

# A Broad-Scale Look at Nutrient Limitation and a Shift toward Co-limitation in United States Lakes

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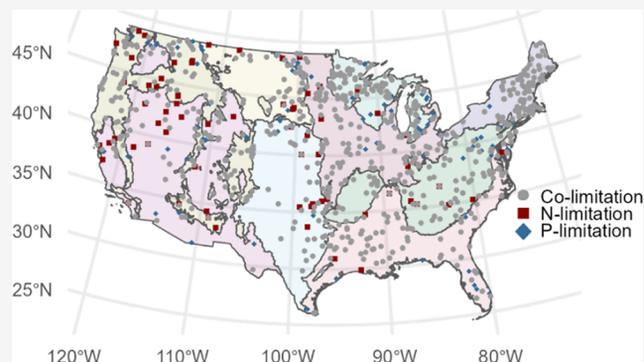
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**ABSTRACT:** There is a longstanding debate about the role of nitrogen (N) vs phosphorus (P) in limiting primary production in lakes and whether co-nutrient limitation should be considered for managing eutrophication. We evaluated nutrient limitation and eutrophication at a subcontinental scale. Using U.S. Environmental Protection Agency National Lakes Assessment data, we assessed broad-scale patterns in nutrient limitation and compared samples of all surveyed lakes and lakes resurveyed in multiple surveys. We found that N correlated more strongly with productivity in the western U.S., while P correlated more strongly in the eastern U.S. The aggregated subcontinental effect suggests the importance of factors like N-deposition, terrestrial vegetation, underlying geology, and land use for understanding drivers of nutrient dynamics in lakes. Our study showed how patterns can aggregate across subcontinental scales yet still demonstrate considerable variation when more deeply examined on an individual lake level. Overall, we found that nutrient limitation is dynamic over space and time, with most lakes being co-limited. The prevalence of co-limitation also increased from 2007 to 2017. Trophic states within each limitation category varied substantially. Our findings underscore the need for combined N and P reductions to mitigate accelerated eutrophication.

**KEYWORDS:** biogeochemistry, nutrient limitation, National Lakes Assessment, water quality management, eutrophication



## INTRODUCTION

Enrichments of nitrogen (N) and phosphorus (P) are often responsible for accelerating eutrophication, a major threat to freshwater ecosystem health, biodiversity, and ecosystem services across the globe.<sup>1–3</sup> Eutrophication often occurs due to an increase in the limiting nutrient or the nutrient in the lowest supply relative to the nutrient demands by organisms.<sup>4</sup> There is an ongoing debate about whether nutrient reductions for eutrophication management should solely focus on P or whether an approach reducing and balancing both N and P is more useful.<sup>5–13</sup> The paradigm of P being the dominant limiting nutrient in lakes has been based on experimental evidence, lower cost of reducing P, and the assumption that biological N-fixation prolongs P-limitation.<sup>14–16</sup> Furthermore, the use of the Redfield Ratio (16N:1P molar)<sup>17</sup> may lead to the assumption of primary P-limitation as the ratio is typically too low for freshwaters, which are often closer to 20N:1P.<sup>18</sup> However, management-driven P reductions have resulted in accumulation of N in large lakes worldwide, leading to an additional nutrient problem.<sup>19</sup>

Despite the longstanding P paradigm, the importance of N in regulating primary productivity is becoming more widely recognized and focusing on P reduction alone may not be an adequate solution to manage eutrophication. In fact, there is

evidence that northern hemisphere,<sup>20</sup> high-latitude, high-altitude,<sup>21</sup> and alpine<sup>22</sup> lakes are N-limited in their natural states. Moreover, N and P together result in significantly more productivity than single nutrient additions, highlighting how stoichiometrically balanced management is beneficial. The importance of N and P together has been extensively demonstrated via experiments, including within varying phytoplankton communities in a controlled laboratory environment<sup>23</sup> to natural phytoplankton communities in nutrient enrichment bioassays in lakes and reservoirs across North America.<sup>24</sup> The importance of N and P together for enhancing productivity was further demonstrated globally in a meta-analysis of freshwater, marine, and terrestrial nutrient enrichment experiments.<sup>25</sup>

In addition to macronutrients, such as N and P, in-lake productivity may also be mediated by micronutrients, trace elements, light, or other factors, such as competition and

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predation. Nutrients and light often directly limit primary productivity, whereas zooplankton grazing and lake turbulence may indirectly constrain productivity. Throughout this manuscript, we use the term “limit” as we assessed macronutrient limitation in lakes using N/P ratios, which quantify the relative availability of nutrients. Primary production depends strongly on the supply rate of the limiting nutrient.<sup>4</sup> Here and in other studies (e.g., Moon et al.<sup>26</sup>), the use of total nutrients and the correlation with chlorophyll-*a* are often used to estimate and compare supply rates among lakes. But we acknowledge the limitations on using N/P ratios alone, which do not account for a variety of confounding factors. For example, worldwide, there is high variability in productivity at similar P concentrations,<sup>27</sup> suggesting how regional or lake-specific factors influence productivity. Productivity can also depend on other elements as responses to N additions in arctic lakes are mediated by increased dissolved organic carbon.<sup>28</sup> Lakes at low latitudes have shown greater productivity in response to similar nutrient concentration as high-latitude lakes, underscoring the importance of light and temperature for phytoplankton growth.<sup>29,30</sup> Nutrient limitation in shallow low-latitude lakes is also influenced by local factors like hydrology, soil type, and macrophytes.<sup>31</sup> Overall, nutrient limitation is complex and varies across scales. While many factors can limit phytoplankton growth, in this study, we examine regional patterns of productivity by inferring limitation by N, P, or both nutrients and other factors (co-limitation) across the continental U.S. because they are often considered the primary controls on productivity. Research at broad spatial scales is critical given the coupled nature of N and P cycles,<sup>19</sup> regional importance of N-deposition,<sup>32</sup> and global climate change.<sup>33</sup>

