECEWISESEM: Piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, *7*, 573–579. https://doi.org/10.1111/2041-210X.12512

Leppi, J. C., Arp, C. D., & Whitman, M. S. (2016). Predicting late winter dissolved oxygen levels in Arctic lakes using morphology and landscape metrics. *Environmental Management*, *57*(2), 463–473. https://doi.org/10.1007/s00267-015-0622-x

Liikanen, A., Murtoniemi, T., Tanskanen, H., Väisänen, T., & Martikainen, P. J. (2002). Effects of temperature and oxygen availability on greenhouse gas and nutrient dynamics in sediment of a eutrophic mid-boreal lake. *Biogeochemistry*, *59*(3), 269–286. https://doi.org/10.1023/A:1016015526712

Luoto, T. P., Rantala, M. V., Henriikka Kivilä, E., & Nevalainen, L. (2019). Recent changes in chironomid communities and hypolimnetic oxygen conditions relate to organic carbon in subarctic ecotonal lakes. *Science of the Total Environment*, *646*, 238–244. https://doi.org/10.1016/j.scitotenv.2018.07.306

Maberly, S. C., Barker, P. A., Stott, A. W., & De Ville, M. M. (2013). Catchment productivity controls CO_2 emissions from lakes. *Nature Climate Change*, *3*(4), 391–394. https://doi.org/10.1038/nclimate1748

Macdonald, G. M., Edwards, T. W. D., Moser, K. A., Pienitz, R., & Smol, J. P. (1993). Rapid response of treeline vegetation and lakes to past climate warming. *Nature*, *361*, 243–246. https://doi.org/10.1038/361243a0

Macintyre, S., Bastviken, D., Arneborg, L., Crowe, A. T., Karlsson, J., Andersson, A., Gålfalk, M., Rutgersson, A., & Podgrajsek, E., & Melack, J. M. (2020). Turbulence in a small boreal lake: Consequences for air–water gas exchange. *Limnology and Oceanography*, *66*(3), 827–854. https://doi.org/10.1002/lno.11645

MacIntyre, S., Fram, J. P., Kushner, P. J., Bettez, N. D., Brien, W. J. O., Hobbie, J. E., & Kling, G. W. (2009). Climate-related variations in mixing dynamics in an Alaskan Arctic lake. *Limnology and Oceanography*, *54*(6_part_2), 2401–2417. https://doi.org/10.4319/lo.2009.54.6_part_2.2401

Mammarella, I., Gavrylenko, G., Zdorovennova, G., Ojala, A., Erkkilä, K. M., Zdorovennov, R., Stepanyuk, O., Palshin, N., Terzhevik, A., & Vesala, T., & Heiskanen, J. (2018). Effects of similar weather patterns on the thermal stratification, mixing regimes and hypolimnetic oxygen depletion in two boreal lakes with different water transparency. *Boreal Environment Research*, *23*, 237–247.

Markfort, C. D., Perez, A. L. S., Thill, J. W., Jaster, D. A., Porté-Agel, F., & Stefan, H. G. (2010). Wind sheltering of a lake by a tree canopy or bluff topography. *Water Resources Research*, *46*(3). https://doi.org/10.1029/2009WR007759

Martinsen, K. T., Andersen, M. R., & Sand-Jensen, K. (2019). Water temperature dynamics and the prevalence of daytime stratification in small temperate shallow lakes. *Hydrobiologia*, *826*(1), 247–262. https://doi.org/10.1007/s10750-018-3737-2

Mathias, J. A., & Barica, J. (1980). Factors controlling oxygen depletion in ice-covered lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, *37*(2), 185–194. https://doi.org/10.1139/f80-024

McGowan, S., Anderson, N. J., Edwards, M. E., Hopla, E., Jones, V., Langdon, P. G., Law, A., Solovieva, N., Turner, S., van Hardenbroek, M., Whiteford, E. J., & Wiik, E. (2018). Vegetation transitions drive the autotrophy–heterotrophy balance in Arctic lakes. *Limnology and Oceanography Letters*, *3*(3), 246–255. https://doi.org/10.1002/lol2.10086

