LIMNOLOGY AND OCEANOGRAPHY
Letters

ASLO
Open Access

Limnology and Oceanography Letters 8, 2023, 639–648

doi: 10.1002/lol2.10318

LETTER

Widespread synchrony in phosphorus concentrations in northern lakes linked to winter temperature and summer precipitation

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Scientific Significance Statement

Phosphorus is one of the most important elements in lakes, and frequently serves as the limiting nutrient for aquatic plants and plankton at the base of the food web. The effect of a changing climate on phosphorus concentrations in lakes at northern latitudes is not well understood. By combining data from almost 400 lakes in 18 regions in North America and Northern Europe, we were able to observe similar patterns of year-to-year variability in phosphorus both within and among regions, indicating that concentrations of this important nutrient are being controlled by large scale climate factors. Using a machine-learning model, we identified winter temperature and summer precipitation as the most important climate influences on phosphorus, and the role of winter climate was reinforced by looking at the relationship of regional median TP with large-scale atmospheric patterns. Taken together, our results suggest that climate is important for lake phosphorus, and that winter warming may be contributing to observed declines in lake TP at high latitudes.

Abstract

In recent years, unexplained declines in lake total phosphorus (TP) concentrations have been observed at northern latitudes (> 42°N latitude) where most of the world's lakes are found. We compiled data from 389 lakes in

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Associate editor: Monika Winder

Author Contribution Statement: PDFI conceived of the study. PDFI, AKB, and IFC contacted partners and collected datasets for the analysis. PDFI performed data preparation, designed and conducted statistical analyses and interpretations, generated figures and tables, and wrote the main text of the document, with feedback from AKB and IFC. FP contributed to statistical analyses and gave feedback on manuscript drafts. DOH, PK, JAR, JV, and MP contributed datasets to the project and gave feedback on manuscript drafts.

Data Availability Statement: The median annual TP data, together with corresponding climate parameters, are available as a citable dataset at: https://doi.org/10.6073/pasta/e0e71e3d371189429956514d29b03d75. Complete climate data used in Fig. 5 are available from the European Center for Mid-Range Weather Forecasts (ECMWF), https://cds.climate.copernicus.eu/cdsapp#!/dataset/reanalysis-era5-land-monthly-means?tab=overview.

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

Fennoscandia and eastern North America to investigate the effects of climate on lake TP concentrations. Synchrony in year-to-year variability is an indicator of climatic influences on lake TP, because other major influences on nutrients (e.g., land use change) are not likely to affect all lakes in the same year. We identified significant synchrony in lake TP both within and among different geographic regions. Using a bootstrapped random forest analysis, we identified winter temperature as the most important factor controlling annual TP, followed by summer precipitation. In Fennoscandia, TP was negatively correlated with the winter East Atlantic Pattern, which is associated with regionally warmer winters. Our results suggest that, in the absence of other overriding factors, lake TP and productivity may decline with continued winter warming in northern lakes.

Phosphorus (P) is the most (Schindler 2012; Schindler et al. 2016), or one of the most (Bergström and Jansson 2006; Elser et al. 2009; Paerl et al. 2016), important elements limiting primary production in lakes and rivers. Many studies have addressed interactions between climate and human land use on lake P (e.g., Zia et al. 2022), but direct climate impacts on P concentrations in relatively undisturbed lakes remain poorly understood.

Climate influences lake P concentrations directly by affecting internal processing of nutrients, and indirectly by affecting catchment processes (Vogt et al. 2011). For example, changes in temperature affect the internal cycling of P by altering stratification dynamics and biological process rates. Changes in precipitation can mediate catchment nutrient loads to lakes and alter lake residence times. Changes in wind speed may affect lake P by altering lake mixing dynamics (Lau et al. 2020). If lake P concentrations are consistently related to changes in climate, there may be widespread changes in P availability and associated changes in lake function with future climate change.

In this study, we examined the effects of climate on lake total phosphorus (TP) concentrations in 389 lakes assigned to 18 regions throughout Fennoscandia, southeastern Canada, and the northeastern United States. We used the period from 1998 to 2017, when most time series were relatively stationary, in order to focus on drivers of year-to-year climate variability rather than climate trends (which may be more susceptible to spurious correlations). Regions were selected in areas that contained lakes with relatively pristine catchments. First, we investigated synchrony of annual median TP within regions. Synchrony (mean pairwise correlation across a set of lakes) is an indicator that regional factors (weather and climate) rather than local factors (land use) are influencing variability in ecosystem properties (Baines et al. 2000; Vogt et al. 2011). We hypothesized that lake TP would be synchronous within regions because of shared climate influences. Second, we investigated synchrony among regions, to assess larger-scale climatic influences. We hypothesized that nearby regions would be more strongly correlated than distant regions due to greater climate similarity. Third, we used random forests to compare TP to seasonal climate variables to determine which factors had the greatest influence on lake TP, and we correlated regional median TP to seasonal climate teleconnection indices to identify large-scale climate controls on TP concentrations.