In this study, we evaluated nutrient limitation of lakes and how nutrient limitation relates to lake trophic state at a subcontinental scale using U.S. Environmental Protection Agency (USEPA) National Lakes Assessment (NLA) data. Previous studies have demonstrated similar prevalence of N- and P-limited freshwaters as well as the prevalence of co-limitation.<sup>25,26</sup> We then extended our analyses to examine spatial and temporal variation in limitation and links between limitation and trophic state. NLA surveys include empirical data from thousands of lakes across the U.S., which allows for comprehensive assessments of lake water quality and ecosystem health across a range of climates and environmental contexts, here defined using USEPA nutrient ecoregions (Figure S1). We examined the following questions: When data are aggregated by ecoregion, which nutrient correlates best with chlorophyll-*a*, an indicator of trophic state? Then, when individual lakes are examined, how does nutrient limitation vary across space and time? Furthermore, we examined how lakes were categorized into trophic states among various forms of nutrient limitation. Finally, since NLA data are intended to represent all lakes in the U.S., we investigated if conclusions drawn from NLA surveys vary depending on the subset of lakes considered, i.e., all surveyed lakes vs resampled lakes.

## METHODS

**NLA Data Collection and Filtering.** The USEPA NLA surveys lakes across the continental U.S. every 5 years to assess their chemical and biological characteristics. The USEPA hand-selects (a priori) approximately 100 reference lakes each year to represent the least-disturbed conditions for total

nutrients (TP, TN) and other assessed parameters to which the other surveyed lakes can be compared.<sup>34</sup> We assessed nutrient data from the 2007, 2012, and 2017 NLA surveys<sup>35–37</sup> and evaluated decadal shifts of limitation and trophic state among limitation types using the 2007 and 2017 surveys. In each survey year, approximately 1000 lakes were surveyed nationwide. Within each survey, approximately 10% of lakes were resampled during the same year. In 2007, lakes greater than 4 ha were sampled. This changed in the later surveys to include surface areas >1 ha. For this analysis, we excluded lakes <4 ha to maintain consistency across surveys.

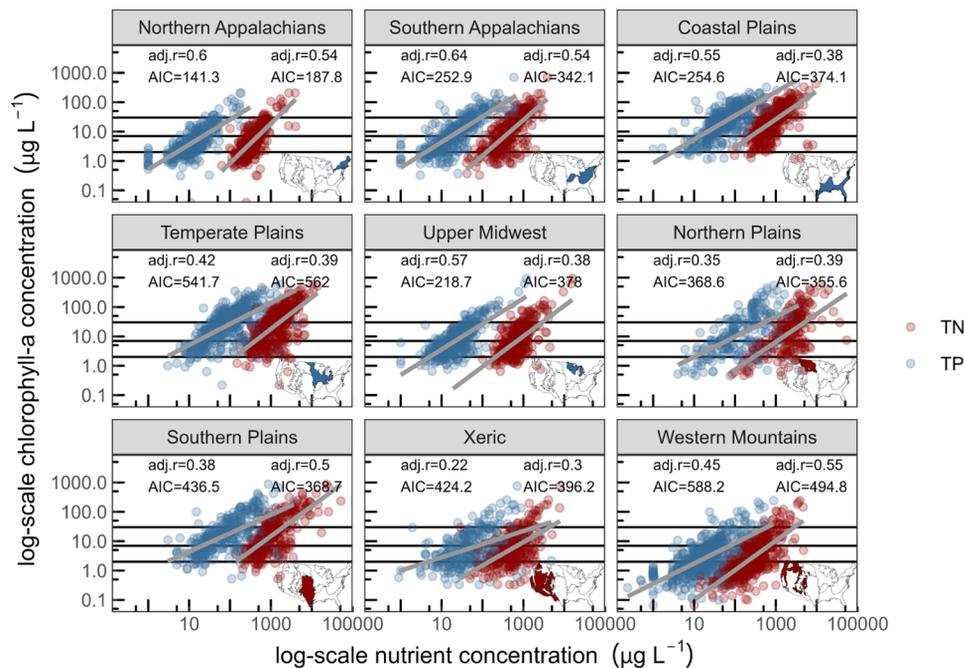
The USEPA used a Generalized Random Tessellation Stratified survey design to randomly choose sampling sites.<sup>34</sup> Stratification was based on Omernik level-3 aggregated ecoregions,<sup>38</sup> state, and lake size.<sup>34</sup> Discretizing the data set into Omerniks nine aggregated ecoregions (Figure S1) provides a qualitative understanding of spatial patterns and regional homogeneities.<sup>38</sup> The USEPA statistically determines a weight to indicate the number of lakes that each surveyed lake represents. This population weight is based on size, state, and ecoregion.<sup>34</sup> Error is assigned around these weights during analyses. The NLA data are specifically designed to assess lakes across the U.S., rather than the individual lakes sampled.<sup>34</sup> We examined if results differed when performing the same analyses on all surveyed lakes and again on only the resampled lakes.

