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Recent Synchronous Declines in DIN:TP in Swedish Lakes

Peter D. F. Isles 1, Irena F. Creed 2, and Ann-Kristin Bergström 1

1 Department of Ecology and Environmental Science, Umeå University, Umeå, Sweden, 2 School of Environment and Sustainability, University of Saskatchewan, Saskatoon, Saskatchewan, Canada

Abstract Declining atmospheric nitrogen (N) deposition in northern Europe and parts of North America, coupled with ongoing changes in climate, has the potential to alter the nutrient limitation status of freshwater ecosystems. In this study we compared time series data of atmospheric N deposition, air temperature, and precipitation with corresponding estimates of dissolved inorganic nitrogen (DIN), total phosphorus (TP), DIN:TP, and total organic carbon from 78 headwater streams and 95 nutrient-poor lakes in Sweden from 1998 to 2013 to assess trends in, and potential drivers of, lake N:P ratios. We found that trends in nutrients were variable at the scale of individual lakes but were highly synchronous at the regional scale, suggesting underlying control by broad-scale environmental drivers mediated by site-specific characteristics. Widespread declines in lake DIN throughout Sweden were correlated with declines in atmospheric N deposition, particularly in northern areas. TP did not have strong directional trends, but interannual variability was synchronous at regional scales, implying that broad-scale climate drivers were affecting these trends. Overall, we observed a significant decline in DIN:TP throughout Sweden over the monitoring period. At the beginning of the study period, 32% of lakes were N limited and 45% colimited by N and P. Proportions increased to 63% of lakes N limited and 20% colimited by N and P at the end of the study period. These results suggest that N limitation is likely to become more widespread in subarctic and boreal areas of Europe in the future if recent trends continue.

Plain Language Summary This article examines the way in which changes in the amount of nitrogen from the atmosphere being delivered to lakes (as a result of fossil fuel combustion) are interacting with global climate change to affect nutrient availability in Swedish lakes. Nitrogen can act as fertilizer in lakes, supporting increased growth of algae and aquatic plants. The amount of nitrogen relative to other important elements such as phosphorus can help to determine which groups of plants and algae dominate lake ecosystems, as well as how much living biomass lakes can sustain. We find that declines in atmospheric deposition of nitrogen, which have resulted from the adoption of policies controlling emissions from fossil fuel combustion, have caused declines in nitrogen concentrations in lakes throughout Sweden. This has changed the balance of nitrogen and phosphorus, which may result in changes to the structure of lake biological communities. At the same time, variability in climate also has subtle but widespread affects on lake nutrient concentrations, suggesting that the availability of nutrients in lakes at northern latitudes is likely to change in the future as the climate warms.

1. Introduction

Human activities have dramatically changed global nitrogen (N) and phosphorus (P) cycles directly through the use of fertilizers and release of N through fossil fuel combustion (Vitousek, 1997) and indirectly through climatic changes affecting nutrient cycling (Jeppesen et al., 2009). These large-scale changes in nutrient cycles are important, because N and P are among the most important resources limiting primary production in both terrestrial and aquatic ecosystems (Elser et al., 2007; Harpole et al., 2011). In lakes specifically, the absolute concentrations of N and P, as well as the ratio of N:P, frequently control plankton community composition, total primary production, and total biomass (Brauer et al., 2012; Downing et al., 2001; Guildford & Hecky, 2000; Smith, 1983). If anthropogenic pressures impact the transport and cycling of N and P differently, lake N:P will change, resulting in corresponding shifts in nutrient limitation (Isles et al., 2017; Penuelas et al., 2013; Yan et al., 2016).

In arctic and boreal regions, which generally have low human population densities and contain the highest density of lakes (Verpoorter et al., 2014), N and P concentrations are likely to be most strongly influenced by diffuse anthropogenic drivers operating at broad spatial scales (Holtgrieve et al., 2011; Vitousek, 1997). These drivers include atmospheric N deposition (Bergström & Jansson, 2006), atmospheric P deposition (Wang...
et al., 2014), atmospheric sulfur deposition (Gerson et al., 2016), and global climate change (Williamson et al., 2009). Of these drivers, changes in N and P deposition may have the most obvious direct impacts on lake nutrient concentrations (Hessen, 2013; Sickman et al., 2003). Atmospheric P deposition remains poorly characterized, but may be increasing, and has been suggested as a potential driver of recent increases in lake total phosphorus (TP) in the United States (Stoddard et al., 2016; Wang et al., 2014). High and increasing atmospheric N deposition can raise N concentrations in lakes, resulting in changes in lake stoichiometry and increased P limitation (Elser et al., 2009; Hobbs et al., 2016; Weyhenmeyer et al., 2014). However, the responses of lakes to atmospheric N deposition are strongly mediated by catchment characteristics (Arvola et al., 2015; Hessen et al., 2009; Meunier et al., 2015), such as size, land cover, slope, and vegetation dynamics (Canham et al., 2012), as well as by lake characteristics such as morphometry and color (Deininger et al., 2017).

Atmospheric N deposition (where N is usually measured as dissolved inorganic nitrogen (DIN), NH₄⁺, and NO₃⁻) has declined recently in North America and Europe as a result of increased controls on NOₓ from fossil fuel combustion beginning in the 1970s and 1980s (Lajtha & Jones, 2013), although DIN deposition is increasing in other areas (Liu et al., 2013). Many lakes impacted by recent decreases in DIN deposition have also experienced recent increases in dissolved organic matter (DOM) inputs (also referred to as lake browning), which are generally attributed to recovery from sulfur deposition as well as climate warming (Monteith et al., 2007; Weyhenmeyer & Karlsson, 2009) (although a number of other factors contribute to DOM inputs, including increased production of catchment vegetation (i.e., catchment greening) (Finstad et al., 2016) and wetter climate (de Wit et al., 2016)). Increases in DOM inputs can directly affect N and P concentrations because both nutrients are complexed with DOM (Kissman et al., 2016; Kortelainen et al., 2006; Seekell et al., 2015). In addition to direct impacts, DOM inputs to lakes can impact N and P concentrations indirectly by inducing light limitation, stimulating bacterial production, and lowering oxygen concentrations (Karlsson et al., 2009; Zwart et al., 2016). Several studies have also suggested that changes in CN ratios resulting from increased dissolved organic carbon may affect denitrification rates (Taylor & Townsend, 2010; Weyhenmeyer & Jeppesen, 2009). Taken together, changes in mass inputs of DIN from deposition and DOM from browning may lead to substantial changes in lake N:P stoichiometry.

