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LETTER

Knowing your limits: Patterns and drivers of nutrient limitation and nutrient–chlorophyll relationships in US lakes

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Scientific Significance Statement

Limnologists have long debated the relative importance of nitrogen vs. phosphorus in limiting or co-limiting primary productivity in lakes. However, much of our nutrient limitation knowledge comes from local studies and few studies have examined the environmental context that may influence nutrient limitation in lakes across broad geographic extents. In our study of 3342 lakes across the conterminous United States, we found that all regions contained a mix of nitrogen-, phosphorus-, and co-limited lakes and that majorities of lakes were phosphorus-limited only in the Northeast, Southeast, and Upper Midwest regions. Moreover, lake, watershed, and regional characteristics combined were related to nutrient limitation. Therefore, successful eutrophication management may require consideration of both nitrogen and phosphorus as well as additional factors operating at local to regional scales.

Abstract

Although understanding nutrient limitation of primary productivity in lakes is among the oldest research priorities in limnology, there have been few broad-scale studies of the characteristics of phosphorus (P)-, nitrogen (N)-, and co-limited lakes and their environmental context. By analyzing 3342 US lakes with concurrent P, N, and chlorophyll *a* (Chl *a*) samples, we showed that US lakes are predominantly co-limited (43%) or P-limited (41%). Majorities of lakes were P-limited in the Northeast, Upper Midwest, and Southeast, and co-limitation was most prevalent in the interior and western United States. N-limitation (16%) was more prevalent than P-limitation in the Great Basin and Central Plains. Nutrient limitation was related to lake, watershed, and regional variables, including Chl *a* concentration, watershed soil, and wet nitrate deposition. N and P concentrations interactively affected nutrient–chlorophyll relationships, which differed by nutrient limitation. Our study demonstrates the value of considering P, N, and environmental context in nutrient limitation and nutrient–chlorophyll relationships.

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Author Contribution Statement: IMM conceived of the manuscript idea, assembled data, and analyzed the prevalence of nutrient limitation across the conterminous United States. XS executed generalized linear mixed models of nutrient–chlorophyll relationships. PJH and XS executed random forest analysis of lake, watershed, and regional drivers of nutrient limitation. IMM, PAS, and XS identified and reviewed relevant literature. IMM, XS, and PJH created figures and tables. All authors wrote portions of the manuscript, provided feedback throughout the writing process, and helped revise figures and tables.

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

Understanding nitrogen (N) vs. phosphorus (P) limitation of primary productivity in lake ecosystems is a long-standing research priority in limnology. Nutrient limitation refers to the primary limiting nutrient of phytoplankton abundance when there is sufficient available energy (light and heat) (Hecky and Kilham 1988). Many studies have argued that lakes are predominantly P-limited based on N fixation increasing N concentrations relative to P concentrations, thus promoting P-limitation (Schindler 1977; Correll 1998; Carvalho et al. 2013; Fastner et al. 2016; Schindler et al. 2016). However, other studies have argued that limnologists underestimate N-limitation or co-limitation (Downing and McCauley 1992; Sterner 2008; Paerl et al. 2016; Myrstener et al. 2022). Explanations include recent declines in atmospheric N deposition (Isles et al. 2018), the potential for denitrification rates to exceed N fixation rates (Scott et al. 2019), or research bias toward certain lake types or regions (Poikane et al. 2022). Taken together, despite decades of research, there is still a lack of consensus among limnologists over the prevalence of N- vs. P-limitation in lake ecosystems.

An important source of this lack of consensus is likely over what can be reasonably inferred from disparate studies with different locations, types of lakes, temporal or spatial scales, or primary methods (e.g., laboratory, mesocosm, whole-lake experiments). However, a complement to these finer-scaled studies that has been used less frequently are studies of thousands of lakes across wide environmental gradients, which could also help identify geographic patterns and potential lake, watershed, or regional drivers of nutrient limitation that cannot be studied at fine scales. For example, previous broad-scale studies have identified lake trophic state as a predictor of nutrient limitation. In a study of 1384 US lakes, Liang et al. (2020) found that P-limitation was more prevalent in oligotrophic, mesotrophic, or eutrophic lakes, whereas co-limitation was more prevalent in hypereutrophic lakes. Related, recent global studies found that the probability of P-limitation declined as lakes become more eutrophic (Zhou et al. 2022, $n = 831$ lakes; Zhao et al. 2023, $n = 2849$ lakes). Supporting these results, Scott et al. (2019) found that eutrophic and hypereutrophic lakes were mostly N-limited because denitrification exceeded N fixation ($n = 1964$ lakes).