Full details on the standardized sampling procedures, laboratory methods, and quality assurance can be found in the NLA field and laboratory operation manuals.<sup>39–44</sup> Briefly, lakes were sampled between May and September of each survey year, and samples were processed at approved laboratories within 24 h of receipt. Sampling included a suite of common water quality chemical and biological indicators, such as Secchi depth, pH, dissolved oxygen, major ions, nutrients, sediment chemistry, zooplankton, phytoplankton, and macroinvertebrates.

The NLA uses chlorophyll-*a* concentration as a proxy for trophic state, while acknowledging trophic state is determined by a variety of characteristics, including nutrients, climate, morphology, etc.<sup>34</sup> Lakes are classified as oligotrophic (chlorophyll-*a* concentrations  $\leq 2 \mu\text{g L}^{-1}$ ), mesotrophic ( $>2$  and  $\leq 7 \mu\text{g L}^{-1}$ ), eutrophic ( $>7$  and  $\leq 30 \mu\text{g L}^{-1}$ ), or hypereutrophic ( $>30 \mu\text{g L}^{-1}$ ). The stratified sampling design ensures a representative snapshot of trophic states were sampled within each region.

**Data Analyses.** All data analyses were performed in the R programming language version 4.4.0<sup>45</sup> using the tidyverse, zoo, patchwork, ggpubr, and colorblindr packages for data wrangling and visualization;<sup>46–50</sup> the sf package for creating maps;<sup>51</sup> and the spsurvey package for generating weighted population estimates.<sup>52</sup> The data and code to run analyses and create all of the figures in this manuscript are available at <https://zenodo.org/doi/10.5281/zenodo.12014772>.

To broadly estimate whether regional lake productivity was limited by N or P at the time of sampling, we used chlorophyll-*a* as a proxy of phytoplankton biomass and evaluated whether total nitrogen (TN) or total phosphorus (TP) best correlated with chlorophyll-*a*. We analyzed all surveyed lakes in 2007, 2012, and 2017 together using log-scale linear models. The  $R^2$  and AIC values for models with TN and TP were compared to determine which nutrient had the best explanatory power of chlorophyll-*a*. We acknowledge the assumption of correlation by using this approach as TN and TP are components of phytoplankton biomass; thus, there is likely some level of



**Figure 1.** Chlorophyll-*a* vs nutrient concentration (on logged axes) in each ecoregion. Color indicates either total nitrogen (red) or total phosphorus (blue). AIC and adjusted  $R^2$  values are displayed on each panel, with values for the phosphorus model on the left and those for nitrogen on the right. Horizontal lines indicate trophic state from oligotrophic (below the lowest line) to hypereutrophic (above the highest line). U.S. map is in the lower right corner of each panel with the ecoregion colored by the nutrient that better correlated with chlorophyll-*a*.

autocorrelation between TN, TP, and chlorophyll-*a*, regardless of limitation.<sup>14,53</sup>