Methods

Epilimnion TP data were aggregated from national, state, provincial, and academic monitoring programs. We chose the period 1998–2017 to maximize overlap between datasets, and because strong directional trends in TP were mostly absent during this period. Eutrophic lakes (median annual TP > 24 $\mu g\ L^{-1}$) and lakes with < 8 yr of data between 1998 and 2017 were excluded from the analysis. Only samples from April to November were used. The lakes in Norway were the least frequently sampled, with a single sample taken each year during fall turnover. Other regions had multiple samples per year (Data S1). If multiple samples were taken annually, median values were used to estimate annual TP concentrations (Isles et al. 2023).

Sampling sites were assigned to regions based on geographic proximity and sampling authority. Geographic proximity was used because nearby lakes are most likely to experience similar variations in weather. Sampling authority was used as an additional constraint to ensure consistency in methods and maximize the number of years with overlapping data within regions. In the large national monitoring programs in Fennoscandia, lakes from the same sampling authority were subdivided into regions based on expert opinion as to differences in climate and geography, as has been done in previous studies (Bergström et al. 2005; Isles et al. 2018; Isles et al. 2020). The size of these regions was chosen such that each region had enough lakes to make robust estimates of annual regional median lake TP but had similar patterns of year-to-year variation in weather.

Within-region synchrony was calculated as the mean pairwise Spearman's correlation among lakes. Synchrony at the annual timescale is likely to be driven by climate variability, whereas variability over longer timescales such as decades may be driven by factors such as farming or forestry practices. Typically, mean synchrony ranges from slightly negative to 1 (Rusak et al. 1999). To assess the significance of regional synchrony estimates, the time series of TP for each lake in each region was randomly permuted 1000 times and mean pairwise correlations were calculated on each permuted matrix, with synchrony over the 95th percentile considered significant.

Among-region synchrony was assessed after first calculating median *z*-scores of TP for lakes within each region. *z*-Scores for each lake were calculated by subtracting the mean and dividing by the standard deviation of TP for each year. Median *z*-scores in each region were correlated with median *z*-scores from all other regions to evaluate synchrony among regions. Comparisons between regions with fewer than 5 yr of overlapping data were excluded. The mean values of the pairwise correlations were calculated to derive synchrony estimates for North America, Fennoscandia, and the entire dataset.

Random forests (Liaw and Wiener 2002) were used to compare standardized seasonal climate variables with TP *z*-scores for individual lakes. Monthly climate data were accessed through the ERA5-Land reanalysis product (Muñoz-Sabater et al. 2021) for 1951–2019, and precipitation, temperature, and wind speed were averaged into four seasons: December–February (djf), March–May (mam), June–August (jja), and September–November (son). Long-term trends were assessed for winter temperature and summer precipitation by calculating the slope of linear regressions for each grid cell from 1951 to 2019. Climate variables were standardized to *z*-scores for each site before running the random forest, so that we could test the *relative* impact of changes in climate on TP (e.g., does a relatively warm winter at lake *X* correspond to relatively high TP for that lake?). For the random forest analysis, 100 separate forests were run, each randomly sampling five lakes from each region to ensure that results were not geographically biased toward regions with more monitored lakes. Each of the 100 forests was run with 1000 trees, testing five variables at each node. The decrease in mean squared error was used to rank the importance of explanatory variables, and the mean rank across 100 random forests was used as an overall variable importance metric. A standard random forest analysis was also run with data from all lakes simultaneously (Fig. S1).

Climate teleconnection indices including the North Atlantic Oscillation (NAO), East Atlantic pattern (EA), East Atlantic/Western Russia pattern (EAWR), Scandinavia pattern (SCA), East Pacific/North Pacific pattern (EPNP), Pacific/North American Pattern (PNA), and El Niño Southern Oscillation (ENSO), were accessed from the US National Oceanic and Atmospheric Administration website https://www.cpc.ncep.noaa.gov/products/precip/CWlink/daily_ao_index/teleconnections.shtml or, in the case of the multivariate ENSO index, https://psl.noaa.gov/enso/mei/. We chose teleconnections for which we could find reports of associations with terrestrial or aquatic ecological processes in the study regions: for North America, NAO, EPNP, PNA, ENSO; for Fennoscandia, NAO, EA, EAWR, and SCA (Chen and Hellström 1999; Sheridan 2003; Kingston et al. 2006; Bai et al. 2012; Moore and Renfrew 2012; Zhu et al. 2017). Other indices may influence regional climate, so our analysis was not exhaustive. For each seasonal index and for each continent, the mean and standard error of correlations of seasonal teleconnections with the regional median TP were calculated. The 95% and 99.7% (following Bonferroni's correction) confidence intervals around the mean estimate were calculated. If the confidence intervals did not include zero, the mean correlation was considered significant (Figs. S2, S3).

To confirm the effect of the most important climate variables identified by random forest analysis, we calculated mean lake TP from years with the warmest half and the coldest half of winters from each lake, and the mean lake TP from the years with wettest half and driest half of summers from each lake. One-sample *t*-tests were used to assess whether the mean of the distributions of TP differences between years with warm and cold winters, and between wet and dry summers, were significantly different from zero.