In addition to changes in DIN deposition and lake browning, climate change may also impact catchment inputs and processing of nutrients within lakes. Delivery rates of N, P, and C from catchments can be affected by both temperature and precipitation changes (Jeppesen et al., 2009, 2010; Weyhenmeyer & Karlsson, 2009). Changes in precipitation are likely to affect lake nutrient stoichiometry by changing both the timing and magnitude of nutrient inputs. In subarctic and boreal regions, nutrient loading to lakes is likely to occur earlier in the year as more nutrients are delivered in the winter months (Bouraoui et al., 2004). Warmer temperatures and longer growing seasons may lead to increased catchment greening and increased watershed retention of N (Hessen et al., 2009; Lucas et al., 2016). Catchment greening may also affect P loading; however, insufficient attention has been given to P dynamics in undisturbed boreal catchments in Scandinavia. Within lakes, warming may affect water temperature and the length of the stratified period (Read et al., 2014), potentially resulting in reduced oxygen, increased internal P loading, and increased denitrification (Myrsten et al., 2016; Vereaart et al., 2011). All of these interacting DIN deposition and climate-driven changes are likely to affect lake nutrient stoichiometry.

Understanding the effects of large-scale environmental drivers is difficult because site-specific features related to catchment properties or lake morphology may mask the signal of these drivers at the scale of individual lakes (Read et al., 2015). Because many sources of variation affect N and P concentrations in individual lakes, comparable data sets from multiple lakes are needed to identify long-term impacts of diffuse environmental drivers. Sweden, which straddles boreal and subarctic biomes, has large gradients of DIN deposition, lake color, temperature, and precipitation, making it well suited for studying the impact of large-scale climatic and depositional changes on lake nutrient stoichiometry (Bergström et al., 2005; Seekell et al., 2015). Sweden also has an extensive water-quality monitoring program, with data from hundreds of lakes and headwater streams analyzed using consistent methods. Moreover, most Swedish lakes are nutrient poor, making them sensitive to changes in nutrient concentrations (Karlsson et al., 2009), and phytoplankton are frequently found to be N limited in both boreal and subarctic areas in Sweden (Bergström et al., 2015, 2008; Elser et al., 2009). Climate is also warming faster in Scandinavia than in other
parts of Europe (Vautard et al., 2014). As a result of all of these factors, Swedish lakes may be particularly sen-
sitive to changes in atmospheric N deposition as well as climate (Elser et al., 2009).

In this study, we compared both spatial and temporal trends in DIN, TP, DIN:TP, and total organic carbon
(TOC) in 78 headwater streams and 95 nutrient-poor Swedish lakes with corresponding estimates of DIN
deposition, air temperature, and precipitation from 1998 to 2013. While several studies have observed declin-
ing DIN deposition in southern Sweden (Lucas et al., 2016) and impacts of changes in DIN deposition on lake
DIN concentrations (Elser et al., 2009; Weyhenmeyer et al., 2007; Weyhenmeyer & Jeppesen, 2009), to our
knowledge none have addressed these changes in the context of simultaneous changes in lake P over time,
or the consequences of these changes for N:P and lake nutrient limitation. We hypothesized that (1) changes
in DIN deposition would be correlated with changes in lake DIN; (2) changes in TP would be positively corre-
lated with changes in lake TOC as a result of cotransport of phosphorus with DOM; and (3) because of these
two processes, lake DIN:TP would decline in areas with browning and declining DIN deposition.

2. Methods

2.1. Meteorological Data

Estimates of daily air temperature and precipitation were downloaded from the interpolated Luftweb data
product (Swedish Meteorological and Hydrological Institute; http://luftweb.smhi.se) for grid cells correspond-
ing to the lake monitoring sites. Mean annual temperature (MAT; °C) and mean annual precipitation (MAP;
mm d\(^{-1}\)) were calculated for each lake. Because air temperature and precipitation were being compared
to July–September averages of lake data, and to capture possible effects on antecedent winter conditions
on lake biogeochemistry, we used water year rather than calendar year in our calculation of MAT and MAP
(so, e.g., water year 2000 is 1 October 1999 to 31 September 2000).

2.2. Atmospheric DIN Deposition Data

Gridded, interpolated estimates of both NH\(_4\)\(^+\) and NO\(_x\) total (wet + dry) deposition were downloaded from
the Swedish Meteorological and Hydrological Institute (http://www.smhi.se/klimatdata/miljo/atmosfarskemi)
as shapefiles for each calendar year from 1998 (the first year data were available) to 2013. Data were extracted
for grid cells corresponding to the monitored lake and stream sites. DIN deposition (DIN\(_{\text{dep}}\)) was calculated as
the sum of NH\(_4\)\(^+\) and NO\(_3\)\(^-\) deposition. Lakes were divided into four regions corresponding to quantiles of
DIN deposition (“low,” 0–25th percentiles; “medium,” 25–50th percentiles; “high,” 50–75th percentiles; and
“highest,” 75–100th percentiles). DIN deposition thresholds corresponding to these quantiles were used to
assign the lake and stream sites to corresponding DIN deposition regions.

2.3. Lake and Stream Data

Summary information about catchment characteristics and lake size is provided in Table 1. Data on nitrate-
nitrite N (NO\(_x\)), ammonium (NH\(_4\)\(^+\)), TP, and TOC from 1998 to 2013 were downloaded from the trend lakes,
reference lakes, trend streams, and reference streams data sets collected by the Swedish long-term monitor-
ing program (http://miljodata.slu.se/mvm/Default.aspx). Lakes were selected that had low proportions of
agricultural land (1 lake had 17%; all others were below 9%) and developed land (consisting of urban devel-
opment, roads, mining, and recreational parks; maximum 4.5%, most below 2%) in their catchments and that
didn’t have data for the entire study period. Only epilimnetic data from lakes were used. Lakes with average
TP > 25 \(\mu\)g L\(^{-1}\) were excluded from the analysis to minimize the effects of anthropogenic eutrophication
on the results (cf. Bergström et al., 2005).