Meinshausen, N. (2017). *quantregForest: Quantile regression forests. R package version 1.3-7*. Available at https://CRAN.R-project.org/package=quantregForest

Michelutti, N., Labaj, A. L., Grooms, C., & Smol, J. P. (2016). Equatorial mountain lakes show extended periods of thermal stratification with recent climate change. *Journal of Limnology*, *75*(2), 403–408. https://doi.org/10.4081/jlimnol.2015.1444

Moen, J., Aune, K., Edenius, L., & Angerbjörn, A. (2004). Potential effects of climate change on treeline position in the Swedish mountains. *Ecology and Society*, *9*(1). https://doi.org/10.5751/ES-00634-090116

Mortimer, C. H. (1942). The exchange of dissolved substances between mud and water in lakes. *Journal of Ecology*, *30*(1), 147–201. https://doi.org/10.2307/2256691

Moser, K. A., Baron, J. S., Brahney, J., Oleksy, I. A., Saros, J. E., Hundey, E. J., Sadro, S., Kopáček, J., Sommaruga, R., Kainz, M. J., Strecker, A. L., Chandra, S., Walters, D. M., Preston, D. L., Michelutti, N., Lepori, F., Spaulding, S. A., Christianson, K. R., Melack, J. M., & Smol, J. P. (2019). Mountain lakes: Eyes on global environmental change. *Global and Planetary Change*, *178*, 77–95. https://doi.org/10.1016/j.gloplacha.2019.04.001

Muggeo, V. M. R. (2008). segmented: An R package to fit regression models with broken-line relationships. *R News*, *8*(1), 20–25.Available at https://cran.r-project.org/doc/Rnews/

Müller, B., Bryant, L. D., Matzinger, A., & Wüest, A. (2012). Hypolimnetic oxygen depletion in eutrophic lakes. *Environmental Science & Technology*, *46*(18), 9964–9971. https://doi.org/10.1021/es301422r

Murphy, M. (2020). *semEff: Automatic calculation of effects for piecewise structural equation models*. R package version 0.3.0. Available at https://CRAN.R-project.org/package=semEff

Nisell, J., Lindsjö, A., & Temnerud, J. (2007). *Rikstäckande virtuellt vattendrags nätverk för flödesbaserad modellering ViVaN* (in Swedish with an English summary). Department of Aquatic Science and Assessment, Swedish University of Agricultural Sciences. Sveriges Lantbruksuniversitet Report, 17.

North, R. P., North, R. L., Livingstone, D. M., Köster, O., & Kipfer, R. (2014). Long-term changes in hypoxia and soluble reactive phosphorus in the hypolimnion of a large temperate lake: Consequences of a climate regime shift. *Global Change Biology*, *20*(3), 811–823. https://doi.org/10.1111/gcb.12371

Nürnberg, G. K. (1995). Quantifying anoxia in lakes. *Limnology and Oceanography*, *40*(6), 1100–1111. https://doi.org/10.4319/lo.1995.40.6.1100

Pearson, R. G., Phillips, S. J., Loranty, M. M., Beck, P. S. A., Damoulas, T., Knight, S. J., & Goetz, S. J. (2013). Shifts in Arctic vegetation and associated feedbacks under climate change. *Nature Climate Change*, *3*, 673–677. https://doi.org/10.1038/nclimate1858

Pienitz, R., Smol, J. P., & Lean, D. R. S. (1997). Physical and chemical limnology of 59 lakes located between the southern Yukon and the Tuktoyaktuk Peninsula, Northwest Territories (Canada). *Canadian Journal of Fisheries and Aquatic Sciences*, *54*(2), 330–346. https://doi.org/10.1139/cjfas-54-2-330