Results

In the 389 lakes selected from our database as having sufficient data for our analyses, median epilimnetic TP ranged from 1 to 22.5 μg L^{-1}, with a median of 6 μg L^{-1} (Fig. 1). Seventy-nine percent of lakes were oligotrophic (TP $< 12\ \mu$g L^{-1}), the rest mesotrophic ($12 <$ TP $< 24\ \mu$g L^{-1}).

Synchrony was significant within all regions (Fig. 2). The highest synchrony was observed in the Turkey Lakes, Ontario, likely because five lakes drain one into the other. Synchrony was lower in regions where not all lakes were measured each year (North America: Maine, Vermont), and in southern areas of Norway and Finland. Across all lakes, TP decreased over the study period (median slope: -0.5% yr^{-1}) but these trends were minor relative to year-to-year variability (median within-site coefficient of variation of 25% among years) (Fig. S4).

At the regional scale, all Fennoscandian regions were positively correlated with each other, except for southern Finland (Fig. 2). The coastal regions of North America (Maine, New Brunswick, and Nova Scotia) were positively correlated with the Fennoscandian regions, with the exception of southern Finland. There was not a consistent pattern of synchrony among the other North American regions.

The bootstrapped random forest analysis explained 16% of variation in TP based on mean out-of-bag variance. The most important variables were winter temperature and summer precipitation, followed by spring temperature (Fig. 3). The partial effects of winter and spring temperatures had flat slopes for years with average temperatures, but large effects at both ends of the distribution, indicating that extreme years were associated with major changes in lake TP, and higher temperatures were associated with lower TP. Summer precipitation was positively associated with lake TP across the upper half of the data distribution, with relatively small effects on the lower half of the distribution. When all data were used in a single random forest, the model explained 18% of the variation in TP, with winter temperature the most important predictor, followed by summer precipitation.

Winter temperature was more important in Fennoscandian lakes than in North American lakes (Fig. S5), with a mean decrease in lake TP of 5.0% from the coldest 50% of winters