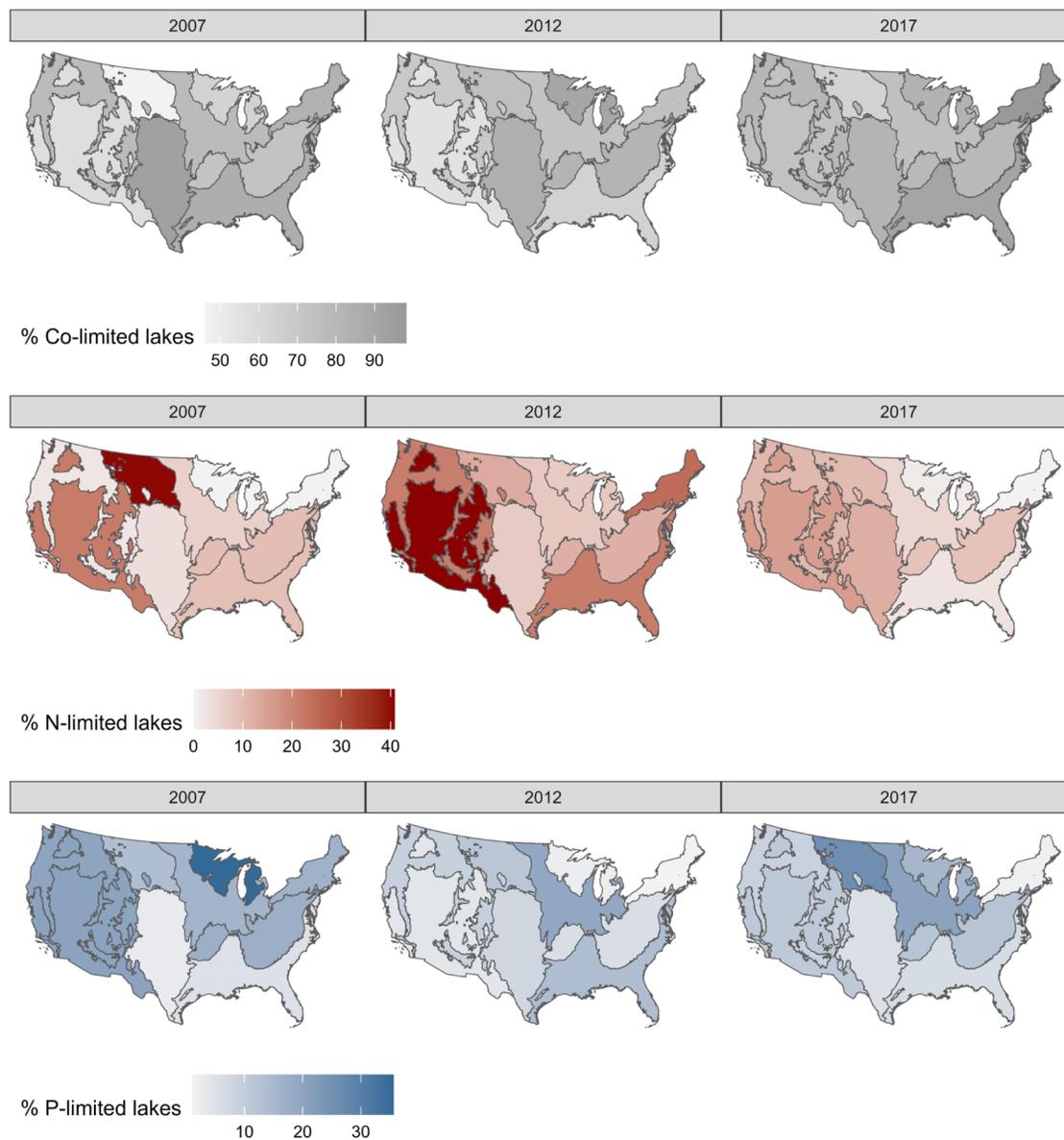
We then calculated nutrient limitation on a sample-by-sample basis using methods adapted from Moon et al.,<sup>26</sup> which were originally inspired by methods to determine trophic state index and nutrient limitation in Abell et al.,<sup>30</sup> Brown et al.,<sup>54</sup> Carlson and Havens,<sup>55</sup> Kratzer and Brezonik.<sup>56</sup> Nutrient ratios have been extensively used to determine limitation.<sup>17,57–61</sup> The Moon et al.<sup>26</sup> methods expand on methods using N/P ratios by normalizing chlorophyll-*a* relationships with TN and TP, putting them on the same scale and allowing for better comparison and development of a tipping point N/P ratio at which limitation may be inferred. We first calculated high-yield chlorophyll-*a*, which is defined as the chlorophyll-*a* concentration that could correspond to a nutrient concentration without other confounding factors present. Next, the fraction yield of chlorophyll-*a* was determined for each sample. Fraction yield is defined as the portion of potential chlorophyll-*a* (i.e., high-yield chlorophyll-*a*) that was observed. The tipping point is defined as the N/P ratio at which the fraction yield of chlorophyll-*a* by TN exactly equals the fraction yield of chlorophyll-*a* by TP. When the observed N/P ratio is greater than the tipping point, the yield of chlorophyll-*a* by TP is greater than that of TN; thus, the lake would be considered P-limited and vice versa for N-limited samples.<sup>26</sup> We performed the following methods within each of the nine ecoregions, developing nine equations to determine tipping point N/P ratios (Table S1).

We first calculated high-yield chlorophyll-*a* vs median TN and TP linear regression lines. Within each ecoregion, TP concentrations were ranked from low to high. Then, using a moving window of  $n$ -samples, we computed the 95th percentile chlorophyll-*a* and median TP concentrations, where  $n = 10\%$  of the total samples in each ecoregion. The paired median TP and 95th percentile chlorophyll-*a* values

were regressed on the log scale. Then, this process was repeated for TN. The 95th percentile chlorophyll-*a* was paired with the median nutrient in each moving window to estimate how midpoint nutrient concentrations would result in a high-yield chlorophyll-*a*. The log-scale regression equations were used to calculate the high-yield chlorophyll-*a* potential of each observed sample of TN and TP in the NLA data.<sup>26</sup> In this step, there were two equations for each ecoregion, one high-yield chlorophyll-*a* vs TP and one high-yield chlorophyll-*a* vs TN, both using log-transformed data (Table S1).

Then, fraction yields of chlorophyll-*a* by TN or TP were calculated by dividing the observed chlorophyll-*a* by the high-yield chlorophyll-*a* corresponding to each sample. This step puts chlorophyll-*a* yields for each nutrient on the same scale (median fraction yields in Table S2). Within this framework, nutrient deficiency is inferred when the fraction yield via one nutrient is significantly greater than the other.<sup>26</sup>