Pienitz, R., Smol, J. P., & MacDonald, G. M. (1999). Paleolimnological reconstruction of holocene climatic trends from two boreal treeline lakes, Northwest Territories, Canada. *Arctic, Antarctic, and Alpine Research*, *31*(1), 82–93. https://doi.org/10.1080/15230430.1999.12003283

Pilla, R. M., Williamson, C. E., Zhang, J., Smyth, R. L., Lenters, J. D., Brentrup, J. A., Knoll, L. B., & Fisher, T. J. (2018). Browning-related decreases in water transparency lead to long-term increases in surface water temperature and thermal stratification in two small lakes. *Journal of Geophysical Research: Biogeosciences*, *123*(5), 1651–1665. https://doi.org/10.1029/2017JG004321

R Development Core Team. (2019). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Available at http://www.R-project.org

Randsalu-Wendrup, L., Conley, D. J., Carstensen, J., & Fritz, S. C. (2016). Paleolimnological records of regime shifts in lakes in response to climate change and anthropogenic activities. *Journal of Paleolimnology*, *56*, 1–14. https://doi.org/10.1007/s10933-016-9884-4

Rasmussen, J. B., Godbout, L., & Schallenberg, M. (1989). The humic content of lake water and its relationship to watershed and lake morphometry. *Limnology and Oceanography*, *34*(7), 1336–1343. https://doi.org/10.4319/lo.1989.34.7.1336

Read, J. S., Hamilton, D. P., Jones, I. D., Muraoka, K., Winslow, L. A., Kroiss, R., Wu, C. H., & Gaiser, E. (2011). Derivation of lake mixing and stratification indices from high-resolution lake buoy data. *Environmental Modelling and Software*, *26*(11), 1325–1336. https://doi.org/10.1016/j.envsoft.2011.05.006

Read, J. S., & Rose, K. C. (2013). Physical responses of small temperate lakes to variation in dissolved organic carbon concentrations. *Limnology and Oceanography*, *58*(3), 921–931. https://doi.org/10.4319/lo.2013.58.3.0921

Read, J. S., Winslow, L. A., Hansen, G. J. A., Van Den Hoek, J., Hanson, P. C., Bruce, L. C., & Markfort, C. D. (2014). Simulating 2368 temperate lakes reveals weak coherence in stratification phenology. *Ecological Modelling*, *291*, 142–150. https://doi.org/10.1016/j.ecolmodel.2014.07.029

Rees, W. G., Hofgaard, A., Boudreau, S., Cairns, D. M., Harper, K., Mamet, S., Mathisen, I., Swirad, Z., & Tutubalina, O. (2020). Is subarctic forest advance able to keep pace with climate change? *Global Change Biology*, *26*(7), 3965–3977. https://doi.org/10.1111/gcb.15113

Reilly, C. M. O., Sharma, S., Gray, D. K., Hampton, S. E., Read, J. S., Rowley, R. J., & Allan, M. G. (2015). Rapid and highly variable warming of lake surface waters around the globe. *Geophysical Research Letters*, *42*(10), 773–781. https://doi.org/10.1002/2015GL066235

Reuss, N. S., Hammarlund, D., Rundgren, M., Segerström, U., Eriksson, L., & Rosén, P. (2010). Lake ecosystem responses to Holocene climate change at the subarctic tree-line in Northern Sweden. *Ecosystems*, *13*(3), 393–409. https://doi.org/10.1007/s10021-010-9326-5

Rose, K. C., Williamson, C. E., Kissman, C. E. H., & Saros, J. E. (2015). Does allochthony in lakes change across an elevation gradient? *Ecology*, *96*(12), 3281–3291. https://doi.org/10.1890/14-1558.1

Sadro, S., Melack, J. M., & MacIntyre, S. (2011). Depth-integrated estimates of ecosystem metabolism in a high-elevation lake (Emerald Lake, Sierra Nevada, California). *Limnology and Oceanography*, *56*(5), 1764–1780. https://doi.org/10.4319/lo.2011.56.5.1764