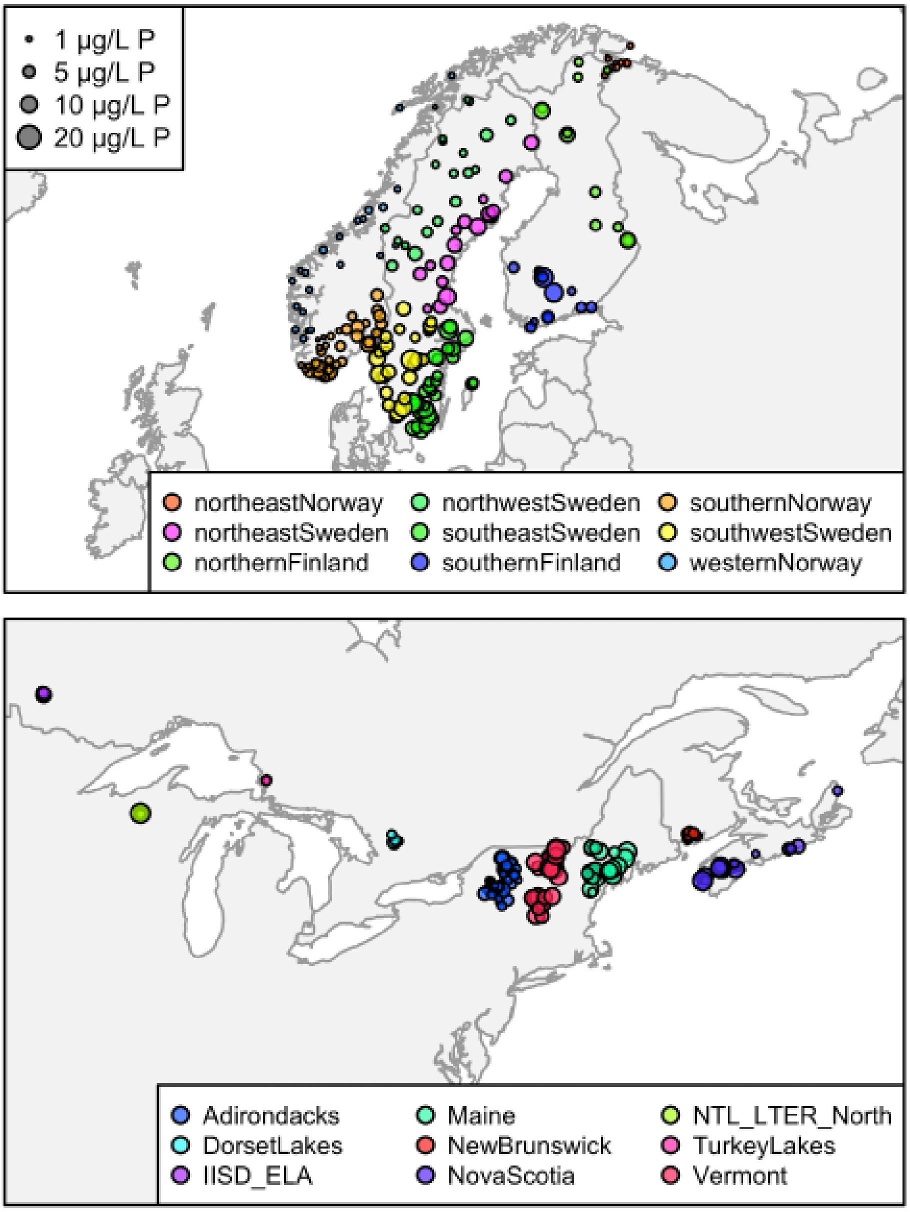

Fig. 1. Map of sites showing regions (colors) and median TP concentrations for each lake in Fennoscandia (top) and North America (bottom). NTL_LTER_North denotes the north temperate lakes long-term ecological research lakes. IISD_ELA denotes the IISD Experimental Lakes Area in Ontario.

relative to the warmest 50% of winters ($p < 0.001$). By contrast, there was a modest (mean decrease of 1.1%), non-significant ($p = 0.33$) difference in lake TP between warm and cold winters in North American lakes. Summer precipitation was more important in North America, with a mean increase in lake TP during wet relative to dry summers of 5.4% ($p < 0.0001$), than in Fennoscandia which had a non-significant mean increase of only 2.3% during wet summers ($p = 0.19$).

Several seasonal climate teleconnection indices influenced regional median lake TP (Fig. 4). In Fennoscandia, winter EA was negatively correlated with TP in all regions (mean correlation −0.42), and this correlation was highly significant (Fig. S2). The spring and fall NAO were also negatively correlated with TP in Fennoscandia. In North America, the winter EPNP was negatively correlated with continental TP ($p < 0.05$) (Fig. S3).

The synchrony and random forest analyses were performed over a relatively period of 20 yr. The longer climate time series of almost 70 yr revealed temporal trends in variables important for lake TP. Winter temperature increased in all regions from 1951 to 2019 (Fig. 5). The range of winter temperatures