Finally, we determined a tipping point N/P ratio regression line for each ecoregion. This tipping point corresponds to the TN and TP concentrations, at which fraction yields are equal. We used the high yield regressions to determine TN concentrations that corresponded to the same high-yield chlorophyll-*a* concentrations determined at TP = 1 and 5000  $\mu\text{g L}^{-1}$  and regressed the TN/TP ratios on TP concentrations on the log scale. The resulting equations were used to estimate the TN/TP tipping point ratios based on observed TP concentrations for each NLA sampling event. The deviation of observed TN/TP ratios from tipping point TN/TP ratios was used to determine nutrient limitation (median tipping point N/P ratios and median deviations in Table S2). We inferred a high likelihood of P-limitation if the deviation was  $>2$  and of N-limitation if the deviation was  $<0.5$ . When the deviation was between 0.5 and 2, we inferred co-limitation, potentially by both nutrients and/or along with other factors that can limit productivity. While many different limitation thresholds could

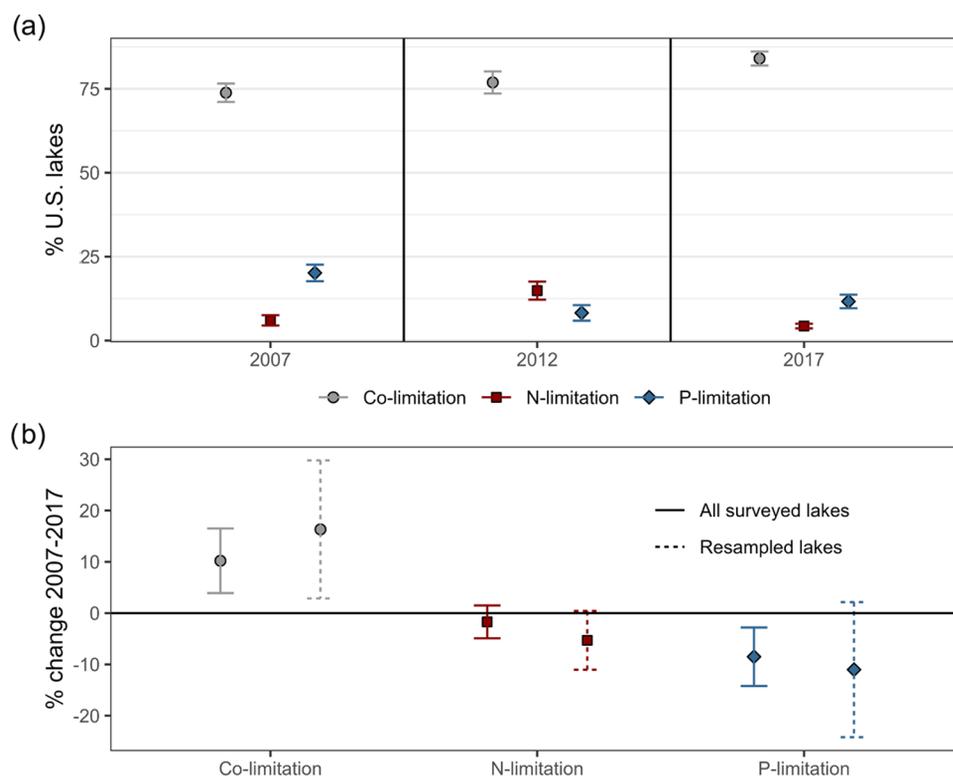


**Figure 2.** Spatial and temporal variability of nutrient limitation mapped across nine ecoregions of the U.S. Percent of lakes that are co- (gray), N- (red), and P- (blue) limited are displayed within each ecoregion and year.

be used, we selected thresholds following the methods established by Moon et al.<sup>26</sup> Within this framework, deviation of 2 indicates the fraction yield chlorophyll-*a* by TP is twice as great as that by TN, while deviation of 0.5 indicates the fraction yield of chlorophyll-*a* by TN is twice as great as that by TP.<sup>26</sup> Of course, there are limitations to using N/P ratios to determine nutrient limitation, including the aforementioned collinearity between N, P, and productivity,<sup>14</sup> and unaccounted for factors that may limit productivity, such as light or temperature.<sup>4</sup>

After determining nutrient limitation on a sample-by-sample basis following Moon et al.,<sup>26</sup> we next assessed spatiotemporal variability in limitation by aggregating limitation at the ecoregional scale. We further examined how lakes were categorized in trophic states among various forms of nutrient limitation by aggregating the limitation within trophic state categories. We used change analyses (change\_analysis function in the spsurvey package<sup>52</sup>), which incorporates the population weights to measure the difference in the proportion of

categories (here, limitation and trophic state were the categories) between the 2007 and 2017 surveys.<sup>34</sup> USEPA-selected reference lakes and observations from second sampling events during the same year were not included in the change analyses. The shifts were analyzed using all surveyed lakes representing lakes across the conterminous U.S. ( $n = 2768$ ) and using lakes sampled in both 2007 and 2017 ( $n = 478$ ), referred to as resampled lakes. Shift estimates were not statistically significant when the 95% confidence interval overlapped with zero. Categorical analyses (cat\_analysis function from the spsurvey package) were used to generate population-weighted estimates of the percentage of lakes in each limitation category and trophic state across survey years. Categorical analyses were also used to generate estimates of trophic states within each limitation category using data from all three surveys. Our study builds on the USEPA's presentation of NLA survey data by assessing spatiotemporal variation in nutrient limitation and how trophic state varies by limitation.