Although the above studies suggest that trophic state is a coarse predictor of nutrient limitation in lakes, other factors are also known to drive relationships of N and P with productivity. It is well established that a combination of in situ and external factors operating across spatial scales from lakes to regions, such as lake depth, watershed land use/cover, and regional climate, combine to influence lake nutrient concentrations and primary productivity (Read et al. 2015; Soranno et al. 2015; King et al. 2019). However, few studies have explicitly examined how such environmental context variables influence nutrient limitation or interact to influence nutrient–chlorophyll relationships at broad scales. For example, P-limitation can shift toward N- or co-limitation with decreasing lake depth (Zhao et al. 2023). Moreover, such factors also combine to influence nutrient–chlorophyll relationships at broad scales. For example, water clarity, mean depth, elevation, and regional air temperature mediated TP–chlorophyll relationships in a study of 3874 lakes across 47 countries (Quinlan et al. 2021). TP–chlorophyll relationships also varied regionally in relation to regional agriculture and wetland cover in a study of 2105 lakes in the midwestern and northeastern US (Filstrup et al. 2014). Additionally, N and P can also interact to influence primary productivity (Harpole et al. 2011), such that the effects of enrichment of one nutrient on phytoplankton may depend on background concentrations of the other (Frost et al. 2023). Collectively, these studies demonstrate that nutrient cycling, nutrient limitation, and nutrient–chlorophyll relationships in lakes are influenced by a combination of lake, watershed, and regional environmental context, including potential N–P interactions. However, rarely has the relative importance of a wide range of environmental context variables been considered in a single, multiscale analysis of nutrient–chlorophyll relationships across thousands of lakes along the spectrum of N-, P-, and co-limitation. Using a large database of 3342 US lakes with concurrent N, P, and chlorophyll *a* (Chl *a*) data and multi-scaled environmental context, we asked:

1. What is the prevalence of P-, N-, and co-limitation across broad gradients of ecological context?
2. What are the lake, watershed, and regional characteristics of P-, N-, and co-limited lakes?
3. How do nutrient–chlorophyll relationships vary across P-, N-, and co-limited lakes?

Methods

Study lakes and limnological data

We analyzed lakes ≥ 4 ha in the conterminous US with same-day epilimnion TP, TN, and Chl *a* samples collected between May and September from 1991 to 2020 (LAGOS-US-LIMNO v. 5; Shuvo et al. 2023). LAGOS-US-LIMNO consists of lake water quality from the US Water Quality Portal, which houses data from federal and state agencies (many of which collaborate with citizen science programs) (National Water Quality Monitoring Council 2021). LAGOS-US-LIMNO also includes data from the 2007, 2012, and 2017 US National Lakes Assessments (NLA; US Environmental Protection Agency 2010, 2016, 2022) and the US National Ecological Observatory Network (NEON; Keller et al. 2008). We used the most recent concurrent samples available (one sample per lake; median year = 2013) and applied water quality QA/QC procedures from LAGOS-NE-LIMNO v. 1.087.3 (Soranno et al. 2019). When TN measurements were unavailable, we calculated TN by combining nitrite, nitrate, and total Kjeldahl nitrogen if they were from the same sample. A total of 3342 lakes passed these criteria, 1905 (57%) of which were sampled by the NLA. We analyzed lakes across NEON regions (hereafter, regions), which are delineated primarily based on climate (Hargrove and

Hoffman 1999). All regions had samples for approximately 1–5% of lakes ≥ 4 ha (22–472 lakes), except the Southern Rockies and Colorado Plateau (13% of lakes with samples; Table 1). Because the Atlantic Neotropical region had only four sampled lakes, we lumped these with the Southeast.

We inferred P-, N-, and co-limitation based on mass TN : TP ratios used by Zhou et al. (2022) derived from Guildford and Hecky (2000). If TN : TP was < 9 or > 22.6, lakes were designated as N-limited and P-limited, respectively. TN : TP ratios that fell between these thresholds were designated as co-limited. TN : TP ratios are imperfect indicators of true limitation of primary productivity in lakes given uncertainty in nutrient bioavailability or the possibility that some other factor (such as light) may be more limiting than nutrients, including conditions when both N and P concentrations are high (Moon et al. 2021). However, ratios are appropriate and practical for estimating nutrient limitation at the macroscale (e.g., Elser et al. 2009*a*; Zhou et al. 2022). Such an approach is necessary when studying the potential mediating effects of lake, watershed, and regional factors on thousands of lakes, for which labor-intensive measures of nutrient limitation are unavailable.