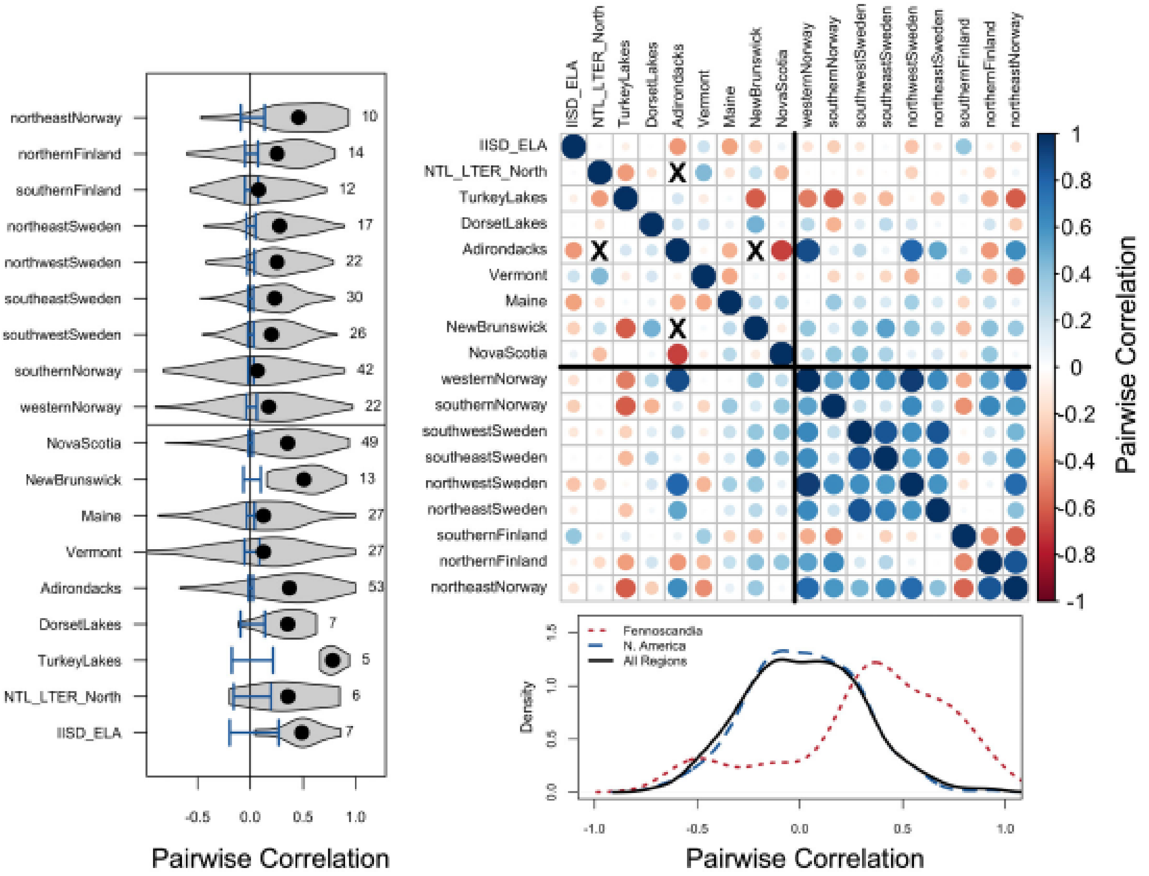

Fig. 2. Synchrony within (left) and among (right) regions. Left: Violin plots of synchrony within regions, showing distributions of pairwise correlations of TP between lakes with each region. Regions are ordered from east (top) to west (bottom). Numbers next to each violin represent the total number of lakes (n) within each region (total number of pairwise correlations = $[n^2 - n]/2$). Black circles represent the mean pairwise correlation for each region. The blue bars represent the 95th percentile range of mean correlations from 1000 randomized permutations of the annual data in each lake (black circles outside of this range indicate significant synchrony). The black horizontal line divides Fennoscandian and North American regions. Top right: Correlation plot showing synchrony among regions. Colors represent pairwise correlations of years with overlapping data from perfect negative correlation (−1, dark red) to no relationship (0, white), to perfect positive correlation (1, dark blue). Regions are ordered from west to east; dark lines divide North American and Fennoscandian regions. X's are shown for comparisons where there were fewer than five overlapping years of data between regions. Bottom right: Same data as above, with kernel density plots of pairwise correlations among North American regions (blue dashed lines), Fennoscandian regions (red dotted lines), and all regions together (solid black line).

was similar in the Fennoscandia and North America regions (Fig. S7); however, the rates of temperature increases were generally larger in Fennoscandia (min slope 0.024, median 0.043, max 0.065°C yr^{-1}) than in North America (min 0.012, median 0.028, and max 0.032°C yr^{-1}). Summer precipitation generally increased, and trends were similar between Fennoscandia (min slope −0.002, median 0.005, max 0.018 mm yr^{-1}) and North America (min slope −0.002, median 0.007, max 0.014 mm yr^{-1}). The winter EA and spring NAO, which both had significant negative correlations with lake TP in Fennoscandia, increased over time (Fig. 5).

Discussion

We found evidence for widespread synchrony in Lake TP concentrations in northern lakes indicating the importance of climate factors in controlling lake nutrient cycling. Previous studies investigating climate impacts on lakes at large spatial scales (Oliver et al. 2017; Collins et al. 2019) have frequently focused on the slopes of long-term trends, which are sometimes estimated from relatively few datapoints over varying time periods and which may be more susceptible to spurious correlations than year-to-year variability. However, year-to-year variability is often much greater than long-term trends in TP concentrations (as well as other analytes), as was the case in this study (Fig. S4). By focusing on year-to-year synchrony, and by constructing our random forest analysis to look at drivers of *relative* changes in *z*-score transformed TP in different lakes, we were able to take advantage of the information contained in the year-to-year variability in TP to uncover relationships with climate variables.

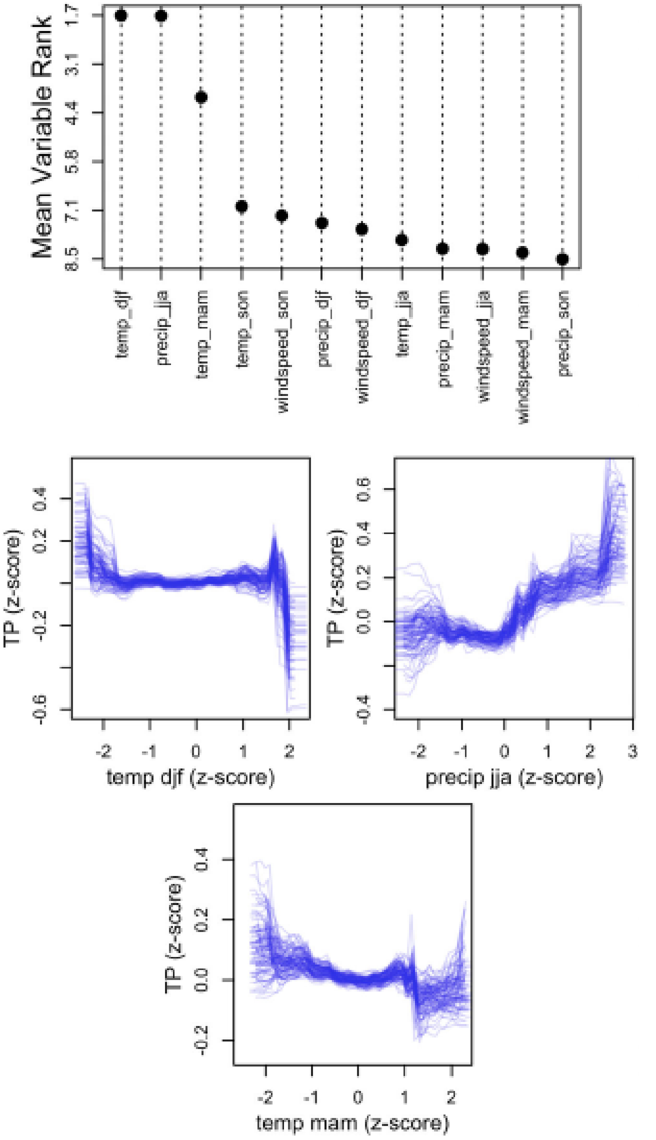

Fig. 3. Top: Mean variable importance rankings (top) across 100 random forests (each sampling five sites from each region). All predictor variables, as well as TP, were standardized to z-scores within each site before running the random forest, to compare relative variations in climate variables to relative variation in TP. Bottom three panels: Partial effects plots for the three most important variables showing partial effects from each of the 100 random forest iterations (transparent blue lines). X-axes represent the range of z-scores for each variable.