**Figure 3.** Aggregated national lake nutrient limitations with (a) percent of lakes that are co- (gray circles), N- (red squares), and P- (blue diamonds) limited in each survey year. (b) Percent change in limitation categories between 2007 and 2017. The change is represented as a percent difference in the population (point) with 95% confidence interval bars. Error bars that cross zero are not statistically significant. There was no significant difference between shifts among all surveyed lakes (solid lines) and resampled lakes (dotted lines).

## RESULTS AND DISCUSSION

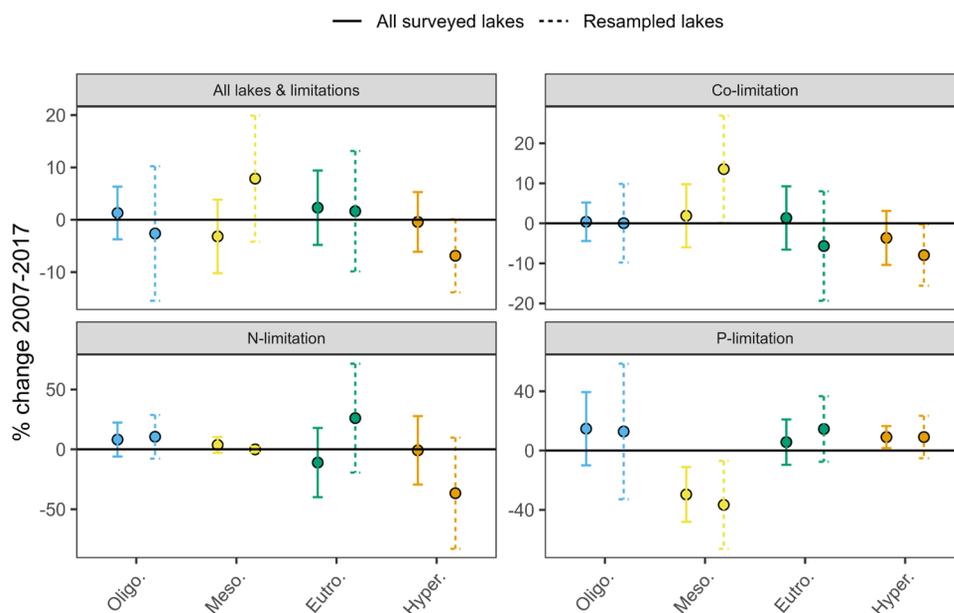
**Controls on Productivity Vary Geographically.** When aggregated at the regional scale, TN and TP correlated with chlorophyll-*a* differently across ecoregions of the U.S. (Figure 1), with a clear geographic divide in the data. In the western U.S. (Northern Plains, Southern Plains, Xeric, and Western Mountains ecoregions), TN explained more variation in chlorophyll-*a* than TP based on the linear models' higher  $R^2$  and lower AIC values. This was contrasted by the Eastern U.S. (Northern Appalachians, Southern Appalachians, Coastal Plains, Temperate Plains, and Upper Midwest ecoregions), where TP explained more variation (Figure 1). Interestingly, both nutrients had the lowest relative power in the Xeric ecoregion, indicating that there may be other factors more greatly influencing productivity in this region like high dissolved solids and salinity.<sup>62–64</sup> While this pattern was largely consistent, there were intersurvey variations. In 2007, productivity in the Coastal Plains was better explained by TN; TN was a better predictor in the Temperate Plains in 2012; and in 2017, productivity in the Western Mountains and Xeric ecoregions better correlated with TP.

The distinct subcontinental pattern supports ideas that processes at finer scales can aggregate to larger extents and that broad processes can influence nutrient dynamics in lakes. Sources, transport, and internal-lake dynamics of nutrients vary across the U.S., with broad distinctions between the east and west. Differences in climate, geology, land use, vegetation,<sup>65–68</sup> and atmospheric deposition<sup>69</sup> likely lead to broad-scale differences in nutrient loading. Furthermore, global nutrient cycling has been substantially amplified due to anthropogenic activity.<sup>70</sup> In fact, anthropogenic-induced high atmospheric N-

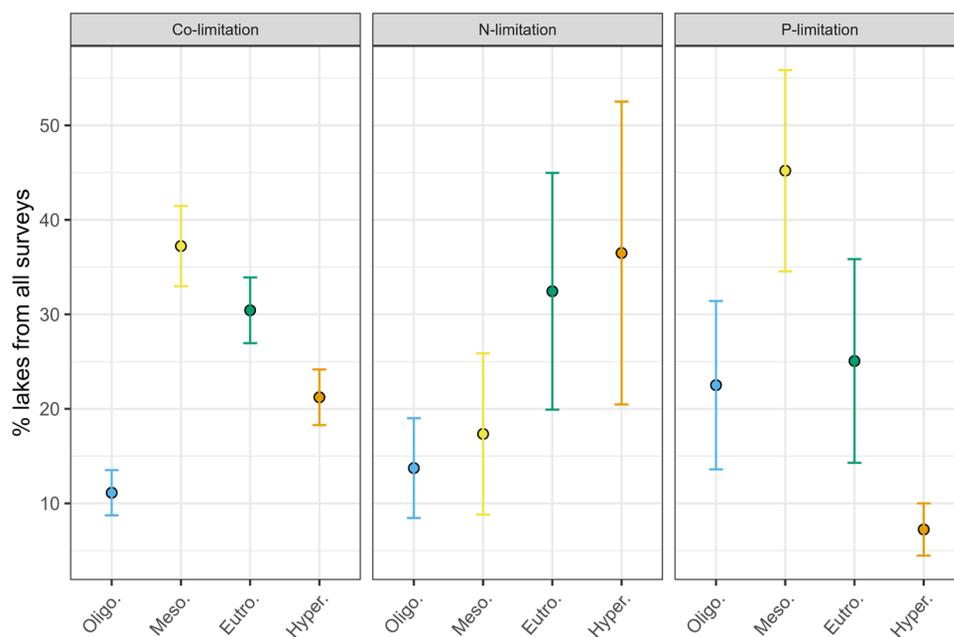
loading has already shifted background N-limitation toward P-limitation globally across many northern hemisphere lakes.<sup>71</sup> Furthermore, at least 60% of NLA surveyed waters were reservoirs in the west, whereas reservoirs make up less than 50% of the waters in the east. Factors that affect internal nutrient cycling and vary between reservoirs and natural lakes include age, residence times, mixing regimes, and morphometry.<sup>72–74</sup>