For lakes, data were averaged from July to September (hereafter referred to as summer). This time window
excludes a substantial fraction of the growing season in southern Sweden; however, many northern lakes
do not become ice free until May or June, making it difficult to compare spring data across regions.
Furthermore, biogeochemical data during the spring snowmelt period are highly variable at short time scales
and sensitive to specific melt events (Pellerin et al., 2011; Sebestyen et al., 2008), so individual samples are
unlikely to represent true seasonal averages (particularly in small lakes with short residence times), and the
high seasonal variance may mask long-term trends.

For streams, data were averaged from May to September. May and June data were included in these averages
because most nutrient loads to lakes are delivered during the spring snowmelt pulse (restricting our analysis
Table 1
Mean Catchment Characteristics for Lakes in the N Deposition Regions (See Figure 1 for Region Definitions)

<table>
<thead>
<tr>
<th>Region</th>
<th>% forest</th>
<th>% wetland</th>
<th>% agriculture</th>
<th>Lake surface area (km²)</th>
<th>Catchment area (km²)</th>
<th>Catchment/lake area</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low</td>
<td>45.6 (22.7)</td>
<td>10.1 (9.8)</td>
<td>0.4 (0.6)</td>
<td>2.6 (4.0)</td>
<td>166.6 (502.3)</td>
<td>20.4</td>
</tr>
<tr>
<td>Medium</td>
<td>64.0 (8.8)</td>
<td>3.1 (4)</td>
<td>1.1 (1.9)</td>
<td>0.8 (0.6)</td>
<td>15.1 (22.2)</td>
<td>11.3</td>
</tr>
<tr>
<td>High</td>
<td>68.4 (7.2)</td>
<td>1.5 (2.3)</td>
<td>1.9 (3)</td>
<td>1.4 (3.0)</td>
<td>8.8 (14.4)</td>
<td>7.3</td>
</tr>
<tr>
<td>Highest</td>
<td>71.9 (10)</td>
<td>2.2 (3.6)</td>
<td>3.2 (4.1)</td>
<td>0.8 (1.2)</td>
<td>15.4 (38.2)</td>
<td>11.5</td>
</tr>
</tbody>
</table>

Note: Values are expressed as arithmetic mean (st. dev) for all variables except for catchment/lake area ratio, which is expressed as the geometric mean.

of stream data to July–September low-flow months would only reflect a small proportion of annual nutrient loading to most Swedish lakes, and spring nutrient loads have been found to be particularly important for the development of summer phytoplankton populations (e.g., Kohler & Hoeg, 2000; Stumpf et al., 2012). Most Swedish lakes have residence times <100 days (Lindström et al., 2006), so input water from May to September likely represent a substantial fraction of the nutrients available to summer production. DINlake, TPlake, TOClake, and log10(DIN:TP)lake refer to annual summer averages (July–September); DINstream, TPstream, TOCstream, and log10(DIN:TP)stream refer to annual May–September averages for all subsequent analyses of spatial gradients, trends, and synchrony unless otherwise stated. For completeness, z scores of April–June averages of chemical variables in both lakes and streams are also presented in supporting information Figure S1.

N to P ratios were represented as molar ratios of DIN:TP. DIN:TP has been shown to be a robust predictor of phytoplankton nutrient limitation in Swedish lakes (Bergström, 2010) and in other areas with high DOM (Axler et al., 1994). DIN in lakes and streams was calculated as the sum of NO3 and NH4+. To avoid averaging errors resulting from the nonnormal distribution of ratio data, DIN:TP was calculated as log10(DIN:TP) of daily observations. The use of log transformations is generally appropriate when calculating statistics with ratio data (Keene, 1995) and is necessary when averaging ratio data to accurately represent nutrient limitation status (Hillebrand et al., 2013; Keene, 1995).

2.4. Data Analysis and Statistical Methods

Total changes in lake nutrients (ΔTPlake, ΔDINlake, ΔTOClake, and Δlog10(DIN:TP)lake) at individual sites were assessed by calculating the slope of the Thiel-Sen regression line using the R package rkt (Marchetto, 2017) and multiplying by the length of the study period. In addition, to quantify the changes in lake nutrient limitation status over the monitoring period and percent changes in lake nutrients, the difference between the average of the first 5 years of the study period (1998–2002) and the average of the last 5 years (2009–2013) was calculated for DINlake, TPlake, TOClake, and log10(DIN:TP)lake. Temporal changes in each variable were used to address hypothesis 3 (DINlake would decline in areas with increasing TOClake and decreasing DINdep).

To test hypothesis 2 (changes in TPlake will be correlated with changes in TOClake) at both spatial and temporal scales, correlations between TPlake (and DINlake) and TOClake were first calculated across the entire data set (including all sites and years). To investigate temporal correlations while controlling for spatial gradients, correlations were also calculated between TPlake and TOClake within each individual lake and between DINlake and TOClake within each individual lake. The averages of the individual lake correlations were then calculated. Average correlations greater than 1.96 standard errors from 0 were considered statistically significant.

Synchrony (S) is a measure of the degree to which different sites show the same patterns of year-to-year variability. To quantify S in temporal trends in individual variables, a full correlation matrix among lakes was calculated for each of the chemical variables (TPlake, DINlake, TOClake, and log10(DIN:TP)lake). For each variable, S was calculated as the average of the correlation matrix. S can range from slightly negative (~−0.1) to 1.0 in the case of perfectly correlated time series among all lakes (Vogt et al., 2011). High values of S suggest that lakes are responding to similar drivers. All correlations were calculated using Pearson’s product-moment correlation. To calculate the significance of S values for each variable, a permutation test was used following Vogt et al. (2011). The observed average S was compared to a distribution of r values derived from 1,000 randomizations of the original time series, and values below the 2.5th or above the 97.5th percentiles were considered significant. For all variables, S was significant when S > 0.04.
To compare relative trends over time across sites with different nutrient concentrations and stoichiometry at the regional scale, nutrient concentrations and log ratios were standardized to z scores for each variable within each lake and stream. For each nutrient N in year i, the z score was calculated as \((N_i - \text{mean}(N))/\text{st. dev}(N)\). Standardized values were then averaged across lakes and streams for each year within each N deposition region (defined in section 2.1). Regional averaging was performed to allow comparisons between stream and lake data (because sampled stream sites were not paired with sampled lake sites) and to filter out lake-specific differences to detect underlying regional trends. Regional average z scores were also used to test hypothesis 1 (DIN\text{lake} will be positively correlated with DIN\text{dep}). To determine temporal trends in each variable, the regional Kendall test was used on regional averages by year, using region as a blocking variable. This nonparametric regression was used to minimize the effects of outliers on the results. Thiel-Sen slopes were also calculated to estimate the rates of increase or decline in nutrients. Kendall tests and Thiel-Sen slopes were calculated using the R package rkt (Marchetto, 2017).