Direct human impacts on lakes are unlikely to be synchronous among lakes either within or across regions at the scale of year-to-year variability, whereas climate- and weather-mediated changes are likely to be synchronous across large geographic areas. The consistently significant within-region synchrony presents strong evidence for the influence of climate variables on TP, as does the high synchrony among regions in Fennoscandia. The large difference in among-region synchrony between Fennoscandia and North America suggests either stronger control of regional climate on Fennoscandian lakes, or more consistent year-to-year variation in climate variables across Fennoscandia relative to the North America study area (which has a complex mix of continental and maritime climate influences; Fig. S6). Previous studies have used synchrony analyses as an indicator of climate influence on lake properties (e.g., Baines et al. 2000; Rusak et al. 2008; Vogt et al. 2011), but we are unaware of other studies in lakes that have used something like the regional approach developed here to identify synchrony across broader spatial scales.

The relatively low amount of variance explained by our random forest analyses (16–18%) is common in large-scale studies (Oliver et al. 2017; Collins et al. 2019), and was not surprising given that many factors known to influence lake TP were not addressed in this study. By focusing on climate factors in this analysis, we do not intend to downplay other factors that may impact TP, including local land-use activities, the mediating role of catchment and lake morphometry and underlying geology, or the specific ecological histories of individual lakes, all of which influence TP. Rather, we intend to quantify the portion of variability in TP that is influenced by climate, with the understanding that relatively small climate-driven changes across large areas can have large cumulative impacts on global biogeochemical cycles.

The positive influence of summer precipitation on lake TP that we observed in North America is consistent with other studies (e.g., Rose et al. 2017) and may indicate increased P loading from catchments during wet years. The strong influence of summer precipitation in the North American lakes may reflect the fact that they generally received higher summer precipitation (Fig. S7), as well as warmer summer temperatures relative to the Fennoscandian lakes, which could lead to more dramatic shifts in wetting and drying (e.g., Senar et al. 2018). It may also reflect a mixed influence of precipitation in parts of Fennoscandia. Previous research has shown that in wetter areas (especially western Norway), high annual precipitation results in dilution and therefore decreasing solute concentrations during wet years, whereas in drier areas, high annual precipitation results in higher solute concentrations (de Wit et al. 2016).

Three distinct approaches were used to explore climatic influences on lake TP (random forest analysis, correlations of TP with seasonal teleconnection indices, and a *t*-test comparison of TP in warm and cold winters), and all indicated that winter conditions are an important driver of year-to-year variability in lake TP, particularly in Fennoscandia. This was remarkable given that no winter TP measurements were included in our analysis, and suggests that winter conditions have a persistent impact on lake TP during the following ice-free period. The winter EA can have a strong influence on European winter climate (Comas Bru and McDermott 2014; Moore and Renfrew 2012; Salmaso and Sarasino 2012), and the positive phase of the EA is associated with warmer winters, so the significant negative correlations observed between