Sánchez, E., Colmenarejo, M. F., Vicente, J., Rubio, A., García, M. G., Travieso, L., & Borja, R. (2007). Use of the water quality index and dissolved oxygen deficit as simple indicators of watersheds pollution. *Ecological Indicators*, *7*(2), 315–328. https://doi.org/10.1016/j.ecolind.2006.02.005

Saros, J. E., Northington, R. M., Osburn, C. L., Burpee, B. T., & John Anderson, N. (2016). Thermal stratification in small Arctic lakes of southwest Greenland affected by water transparency and epilimnetic temperatures. *Limnology and Oceanography*, *61*(4), 1530–1542. https://doi.org/10.1002/lno.10314

Saros, J. E., Stone, J. R., Pederson, G. T., Slemmons, K. E. H., Spanbauer, T., Schliep, A., Cahl, D., Williamson, C. E., & Engstrom, D. R. (2012). Climate-induced changes in lake ecosystem structure inferred from coupled neo- and paleoecological approaches. *Ecology*, *93*(10), 2155–2164. https://doi.org/10.1890/11-2218.1

Schindler, D. W., Bayley, S. E., Parker, B. R., Beaty, K. G., Cruikshank, D. R., Fee, E. J., Schindler, E. U., & Stainton, M. P. (1996). The effects of climatic warming on the properties of boreal lakes and streams at the Experimental Lakes Area, northwestern Ontario. *Limnology and Oceanography*, *41*(5), 1004–1017. https://doi.org/10.4319/lo.1996.41.5.1004

Sepulveda-Jauregui, A., Anthony, K. M. W., Martinez-Cruz, K., Greene, S., & Thalasso, F. (2015). Methane and carbon dioxide emissions from 40 lakes along a north–south latitudinal transect in Alaska. *Biogeosciences*, *12*, 3197–3223. https://doi.org/10.5194/bg-12-3197-2015

Shipley, B. (2013). The AIC model selection method applied to path analytic models compared using a d-separation test. *Ecology*, *94*(3), 560–564. https://doi.org/10.1890/12-0976.1

Simard, M., Pinto, N., Fisher, J. B., & Baccini, A. (2011). Mapping forest canopy height globally with spaceborne lidar. *Journal of Geophysical Research: Biogeosciences*, *116*(4), 1–12. https://doi.org/10.1029/2011JG001708

Siver, P. A., Marsicano, L. J., Lott, A. M., Wagener, S., & Morris, N. (2018). Wind induced impacts on hypolimnetic temperature and thermal structure of Candlewood Lake (Connecticut, U.S.A.) from 1985–2015. *Geo: Geography and Environment*, *5*(2), 1985–2015. https://doi.org/10.1002/geo2.56

Skogsstyrelsen. (2020). Basic forest data – tree height (in Swedish 'Skoglig grunddata – trädhöjd'). Available at https://www.skogsstyrelsen.se/skogligagrunddata

SMHI. (2012). Svensk Vattenarkiv – vattenförekomster-vattendrag Vd_l_2012_2 (Swedish Water Archive - Water courses). https://www.smhi.se/polopoly_fs/1.28869!/Menu/general/extGroup/attachmentColHold/mainCol1/file/vd_l_2012_2.zip

SMHI. (2020). Meteorological data (in Swedish, 'Observationsdata meteorologi'). Available at https://www.SMHI.se/data

Smith, S. D. (1988). Coefficients for sea surface wind stress, heat flux, and wind profiles as a function of wind speed and temperature. *Journal of Geophysical Research: Oceans*, *93*(C12), 15467–15472. https://doi.org/10.1029/JC093iC12p15467

Sobek, S., Tranvik, L. J., Prairie, Y. T., Kortelainen, P., & Cole, J. J. (2007). Patterns and regulation of dissolved organic carbon: An analysis of 7,500 widely distributed lakes. *Limnology and Oceanography*, *52*(3), 1208–1219. https://doi.org/10.4319/lo.2007.52.3.1208