Aggregating data across broad scales can result in an ecological fallacy under which individual context is lost and the results may not apply to all individuals within a group.<sup>75</sup> Individual lakes are unique, each with context-dependent characteristics that must be considered when designing nutrient management targets.<sup>76</sup> For example, despite the general trend of N-limitation in western U.S. lakes, lakes along the front range of the Rocky Mountains tend to be P-limited because of a history of high N-deposition and legacy accumulation.<sup>77–79</sup> Nutrient dynamics vary at local scales based on depth, surrounding landscape, hydrologic connectivity, and more.<sup>80</sup> Despite localized variances, broad-scale patterns give a holistic overview of interacting processes across the continental U.S.<sup>81</sup>

**Nutrient Limitation Varies Spatiotemporally, with High Proportions of Co-limitation.** There were 436 observations of P-limited lakes, 350 N-limited lakes, and 2484 co-limited lakes across the entire data set. The population-weighted proportion of lakes in each limitation status varies across ecoregions and survey years (Figures 2 and S2a). At the national scale in the most recent survey (2017), 84% of lakes were co-limited, followed by 12% P-limited and 4% N-limited (Figure 3a). Between 2007 and 2017, lakes



**Figure 4.** Minimal changes in trophic state between 2007 and 2017. Panels separated to show all lakes at all limitations in the top left and then separated by co-limitation, N-limitation, and P-limitation in the following three panels. The change is represented as a percent difference in the population (point) with 95% confidence interval bars. Error bars that cross zero are not statistically significant. There were no significant differences between shifts among all surveyed lakes (solid lines) and resampled lakes (dotted lines).



**Figure 5.** Percent of lakes from all NLA surveys in each trophic state distinguished by co-limited lakes, N-limited lakes, and P-limited lakes in the three panels. The 95% confidence intervals represent the error. Eutrophication occurs more among single nutrient limitation than co-limitation, which is more commonly mesotrophic. Hypereutrophication is most common among N-limited lakes compared to co- or P-limited lakes.

shifted away from P-limitation and toward co-limitation, with no change in N-limitation (Figure 3b). The nature of our analysis does not allow for determining if individual lakes are shifting over time but rather provides an overall characterization of national and regional shifts. Among the ecoregions, the largest changes in single nutrient limitation occurred in the Northern Plains (30% decrease in N-limited lakes) and Upper Midwest (20% decrease in P-limited lakes), with the greatest shift in co-limitation occurring as a 19% increase in the Upper Midwest (Figure S2b). There were no statistical differences between all surveyed lakes and resampled lakes (solid and

dotted lines, respectively, in Figures 3b and S2b); however, there were differences in shift significance as indicated by error bars crossing zero. For example, among all surveyed lakes nationally, we observed a 9% decrease in P-limitation. Yet, among resampled lakes, there was no statistical change in P-limitation (Figure 3b).

The prevalence of and shift toward more co-limited lakes across the U.S. (Figure 3) suggests the critical importance of both nutrients when assessing water quality, the potential for these lakes to vacillate between limitation statuses as nutrients are stored or transformed (e.g., P accumulation leading to

accelerated denitrification<sup>82,83</sup>), and the potential for other factors to be limiting. Co-limitation occurs commonly because of spatial heterogeneity of nutrients and phytoplankton within lakes.<sup>84</sup> It can occur when both nutrients are at low concentrations, and both are required for growth. It can also occur when adding a single nutrient spurs phytoplankton growth by stoichiometrically balancing resources and facilitating greater assimilation.<sup>85–87</sup> There is substantial evidence that additions of N and P together result in significantly greater primary production than either nutrient alone,<sup>11,23–25,83</sup> likely due to varying roles, resource utilization, and interactions among phytoplankton species coexisting within a single lake.<sup>88</sup> Thus, with a greater imbalance of N/P, there may be less diversity of phytoplankton species. Co-limitation may also occur seasonally within a lake, as external sourcing and internal recycling vary<sup>89</sup> and as phytoplankton blooms deplete resources and shift limitations into new statuses.<sup>90</sup> Likely, multiple scenarios are occurring across U.S. lakes and are context-dependent. Knowing where and when shifts are occurring, the magnitudes, and the corresponding trophic states can help prioritize areas for management.