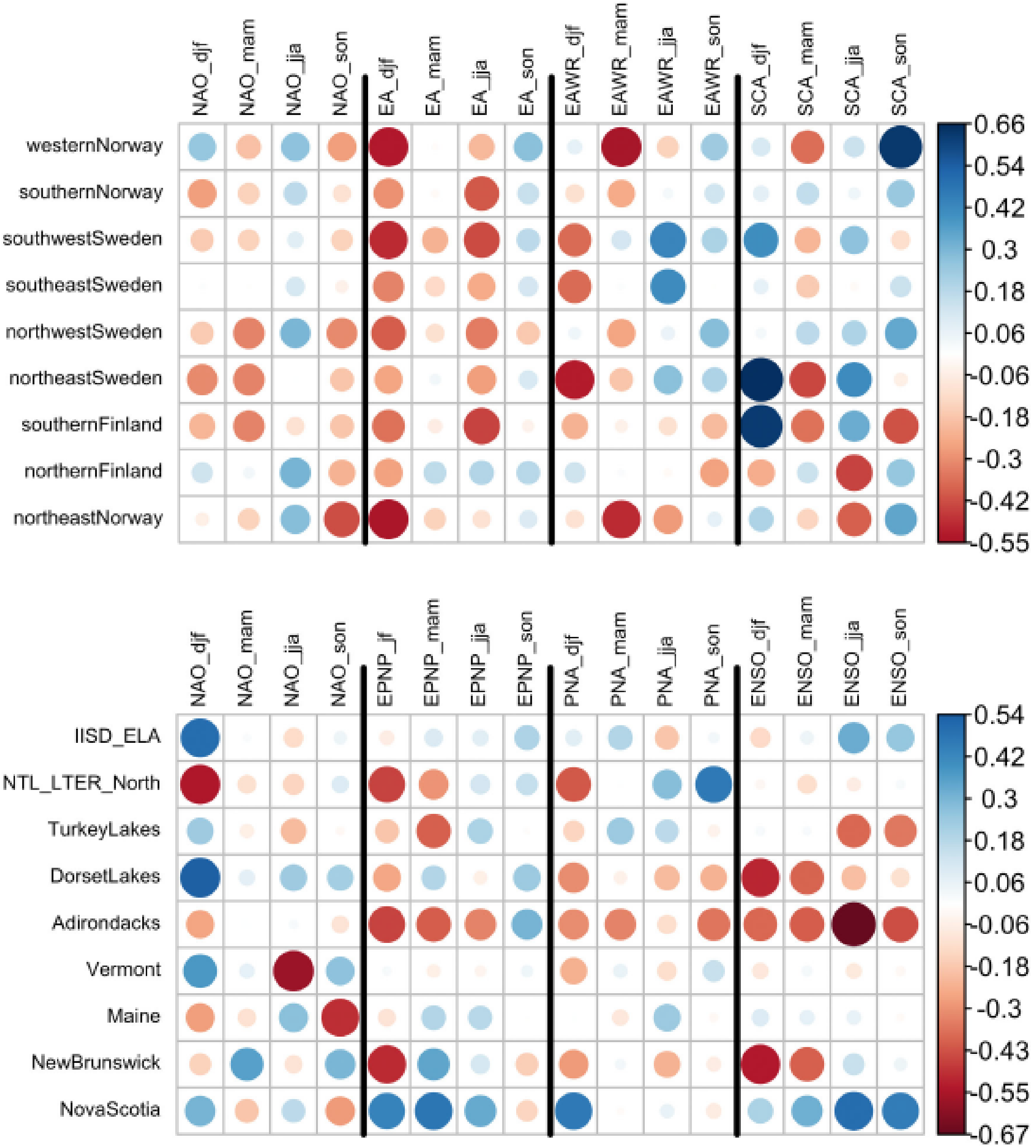

Fig. 4. Pearson correlations of median lake TP in regions in Fennoscandia (top panel) and North America (bottom panel) with atmospheric teleconnection indices likely to influence regional weather, separated by season. Size and color of circles reflect magnitude and direction of correlation. NAO = North Atlantic Oscillation, EA = East Atlantic pattern, EAWR = East Atlantic/Western Russia pattern, SCA = Scandinavia pattern, EPNP = East Pacific/ North Pacific pattern, PNA = Pacific/North American Pattern, ENSO = El Niño Southern Oscillation.

the EA and TP in Fennoscandia provide further support that warmer winters are associated with lower lake TP.

Catchment processes, in-lake processes, or a combination of both may explain the negative effect of winter temperature on lake TP. In catchments, differences in snowmelt timing may have a lasting effect on lake biogeochemistry during subsequent summers (Cortés et al. 2017; Hrycik et al. 2021). More frequent freeze–thaw cycles and changes in the structure of the snowpack (Pulliainen et al. 2020) during winter may result in a variety of biogeochemical changes in soils, including changes in the mobilization of redox-sensitive P pools (Björnerås et al. 2017; Rosenberg and Schroth 2017). Warmer winters may also result in extended terrestrial growing seasons, increasing retention of P and other nutrients by terrestrial plants (Finstad et al. 2016). In lakes, biotic and abiotic processes may remove P delivered during winter (Schroth