2.5. Estimating the Importance of Direct Deposition

To estimate the contribution of DIN\text{dep} to a typical lake (i.e., direct DIN input via DIN deposition onto the lake surface) relative to surface water inputs, a simple model was developed based on median DIN deposition (DIN\text{dep}, mg m\(^{-2}\) lake yr\(^{-1}\)), area-normalized lake volume based on average lake depth (expressed as \(z, m^3\ m_{\text{lake}}^2,\) the volume of a column of water with surface area of 1 m\(^2\) and depth \(z\)), median stream DIN concentrations (DIN\text{stream}, mg m\(^{-3}\)), and published estimates of lake turnover times in Sweden (T\text{lake} yr\(^{-1}\)) (Lindström et al., 2006). First, surface water input volumes \(V_{\text{stream}} (m^3\ m_{\text{lake}}^2\ yr^{-1})\) were calculated as the product of lake turnover time and lake depth (equation (1)). Stream load \((\text{DIN}_{\text{streamLoad}}, mg \ m_{\text{lake}}^2\ yr^{-1})\) was then calculated as the product of \(V_{\text{stream}}\) and [DIN\text{stream}] (equation (2)). Percent DIN inputs from direct DIN deposition for a hypothetical lake (%Deposition) were then calculated from DIN deposition rates and estimated surface water fluxes (equation (3)). %Deposition was calculated across a gradient of lake sizes and depths using median [DIN\text{stream}] and median DIN deposition from this data set. A graphical explanation of the model is provided in supporting information Figure S2.

\[
V_{\text{stream}} = T_{\text{lake}} \times z 
\]

\[
\text{DIN}_{\text{streamLoad}} = V_{\text{stream}} \times [\text{DIN}_{\text{stream}}] 
\]

\[
\%\text{Deposition} = \frac{\text{DIN}_{\text{dep}}}{(\text{DIN}_{\text{streamLoad}} + \text{DIN}_{\text{dep}})} \times 100 
\]

A similar model was constructed to estimate the importance of direct total atmospheric N (organic + inorganic) deposition relative to total N (TN) inputs using the median stream concentration of TN from 2007 to 2016 (when data were available). Assuming that 15% of total atmospheric N deposition is organic (based on the low end of estimates for Europe reported in Cornell et al., 2003), TN\text{dep} was calculated as DIN\text{dep}/0.85. Both DIN and TN models ignored contributions from groundwater, N fixation, and lake sediments.

3. Results

DIN\text{dep} had a strong spatial gradient, with high deposition in the southeast, moderate deposition in central Sweden and along the Baltic coast, and low deposition in the north (Figure 1). Average DIN\text{dep} decreased significantly over the study period in each defined DIN deposition region (p values of regressions of deposition \(\times\) year were 0.0019, 0.0006, 0.0004, and 0.00001 in the low, medium, high, and highest DIN deposition areas, respectively). The average rate of decline ranged from \(-10.74\) mg N m\(^{-2}\) yr\(^{-1}\) in the low deposition region to \(-32\) mg N m\(^{-2}\) yr\(^{-1}\) in the highest deposition region; however, proportional declines (relative to the mean of the first 5 years) were greatest in the low region (43%), followed by medium (38%), highest (37%), and high (30%).