**Subtle Trophic State Shifts, yet Observable Effects of Nutrient Limitation.** Using chlorophyll-*a* as a proxy for trophic state, the raw survey data indicate that there were 520 oligotrophic observations (oligo.), 1047 mesotrophic observations (meso.), 990 eutrophic observations (eutro.), and 713 hypereutrophic observations (hyper.) among lakes from all surveys. The population weights for these raw data generated the overall proportion of lakes in each trophic category across the U.S. (Figure S3). In 2017, eutrophic and hypereutrophic lakes made up 53% of lakes in the U.S. (Figure S3), indicating the extent of nutrient excess plaguing our freshwaters.<sup>3,91</sup> Trophic states varied substantially across ecoregions (Figure S3). Between 2007 and 2017, lakes across the conterminous U.S. showed negligible changes in trophic state, regardless of nutrient limitation category, with the exception of a 9% increase in hypereutrophy and a 30% decrease in mesotrophy within P-limited lakes (Figure 4). The overall lack of change (panel 1 in Figure 4) confirms previous work done on a smaller scale, finding no phytoplankton bloom intensification over the past 40 years in Northeastern U.S. lakes.<sup>92</sup>

Nutrient limitation influences trophic state in U.S. lakes. Co-limited lakes (first panel in Figure 5) are more commonly mesotrophic and eutrophic, suggesting that there may be shifts between insufficient and excess nutrients. We found a positive correlation between trophic state and N-limitation (second panel in Figure 5). This correlation is consistent with previous reports and is linked to increased metabolism of N and denitrification as a result of P accumulation.<sup>57,74,82,83,93</sup> We also found significantly fewer hypereutrophic lakes that were P-limited than the other three trophic state categories (third panel in Figure 5). High proportions of eutrophication among all limitation categories (Figure 5) along with spatially and temporally variable limitation (Figures 2 and S2) suggest that a focus on a single nutrient could be counterproductive for eutrophication management across broad scales. Consistent with our results but in U.S. streams, previous researchers suggested dual consideration of N and P for eutrophication management after finding high nutrient loading and simultaneous roles of N and P in eutrophication.<sup>94</sup> Balanced nutrient management is critical considering the extreme changes to global nutrient cycles with increased fluxes of N by ~100% and

P by ~400% due to activities like agriculture, fertilizer production, mining, and fossil fuel burning.<sup>70</sup>

One consequence of the global nutrient imbalance is preferential accumulation of P relative to N within lakes worldwide.<sup>95</sup> In addition to accelerated eutrophication, P buildup and long-term internal cycling within lakes can lead to greater losses of N via denitrification.<sup>19,74,82,83,93</sup> N loss at high denitrification rates is often greater than N inputs via N-fixation, further prolonging N-limitation in hypereutrophic conditions.<sup>82,83</sup> Nutrient dynamics are complex on the continuum of headwaters to the ocean. Single nutrient management strategies may work for single lakes but can lead to shifts in nutrient limitation, intensifying water quality problems over larger spatial and temporal scales<sup>19,96–98</sup> and perpetuating the global nutrient imbalance.<sup>95,99</sup>

**Implications.** Broad-scale ecological patterns provide information to create regional or national policies and help elucidate influences of major environmental changes, like climate change.<sup>81</sup> Human activities across the U.S. have led to differential impacts on nutrient cycling like N-deposition having detrimental impacts on western grassland and pastureland ecosystems,<sup>32</sup> while legacy accumulation of P has led to water quality impairments in the forested and agricultural eastern U.S.<sup>100</sup> Our research suggests that broad-scale patterns are reflected in nutrient dynamics of lakes across the U.S., with regional differences in nutrient limitation and trophic state. The USEPA NLA surveys provide data to make this research possible and are well suited to avoid typical biases in lake water quality sampling, such as biases toward large lakes in human-impacted watersheds.<sup>101</sup> The USEPA also uses consistent sampling and laboratory methods across surveys, avoiding problems with aggregating large data sets from multiple sources.<sup>39–44</sup>

Broad-scale patterns are useful for management strategies that stretch beyond site-specifics and must account for variable conditions.<sup>102</sup> Our study showed how patterns can aggregate across subcontinental scales (Figure 1) yet still demonstrate considerable variation when more deeply examined within ecoregions (Figure 2). Overall, we found that nutrient limitation is dynamic over space and time with a high prevalence in lakes limited by both nutrients and/or other factors, and a combined N and P reduction approach to eutrophication management is likely beneficial in most U.S. lakes. Focusing on a single nutrient could increase availability of the other limiting nutrient in subsequent waters and intensify downstream problems.<sup>83,96–98</sup> There is a critical need for balanced nutrient remediation while controlling the input of excess nutrients,<sup>103</sup> especially as climate change and other anthropogenic stressors will exacerbate eutrophication and the global N/P imbalance.

## ■ ASSOCIATED CONTENT

### SI Supporting Information

The Supporting Information is available free of charge at <https://pubs.acs.org/doi/10.1021/acs.est.4c03135>.

Map of U.S. ecoregions, spatiotemporal variability of nutrient limitation among ecoregions, and distribution of trophic states among regions; and supporting tables displaying equations to determine limitation and median values from calculations (PDF)

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### Notes

The authors declare no competing financial interest.

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