Characteristics of P-, N-, and co-limited lakes

We applied Random Forest (RF) and Boruta feature selection to identify characteristics of P-, N-, and co-limited lakes using TN : TP as the response variable and the "Boruta" R package (Kursa et al. 2010). Boruta feature selection uses an ensemble of trees to identify relevant predictors by removing unimportant ones based on exceeding the importance of permuted copies of the data known as shadow features (Kursa et al. 2010). The algorithm iteratively and randomly permutes each feature value, checking if tested features have greater or lesser importance than the best shadow feature a significant number of times until either accepted or dropped. Features with no selection decision after the chosen number of iterations are considered tentative. We examined 58 environmental context variables at lake, watershed, or regional scales (Supporting Information Table S1). Lake variables reflected lake area, elevation, shape, hydrologic connectivity (LAGOS-US-LOCUS v1.0; Smith et al. 2021), natural lake vs. reservoir status (LAGOS-US-RESERVOIR v2; Polus et al. 2022), and maximum depth (available for 76% of lakes) (LAGOS-US DEPTH v1.0; Stachelek et al. 2021). Including maximum depth reduced our analysis to 2551 lakes. Watershed variables represented local watershed land use/land cover, watershed area and drainage ratio, hydrology, topography, point-source pollution, and soil properties, whereas regional variables included latitude, longitude, region membership, atmospheric deposition, climate, and hydrology (LAGOS-US-GEO v1.0; Smith et al. 2022). Regional deposition, climate, and hydrology variables were measured at the HU12 watershed scale. After 1000 Boruta iterations, 50 variables were accepted, 7 unimportant variables were dropped,

Table 1. Lakes, sampling effort, and nutrient information across NEON regions.

NEON region	Sampled lakes ≥ 4 ha	All lakes ≥ 4 ha	Sampling rate (%)	TP mean ($\mu g\ L^{-1}$)	TP SD ($\mu g\ L^{-1}$)	TN mean ($\mu g\ L^{-1}$)	TN SD ($\mu g\ L^{-1}$)	TN : TP mean	TN : TP SD
1. Northeast	335	13,641	2.46	23	40	430	380	36	48
2. Mid-Atlantic	246	6522	3.77	53	66	1047	1116	32	49
3. Southeast*	375	21,449	1.75	41	59	773	564	40	58
5. Great Lakes	469	20,808	2.25	33	47	817	668	45	55
6. Prairie Peninsula	472	11,478	4.11	109	137	1450	1098	25	26
7. Appalachians and Cumberland Plateau	97	3258	2.98	59	121	642	670	19	14
8. Ozarks Complex	147	15,205	0.97	77	93	769	536	19	24
9. Northern Plains	309	18,975	1.63	231	236	2779	2515	22	18
10. Central Plains	83	2126	3.90	93	125	790	647	17	15
11. Southern Plains	110	7991	1.38	101	145	1040	774	19	15
12. Northern Rockies	109	2724	4.00	36	88	491	923	23	28
13. Southern Rockies and Colorado Plateau	255	1944	13.12	58	135	470	576	18	16
14. Desert Southwest	22	477	4.61	84	140	1027	1073	29	26
15. Great Basin	179	4349	4.12	89	143	713	821	19	25
16. Pacific Northwest	88	2111	4.17	33	44	380	476	21	24
17. Pacific Southwest	46	2801	1.64	72	177	399	345	19	12
Combined regions	3342	135,859	2.46	76	132	1002	1240	29	40

and 1 variable (lake area) was identified as "Tentative" (retained in the final RF model) (Supporting Information Fig. S1). The final model used 5-fold repeated cross-validation and explained 21.8% of variance in TN : TP. We estimated the combined importance of each spatial scale (lake, watershed, regional) by calculating a grouped mean decrease in Gini index weighted by the number of node splits that contain variables within each spatial scale. We compared differences among N-, P-, and co-limited lakes for the top two lake, watershed, and regional predictors of nutrient limitation using Tukey's contrasts on generalized linear models (Gaussian or Gamma distribution) and the "multcomp" R package (Hothorn et al. 2008).

Nutrient–chlorophyll relationships

We used generalized linear mixed models (GLMMs) with the gamma distribution to examine nutrient–chlorophyll relationships using the lme4 R package (Bates et al. 2015). We treated TN and TP (both log$_{10}$-transformed) as fixed variables and region and nutrient limitation class (P-, N-, or co-limited) as random factors to account for regional variation and the effects of nutrient ratios. We applied chi-square tests ("anova" function) to select best-fitting models (Supporting Information Table S2). All analyses were performed in R 4.3.0 (R Core Team 2023). Data, metadata, and R code are publicly available here (McCullough et al. 2024, https://doi.org/10.5281/zenodo.11049100).