Spatial patterns were different for ΔDIN\text{lake}, ΔTP\text{lake} and ΔTOC\text{lake} (Figure 2). DIN\text{lake} declined in most sites over the monitoring period (12 increasing, 7 no trend, and 76 decreasing; Figure 2). The largest absolute declines were in the southeast, where DIN deposition was highest and where DIN\text{lake} concentrations were also highest. More lakes had declining TP\text{lake} than increasing TP\text{lake} (28 increasing, 28 no trend, and 39 decreasing), but there was no clear spatial pattern across Sweden distinguishing areas with increases or decreases. Most lakes had inclining TOC\text{lake} (83 increasing, 3 no trend, and 9 decreasing), but there was a strong spatial gradient, as reported in previous studies (Weyhenmeyer & Jeppesen, 2009). TOC\text{lake} increased substantially over the
study period in the south and southeast in areas where DIN deposition was highest, but lakes in the northeast tended to have no change or declining TOClake (Figure 2). log10(DIN:TP)lake declined in most lakes (22 increasing, 1 no trend, and 72 decreasing), resulting in a shift in the distribution of lakes toward greater N limitation. In the first 5 years of the study period, 32% of lakes were primarily N limited and 45% were colimited by N and P during the summer using thresholds from Bergström (2010) (i.e., N limited below 3.3; NP limited between 3.3 and 7.5; and P limited above 7.5); however, in the last 5 years, the percentage increased to 63% of lakes primarily N limited and 20% colimited by N and P during the summer (Figure 3). The degree of synchrony among lakes was significant for all variables (DINlake, TPlake, TOClake, and log10DIN:TPlake; Figure 4), but values of S differed among chemical variables and were relatively low compared to other studies of synchrony in lake time series (Rusak et al., 1999; Vogt et al., 2011). DINlake had the lowest synchrony (S = 0.12), and 40% of pairwise correlations were negative. Synchrony in TPlake was somewhat higher (S = 0.20). Correlations of TPlake among lakes were more likely to be positive (71%) than negative (29%). TOClake had a similar degree of synchrony to TPlake (S = 0.23), and 72% of lakes had positive correlations. log10DIN:TPlake had low synchrony (S = 0.08) resulting from the low synchrony in DINlake. Although annual log10TPlake and log10TOClake across the entire data set (including all sites and all years) were significantly correlated (r = 0.55, p < 0.0001; Figure 5a), the average of the correlations of TOClake and TPlake within individual lakes was significantly different from 0 (average r = 0.068, p = 0.02; Figure 5c), but still low, suggesting that while TOClake and TPlake covary spatially, they were not responding strongly to the same drivers over time. Furthermore, long-term changes in TPlake and TOClake (ΔTPlake and ΔTOClake) were not significantly correlated (r = 0.039, p = 0.71; Figure 2). Annual log10DINlake and log10TOClake were not correlated across the entire lake data set (r = 0.04, p = 0.17; Figure 5b) nor were DINlake and TOClake correlated within individual lakes (average r = −0.041, p = 0.20; Figure 5d). The total changes over time (ΔDINlake and ΔTOClake) across all lakes were also not significantly correlated (r = −0.20, p = 0.055; Figure 2). Although synchrony among individual lakes was relatively low for all chemical variables (Figure 4), averages of standardized variables (i.e., z scores) within each N-deposition region behaved very similarly on a year-to-year basis (Figure 6). All pairwise correlations between each region were significant for DINlake and TPlake (Table 2). Correlations were almost always stronger for regional averages between adjacent regions than distant regions (e.g., low was most strongly correlated with medium, and highest was most strongly correlated with high).
Figure 2. Changes in $\Delta$TP$_{lake}$, $\Delta$DIN$_{lake}$, TOC$_{lake}$, and $\log_{10}$(DIN:TP)$_{lake}$ over the monitoring period based on the slope of the Thiel-Sen regression line for each lake. Areas of the circles are proportional to changes in concentration. Increases are shown in blue, decreases in red. Sites with significant ($p < 0.05$) Sen’s slopes are outlined with dark black lines. Sites with no trend are marked with $\times$. 
correlated with high); this was particularly true with $\text{TOC}_{\text{lake}}$, where all correlations between adjacent regions were highly significant, but correlations between distant regions were nonsignificant (but still positive; Table 2). $\text{DIN}_{\text{lake}}$ in all regions initially increased until 2003–2005, then decreased consistently for the remainder of the study period (Figure 6). Although absolute declines in $\text{DIN}_{\text{lake}}$ were greatest in the southeast where $\text{DIN}$ deposition was highest, proportional decreases in $\text{DIN}_{\text{lake}}$ relative to the mean of the first 5 years were greatest in the low deposition region (35.6%), followed by highest (30.4%), medium (24.4%), and high (19.8%). These declines were similar to the proportional declines in $\text{DIN}_{\text{dep}}$ in each region (low 43%, highest 37%, medium 38%, and high 30%). The correlation between $\text{DIN}_{\text{lake}}$ and $\text{DIN}_{\text{dep}}$ was strongest in the northern low deposition region ($r = 0.61$, $p = 0.013$) and positive but not significant in the medium ($r = 0.39$, $p = 0.133$), high ($r = 0.40$, $p = 0.120$), and highest ($r = 0.44$, $p = 0.088$) deposition regions.

There was a significant decline in mean $\text{TP}_{\text{lake}}$ $z$ scores across all DIN deposition regions using the Kendall test with region as a blocking variable ($p = 0.041$). Although long-term temporal trends in $\text{TP}_{\text{lake}}$ were weaker than trends in $\text{DIN}_{\text{lake}}$, there was considerable interannual variability, and average $z$ scores in different regions had very similar patterns of variability, resulting in high correlations between regions (Table 2). The most striking example of this is 2007; in this year, $\text{TP}_{\text{lake}}$ was extremely low in all regions (Figure 6). $\text{TOC}_{\text{lake}}$ generally declined in all regions until 2003–2004, then increased through the remainder of the study period.

In contrast to $\text{DIN}_{\text{lake}}$, $\text{DIN}_{\text{stream}}$ did not decline significantly over the monitoring period (Figure 6). Generally, $\text{DIN}$ behaved similarly in streams and lakes, increasing in the first several years of the monitoring period and declining after 2005–2006, but the trends diverged in the last several years of the study period (Figure 6). In the highest deposition region, $\text{DIN}_{\text{stream}}$ behaved differently from other regions or from lakes. $\text{TP}_{\text{stream}}$ behaved similarly to $\text{TP}_{\text{lake}}$, with the highest TP in 2005 in most regions, and the lowest in 2007. $\text{DIN:TP}$
had a similar temporal pattern in streams as in lakes in the low, medium, and high deposition regions (rising initially until 2003–2005, then falling) but did not decline as steeply at the end of the study period in the streams. In the highest deposition region the trend in DIN:TPstream was very different from the other regions, and DIN:TPstream was highly variable and increasing. TOC appeared to follow similar patterns in streams and lakes, with low or declining concentrations in the first few years followed by increasing concentrations for most of the study period. Average $z$ scores of DIN, TP, and DIN:TP were highly significantly correlated between streams and lakes on an annual basis in the low deposition region (Figure 6 and Table 3). However, average annual $z$ scores of DIN and TP were generally only weakly correlated between lakes and streams in other regions. In the highest deposition region, average annual $z$ scores of DIN were uncorrelated between streams and lakes ($r = 0.127$). For TOC, average annual $z$ scores were most highly correlated between lakes and streams in the medium and highest deposition regions (cf. Table 3). Trends in spring (April–June) data were similar to summer trends for all stream variables and for TP$_{lake}$ and TOC$_{lake}$, but DIN$_{lake}$ and DIN:TP$_{lake}$ did not decline at the end of the monitoring period during the spring as they did during the summer (supporting information Figure S1). However, DIN$_{lake}$ concentrations were much higher and more variable during the spring, and this variability may have obscured long-term trends. TP$_{lake}$ was very low in 2007 in the spring as well as in the summer data.

The model developed to estimate proportional contribution of direct DIN deposition to the lake surface relative to catchment DIN inputs suggests that for a typical lake in this study (median depth 3.3 m, average DIN deposition 686 mg N m$^{-2}$ yr$^{-1}$, median stream nutrient concentration 25 mg m$^{-3}$, residence time 50–100 days; Lindström et al., 2006), direct DIN deposition likely accounts for 50–70% of annual DIN inputs.
and between 10 and 20% of TN inputs (excluding N fixation and sediment loading). The importance of direct DIN deposition increases with lake residence time and is greater for shallow than for deep lakes (Figure 7).