Solomon, C. T., Jones, S. E., Weidel, B. C., Buffam, I., Fork, M. L., Karlsson, J., Larsen, S., Lennon, J. T., Read, J. S., Sadro, S., & Saros, J. E. (2015). Ecosystem consequences of changing inputs of terrestrial dissolved organic matter to lakes: Current knowledge and future challenges. *Ecosystems*, *18*(3), 376–389. https://doi.org/10.1007/s10021-015-9848-y

Swedish National Land Survey. (2016). GSD elevation data, grid 2+. Available at https://www.lantmateriet.se/en/maps-and-geographic-information/Hojddata/GSD-Hojddata-grid-2/

Van Bogaert, R., Haneca, K., Hoogesteger, J., Jonasson, C., De Dapper, M., & Callaghan, T. V. (2011). A century of tree line changes in sub-Arctic Sweden shows local and regional variability and only a minor influence of 20th century climate warming. *Journal of Biogeography*, *38*(5), 907–921. https://doi.org/10.1111/j.1365-2699.2010.02453.x

Vaquer-Sunyer, R., & Duarte, C. M. (2008). Thresholds of hypoxia for marine biodiversity. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(40), 15452–15457. https://doi.org/10.1073/pnas.0803833105

Vonk, J. E., Tank, S. E., Bowden, W. B., Laurion, I., Vincent, W. F., Alekseychik, P., Amyot, M., Billet, M. F., Canário, J., Cory, R. M., Deshpande, B. N., Helbig, M., Jammet, M., Karlsson, J., Larouche, J., MacMillan, G., Rautio, M., Walter Anthony, K. M., & Wickland, K. P. (2015). Reviews and syntheses: Effects of permafrost thaw on Arctic aquatic ecosystems. *Biogeosciences*, *12*(23), 7129–7167. https://doi.org/10.5194/bg-12-7129-2015

Walker, W. W. (1979). Use of hypolimnetic oxygen depletion rate as a trophic state index for lakes. *Water Resources Research*, *15*(6), 1463–1470. https://doi.org/10.1029/WR015i006p01463

Wetzel, R. G. (2001). *Limnology – Lake and river ecosystems* (3rd ed.). Academic Press.

Weyhenmeyer, G. A., & Karlsson, J. (2009). Nonlinear response of dissolved organic carbon concentrations in boreal lakes to increasing temperatures. *Limnology and Oceanography*, *54*(6part2), 2513–2519. https://doi.org/10.4319/lo.2009.54.6_part_2.2513

Wilhelm, S., & Adrian, R. (2008). Impact of summer warming on the thermal characteristics of a polymictic lake and consequences for oxygen, nutrients and phytoplankton. *Freshwater Biology*, *53*, 226–237. https://doi.org/10.1111/j.1365-2427.2007.01887.x

Wolf, A., Callaghan, T. V., & Larson, K. (2008). Future changes in vegetation and ecosystem function of the Barents Region. *Climatic Change*, *87*(1–2), 51–73. https://doi.org/10.1007/s10584-007-9342-4

Wolfe, B. B., Edwards, T. W. D., & Aravena, R. (1999). Changes in carbon and nitrogen cycling during tree-line retreat recorded in the isotopic content of lacustrine organic matter, western Taimyr Peninsula, Russia. *The Holocene*, *9*(2), 215–222. https://doi.org/10.1191/095968399669823431

Woolway, R. I., & Merchant, C. J. (2019). Worldwide alteration of lake mixing regimes in response to climate change. *Nature Geoscience*, *12*(4), 271–276. https://doi.org/10.1038/s41561-019-0322-x

Zeileis, A., & Hothorn, T. (2002). Diagnostic checking in regression relationships. *R News*, *2*(3), 7–10.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Klaus M, Karlsson J, Seekell D. Tree line advance reduces mixing and oxygen concentrations in arctic–alpine lakes through wind sheltering and organic carbon supply. *Glob Change Biol*. 2021;27:4238–4253. https://doi.org/10.1111/gcb.15660