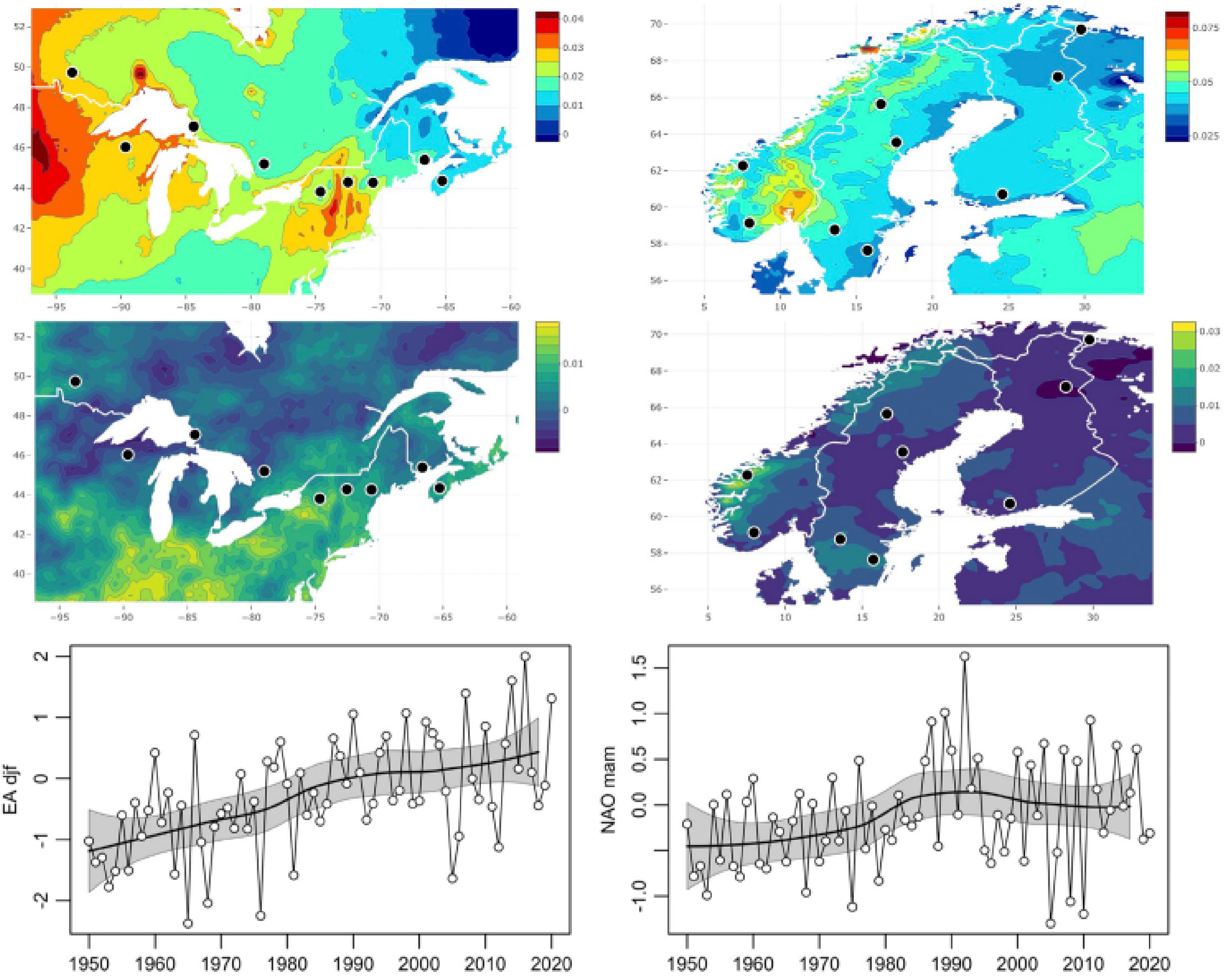

Fig. 5. Top panels: Maps depicting changes in winter (djf) temperature in Eastern North America and Fennoscandia. Colors represent the linear slope (in °C yr^{-1}) from 1951 to 2019. Points represent centroids of study regions. Middle panels: Maps depicting changes in summer (jja) precipitation in Eastern North America and Fennoscandia. Colors represent the linear slope (in mm yr^{-1}) from 1951 to 2019. Bottom panels: Long-term trends (1950–2020) in the most important seasonal teleconnection indices in Fennoscandia (East Atlantic pattern [EA]) djf (left0), and North Atlantic Oscillation (NAO) mam (right). Values of the indices are relative values standardized to the mean of the 1980–2010 reference period. The thick black line is a trend by loess regression, and the shaded area around the trend represents the 95% confidence interval around the mean.

et al. 2015; Joung et al. 2017), and increased light availability resulting from decreased snowpack on the frozen lake surface may increase under-ice primary production (Salmi and Salonen 2016), thereby reducing available nutrients later in the season.

Climatic factors that influence year-to-year variation in lake TP may also influence long-term trends. We selected short time series during which declines in lake TP were modest (Fig. S4). However, over longer time series, the substantial trends in climate variables that we identified as important suggest that if the correlations observed in this study represent causal relationships, changes in winter temperature may have contributed to previously observed longer-term declines in lake TP in some of our study regions (Crossman et al. 2016; Huser et al. 2018). If winters continue to warm, as is expected, it could predispose northern lakes to reduced TP concentrations, although other changes such as increased summer precipitation could offset this effect. Taken together, our findings suggest that climate has a strong influence on P cycling in northern landscapes.

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Acknowledgments

We gratefully acknowledge all monitoring agencies making data available for this project. We thank Kellie Merrell and Leslie Matthews at the Lakes and Ponds division of the Vermont Department of Environmental Conservation for preparation of those datasets for the analysis and for helpful feedback. PDFI was supported by the Swedish Research Council (dnr: 621-2014-5909), the Carl Trygger Foundation, and the Swiss Federal Institute of Aquatic Sciences and Technology (Eawag). IFC acknowledges support from NSERC DG RGPIN-2019-05265. DOH acknowledges the Norwegian Institute for Water Research for providing data for the national long-term monitoring sites, PK and JV acknowledge the Finnish Environment Institute and regional Centres for Economic Development, Transport and the Environment for long-term monitoring of lakes, and JAR acknowledges data collection supported by the Ontario Ministry of the Environment Conservation and Parks. Fisheries and Oceans Canada and the Province of Ontario supported the monitoring of lakes at the IISD-ELA. We thank Dr. Benjamin Kraemer and an anonymous reviewer for useful comments to improve this manuscript.

Submitted 22 July 2022
Revised 17 February 2023
Accepted 20 February 2023