MAT ranged from 0.86°C in the northern low deposition region, to 7.12°C in the southern highest deposition region. MAP did not have such a strong regional gradient and ranged from 2.1 mm d\(^{-1}\) in the medium deposition region to 2.7 mm d\(^{-1}\) in the highest deposition region. Although there is a strong air temperature gradient from southern to northern Sweden, MAT was highly synchronous throughout Sweden, and warmer years in one area were warm everywhere (\(S = 0.90\); Figure 8). MAP was much more variable than MAT.

Figure 6. Left column: Regional summer means (July–September) of standardized total phosphorus (TP), dissolved inorganic nitrogen (DIN), total organic carbon (TOC), and log DIN:TP in lakes (grouped by N deposition). Z scores are first calculated from summer averages within each lake and stream across the monitoring period, then averaged for each year across lakes in each region. Right column: Regional spring-summer averages (May–September) for streams in corresponding N-deposition regions. Circles = low deposition, squares = medium, triangles = high, and diamonds = highest.
Declining DIN:TPlake was observed throughout Sweden, indicating that N limitation in Sweden is becoming more widespread and severe (Figures 2, 3, and 6). This finding supports previous research suggesting that DIN deposition may alter lake N:P stoichiometry (Elser et al., 2009; Hessen, 2013). However, whereas previous studies using space-for-time approaches highlighted the role of DIN deposition in southern Sweden (Bergström et al., 2005; Elser et al., 2009), using time series data, we found the strongest effect of declining DIN deposition in northern Sweden where deposition rates have been historically relatively low. In addition to overall declines in DIN:TPlake, we also found a surprisingly high level of synchrony in year-to-year variability in all of the chemical variables when considered at the regional scale (Figure 6 and Table 2). This synchrony suggests that lake stoichiometry is being partially controlled by climatic and environmental drivers operating at large spatial scales.

There was considerable variability in summer concentrations of chemical variables at the scale of individual lakes (S < 0.3 for all chemical variables; Figure 4). Variability observed at the scale of individual lakes may be the result of either catchment or lake properties. Catchment variability was likely important in filtering (cf. Hessen et al., 2009) the effects of changes to mass inputs such as DINdep (which is known to be retained efficiently by many terrestrial ecosystems) (Lucas et al., 2016) and runoff (which is highly dependent on catchment size and composition) (Blenckner, 2005; Leavitt et al., 2009; Vogt et al., 2011). Changes in energy inputs, such as increasing air temperatures, are expected to have more synchronous impacts on lakes (Read et al., 2014); however, the impacts of energy fluxes on chemical variables are mediated by individual lake morphometry and ecological status (Arnott et al., 2003). Hence, the high variability of DINlake, TPlake, and TOClake at the scale of individual lakes in this study was likely the result of heterogeneity in both catchment and lake properties (Figure 4 and Table 1). Despite the relative lack of synchrony at the individual lake scale, DINlake, TPlake, TOClake, and DIN:TPlake all behaved synchronously at the scale of the four DIN deposition regions (Figure 6 and Table 2). The coherent behavior of nutrients at the regional scale suggests that although there are many lake- and catchment-specific differences, there seems to be an underlying signal from broad-scale environmental drivers such as climate or DIN deposition that lakes are responding to at the landscape scale. Geographic patterns of air temperature, precipitation, and acidic deposition further follow a similar north-south and east-west gradient to DIN deposition (Figure 1) (Weyhenmeyer, 2008). The fact that for all variables trends were almost always more highly correlated with neighboring regions than with distant regions (Table 2) further reinforces the conclusion that broad-scale drivers were responsible for the observed trends.

Table 2
Pairwise Correlations Between DIN Deposition Regions of Average z Scores for Summer DINlake, TPlake, and TOClake

<table>
<thead>
<tr>
<th></th>
<th>Medium</th>
<th>High</th>
<th>Highest</th>
</tr>
</thead>
<tbody>
<tr>
<td>DINlake</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Low</td>
<td>0.717***</td>
<td>0.682**</td>
<td>0.558*</td>
</tr>
<tr>
<td>Medium</td>
<td>0.593*</td>
<td>0.636**</td>
<td></td>
</tr>
<tr>
<td>High</td>
<td>0.704**</td>
<td></td>
<td></td>
</tr>
<tr>
<td>TPlake</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Low</td>
<td>0.786***</td>
<td>0.673**</td>
<td>0.530*</td>
</tr>
<tr>
<td>Medium</td>
<td>0.677**</td>
<td>0.721**</td>
<td></td>
</tr>
<tr>
<td>High</td>
<td></td>
<td>0.771***</td>
<td></td>
</tr>
<tr>
<td>TOClake</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Low</td>
<td>0.752***</td>
<td>0.559*</td>
<td>0.171</td>
</tr>
<tr>
<td>Medium</td>
<td>0.759***</td>
<td>0.463</td>
<td></td>
</tr>
<tr>
<td>High</td>
<td></td>
<td>0.690**</td>
<td></td>
</tr>
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</table>

*p < 0.05. **p < 0.01. ***p < 0.001.
In DIN\textsubscript{lake} and DIN\textsubscript{dep}, were similar throughout Sweden, annual DIN\textsubscript{dep} was only significantly correlated with DIN\textsubscript{lake} in the low deposition region.

The lack of significant correlations of DIN\textsubscript{dep} with DIN\textsubscript{lake} in medium, high, and highest deposition regions at the annual scale is likely the result of different catchment characteristics, which can strongly influence N loading (Crowley et al., 2012; de Wit et al., 2008; Hu et al., 2014). Boreal forests, which are usually N limited, retain DIN efficiently, although some added DIN may be subsequently released as dissolved organic nitrogen (DON) later (Lucas et al., 2016; Sponseller et al., 2017); this may mask the annual signal of DIN deposition. Many lakes in the low deposition region were in mountainous areas or in the sub-arctic, so surrounding catchments contained less forest cover than in other regions (Table 1); this may help to explain the stronger response of the northern lakes to changes in DIN deposition. The signal of reduced deposition in the southern regions may also be obscured by increased DON loading in areas where browning has occurred. In boreal catchments in Scandinavia, 74–95% of TN may be associated with DON (Kortelainen et al., 2006; Sponseller et al., 2014); even a relatively small fraction of this organic N is mineralized to DIN, this may be sufficient to mask the signal from DIN deposition. Increasing DIC\textsubscript{lake} may also promote denitrification in lakes with low C:N\textsubscript{lake} ratios (Weyhenmeyer & Jeppesen, 2009); however, the spatial patterns of changes of DIC\textsubscript{lake} and DIN\textsubscript{lake} are very different (Figures 2 and 6), particularly in the north where the largest DIN\textsubscript{lake} declines occurred but where TOC\textsubscript{lake} was unchanged or decreasing. Temporal patterns were also different, and we saw no significant correlation of DIN\textsubscript{lake} and DIC\textsubscript{lake} within individual lakes (Figure 5). Taken together, the similar long-term trajectories and proportional declines of DIN\textsubscript{dep} and DIN\textsubscript{lake} support hypothesis 1 (declining DIN\textsubscript{dep} was a contributor to declining DIN\textsubscript{lake} although the effects of DIN\textsubscript{dep} were spatially variable and likely modified by catchment processes and lake morphometry for individual lake sites.

DIN\textsubscript{stream} followed similar temporal patterns to DIN\textsubscript{lake} in some regions (Figure 6 and Table 3) but generally declined less than DIN\textsubscript{lake} over the monitoring period (although declining DIN has been observed in northern Swedish streams in previous studies over longer time scales; Lucas et al., 2016). As with DIN\textsubscript{dep}, DIN\textsubscript{stream} was...
most highly correlated with DIN\textsubscript{lake} in the low deposition area ($r = 0.80$), suggesting that there is a closer coupling between DIN\textsubscript{dep}, DIN\textsubscript{stream}, and DIN\textsubscript{lake} in northern than southern areas of Sweden. By contrast, in the highest deposition region, DIN\textsubscript{stream} and DIN\textsubscript{lake} were completely uncorrelated (Table 2). Where DIN\textsubscript{stream} did decline, these declines were less dramatic than the declines in DIN\textsubscript{lake} (Figure 6). Several factors may help to explain greater declines in DIN\textsubscript{lake} relative to DIN\textsubscript{stream}. Lakes may respond to changes in DIN deposition more directly than streams because higher fractions of the DIN loads are delivered to lakes by direct deposition to the lake surface. Our model (Figure 7) suggests that for a typical Swedish lake experiencing average DIN deposition and stream nutrient concentrations and a residence time of 50–100 days, direct DIN deposition may account for as much as 53–69% of annual DIN inputs. Direct DIN deposition accounts for a substantially lower fraction of TN inputs (9–16%, similar to the proportion observed in Canham et al., 2012), but much of the organic N pool is likely unavailable (Stepanauskas et al., 2000). Even assuming that 25% of stream DON may be bioavailable (Stepanauskas et al., 2000), DIN deposition would still account for 28–44% of bioavailable N inputs. In contrast, essentially all nutrients delivered to streams must be filtered through the catchment.

In-lake processes may also contribute to the larger declines in DIN\textsubscript{lake} relative to DIN\textsubscript{stream}. Previous studies have found that warming increases denitrification rates in Swedish lakes directly (Myrstener et al., 2016), which combined with browning may stimulate denitrification and further reduce DIN\textsubscript{lake} (Weyhenmeyer & Jeppesen, 2009). Increased production may also reduce DIN\textsubscript{lake} as a result of phytoplankton and bacterial uptake. Hence, while some of the interannual variability in DIN\textsubscript{lake} can be attributed to stream inputs, it is likely that direct DIN deposition and in-lake processes further modified DIN\textsubscript{lake} Concentrations. The relatively greater declines in DIN\textsubscript{lake} during summer than during spring suggest that in-lake removal processes during the growing season may have also contributed to the observed declines.

While the declines in DIN\textsubscript{lake} can be at least partly attributed to declining DIN deposition, the drivers of interannual variability in TP\textsubscript{lake} were less clear. Surprisingly, ΔTP\textsubscript{lake} was not correlated with ΔTOC\textsubscript{lake} ($p = 0.79$; Figure 2). This result did not support hypothesis 2 (changes in TP\textsubscript{lake} would be correlated with changes in TOC\textsubscript{lake}). Although TP\textsubscript{lake} and TOC\textsubscript{lake} co-variety spatially (Figure 5a), when examined within individual lakes temporal trends in TP\textsubscript{lake} and TOC\textsubscript{lake} were not strongly correlated (Figure 5c) suggesting that lake browning is not a dominant driver of changes in TP\textsubscript{lake} in Swedish lakes. It is surprising that TP\textsubscript{lake} and TOC\textsubscript{lake} dynamics appear to be uncoupled, given that a previous study found that TOC\textsubscript{lake} export explains 61–73% of the variance in TP\textsubscript{lake} (Kortelainen et al., 2006), and other studies have suggested a link between changes in TP\textsubscript{lake} and TOC\textsubscript{lake} in Sweden (Huser et al., 2018). It is likely that changing climatic conditions have affected hydrological properties of catchments and as a result the mobility of terrestrial P, which is closely linked to soil moisture (Macrae et al., 2005). Enhanced forest growth and catchment greening as a result of warming may reduce P export by increasing forest demands for P as well as for N, which has been demonstrated previously (Finstad et al., 2016; Lucas et al., 2016). It is also possible that declining DIN in N-limited lakes may reduce phytoplankton biomass (Deininger et al., 2017), resulting in decreased particulate P and TP. Changes in atmospheric P deposition may also be important, as has been suggested in the United States (Stoddard et al., 2016), although a recent study identified no significant relationship between modeled atmospheric P deposition and lake P concentrations in Swedish lakes (Huser et al., 2018).

Although the declines in TP\textsubscript{lake} were less widespread than the declines in DIN\textsubscript{lake}, the TP\textsubscript{lake} signal was more synchronous among lakes than the DIN\textsubscript{lake} signal both at the scale of individual lakes (Figure 4) and at the scale of regions (Table 2), suggesting that broad-scale forcing variables (which may include other climate-related or deposition drivers not tested) were impacting the year-to-year variability in TP\textsubscript{lake}. Although there were no significant correlations between climate forcing variables (MAT or MAP) and lake chemistry variables, annual averages are rough metrics and may mask important changes at shorter time scales (e.g., seasonal; Palmer et al., 2014, or episodic extreme events; Jennings et al., 2012; Strock et al., 2016). The anomalously low TP in 2007 in lakes and streams throughout Sweden (Figure 6) coincided with the water year with the highest MAT of any year in the study period (Figure 8), as a result of extremely warm temperatures during the fall and winter months. Indeed, most of Europe experienced extremely warm temperatures from fall 2006 to winter 2007 (Luterbacher et al., 2007; You et al., 2007), which might have been an important climate driver contributing to very low soluble reactive P in 2007 noted in several large lakes in the southern Alps (Salmaso et al., 2013). Interestingly, those lakes had similar trends in P concentrations in surrounding years to those observed in regional averages presented here, and interannual variability in that study was...
attributed to broad-scale climatic indices affecting winter weather conditions. The hypothesis that winter conditions may be partly responsible for trends in summer TP\textsubscript{lake} is supported by the data from the spring months, which are similar to summer data and also have low TP\textsubscript{lake} in all regions in 2007 (supporting information Figure S1). The similarity between spring and summer data suggests that the observed patterns are not driven by summer growing season processes (e.g., decreasing production or changes to internal loading). Winter conditions have been shown to affect plankton and nutrient dynamics in subsequent growing seasons (Hampton et al., 2016; Weyhenmeyer, 2004), and warm winters have been found to decrease lake TP in subsequent years (Blennner et al., 2007). Further analysis over a longer monitoring period is required to understand the effects of warm winters on TP\textsubscript{lake}; however, if this is important, it suggests that TP\textsubscript{lake} in northern lakes may be expected to decline with continued climate warming. Several previous studies have observed declining TP in forested boreal catchments in North America and Europe (Arvola et al., 2010; Crossman et al., 2016; Eimers et al., 2009; Huser et al., 2018; Stammler et al., 2017), suggesting that the patterns observed in Sweden may be broadly relevant, although contrasting patterns have been observed in the United States (excluding Alaska and Hawaii) where TP in lakes and streams in relatively undisturbed catchments has increased in recent years (Stoddard et al., 2016).

The significant decline in DIN:TP\textsubscript{lake} throughout Sweden, resulting from declining DIN\textsubscript{lake} coupled with only modest declines in TP\textsubscript{lake}, indicates that N limitation in phytoplankton is increasing throughout Sweden (Bergström, 2010) (Figures 2 and 3). This generally supports hypothesis 3 (DIN:TP\textsubscript{lake} would decline in areas with reduced DIN\textsubscript{dep} and increased TOC\textsubscript{lake}), although browning had less effect on the results than we hypothesized. In regions that are already N deficient, particularly in northern Sweden (Bergström et al., 2008), declining DIN\textsubscript{lake} and DIN:TP\textsubscript{lake} are therefore contributing to an intensified N limitation, potentially reducing pelagic primary production and biomass accumulation at higher trophic levels in northern lakes (Deininger et al., 2017; Elser et al., 2010). At the same time, reduced DIN loadings could lower phytoplankton (i.e., seston) N:P ratios and increase their quality as prey items especially for P demanding crustacean zooplankton (Hessen et al., 2013). This change in phytoplankton N:P stoichiometry should be of special relevance in regions with initially P-limited phytoplankton, particularly southern Sweden (Bergström et al., 2008), where declining DIN:TP\textsubscript{lake} may shift the nutrient limitation status from P toward NP or N limitation. A shift toward N limitation may also promote increases in cyanobacteria populations (Downing et al., 2001), particularly if it is accompanied by significant temperature increases (Paerl & Huisman, 2008), reducing food quality for upper trophic levels (Brett & Müller-Navarra, 1997) and increasing the risk of potential toxic effects (Beversdorf et al., 2015). Trends of increasing cyanobacteria have already been observed in some lakes in southern Sweden (Weyhenmeyer, 2001), and it is possible that declining N:P may exacerbate this trend with potential threats for water quality and lake ecosystem production.

It is uncertain how future changes in climate, atmospheric N deposition, catchment greening, and lake browning may result in further alterations of lake N:P in boreal and subarctic areas. The time period of the current study is too short to definitively ascribe observed changes to long-term trends rather than decadale-scale fluctuations. Some factors that may contribute to the observed trends (decreasing DIN\textsubscript{dep} and possibly winter warming) are likely to continue with continued controls on NO\textsubscript{x} emissions and future climate change, whereas it is not clear for how long browning trends will continue following recovery from acidification (Monteith et al., 2007). The reductions in DIN\textsubscript{dep} experienced in Sweden are similar to those seen in parts of North America (Simpson et al., 2014). Other parts of the world, particularly east Asia, are experiencing large increases in DIN\textsubscript{dep} (Liu et al., 2013) and so will likely have increases in DIN:TP\textsubscript{lake}. The impacts of DIN\textsubscript{dep} may also be affected by the form of N in atmospheric loads; NO\textsubscript{3} and NH\textsubscript{4}+ may be transported differently through catchments (Dillon & Molot, 1990) and have different effects on phytoplankton nutrient limitation (Blomqvist et al., 1994; Ferber et al., 2004). Recently, the proportion of NH\textsubscript{4}+ relative to NO\textsubscript{3} in DIN deposition has increased in North America and Europe (Du et al., 2014; Li et al., 2016; Simpson et al., 2014). The impacts of climate change on P transport and accumulation in surface waters in undisturbed boreal and subarctic/mountain areas have received less attention than N transport, in part because P-centric literature has focused primarily on land use-driven eutrophication. The potential link between warm winters and low TP\textsubscript{lake} observed here and elsewhere may suggest that northern lakes will become more oligotrophic in the absence of other anthropogenic impacts; however, this topic requires substantial future research using longer time series and a variety of methodological approaches. Ultimately, this study suggests that in
Sweden and probably other parts of Scandinavia, N limitation is becoming more severe. In other areas experiencing different trends in climate and DIN deposition, lakes may respond differently. However, both N and P concentration in lakes appear to be influenced by these broad-scale drivers, so it is likely that lake nutrient limitation will respond to these changes coherently at large regional scales.

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