Results

Prevalence of P-, N-, and co-limitation

Across the conterminous US, lakes were primarily co-limited (TN : TP between 9 and 22.6; 42.8%; $n = 1432$) or P-limited (TN : TP > 22.6; 41.5%; $n = 1386$) rather than N-limited (TN : TP < 9; 15.7%; $n = 524$). Although all regions contained a mix of P-, N-, and co-limitation, some regional patterns emerged (Fig. 1). Narrow majorities of lakes were co-limited in the Appalachians and Cumberland Plateau (63.9%), Mid-Atlantic (56.1%), Ozarks Complex (55.8%), Southern Plains (53.6%), and Pacific Southwest (52.2%) regions. In contrast, co-limitation was least prevalent in the Southeast (27.5%) and Great Lakes (28.1%) regions where P-limitation was most prevalent (61.3% and 67.6%, respectively). A narrow majority of lakes were also P-limited in the Northeast (56.1%), whereas a minority of lakes across all other regions were P-limited, including ≤ 25% of lakes in the Ozarks Complex, Central Plains, Northern Rockies, Southern Rockies, and Great Basin. N-limitation ranged from 2.7% of lakes (Northeast) to a high of 38.0% (Great Basin). Results were generally consistent when compared to an analysis of NLA data only ($n = 1905$ lakes) (Supporting Information Fig. S2; Table S3). Overall, most US lakes were either co-limited or P-limited, with co-limitation most common in the interior and western US and P-limitation most common in the Upper Midwest, Northeast, and Southeast.

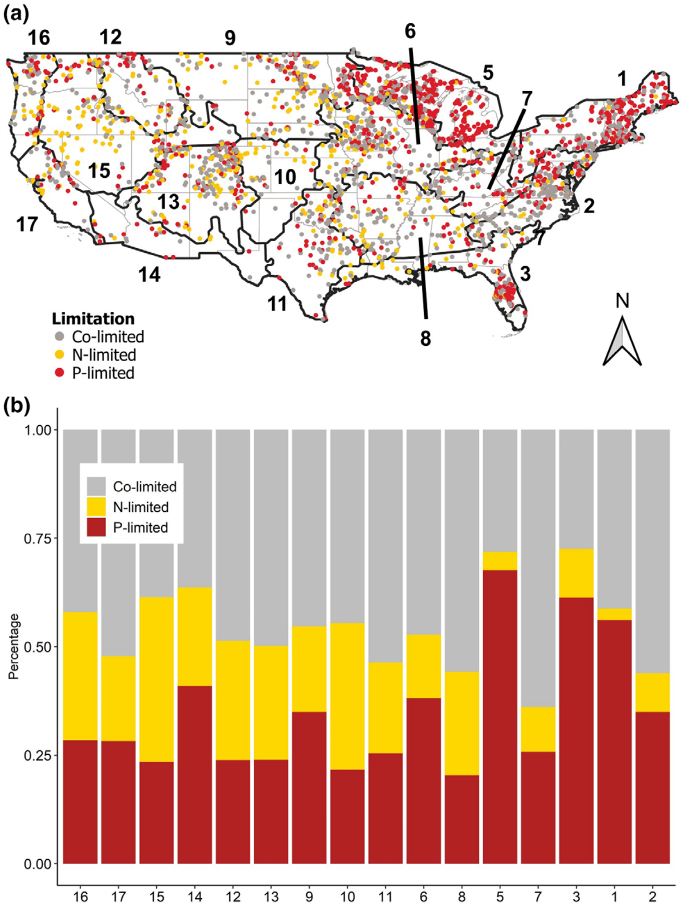

Fig. 1. (**a**) Study lakes by nutrient limitation and NEON region, indicated by bold numbers. (**b**) Percentage of lakes by nutrient limitation across NEON regions, arranged approximately west to east along the *x*-axis. 1 = Northeast, 2 = Mid-Atlantic, 3 = Southeast (includes four lakes from #4 Atlantic Neotropical), 5 = Great Lakes, 6 = Prairie Peninsula, 7 = Appalachians and Cumberland Plateau, 8 = Ozarks Complex, 9 = Northern Plains, 10 = Central Plains, 11 = Southern Plains, 12 = Northern Rockies, 13 = Southern Rockies and Colorado Plateau, 14 = Desert Southwest, 15 = Great Basin, 16 = Pacific Northwest, 17 = Pacific Southwest.

Characteristics of P-, N-, and co-limited lakes

Environmental context at lake, watershed, and regional scales all predicted lake nutrient limitation. Chl *a* concentration was the most important predictor of nutrient limitation, followed by longitude, watershed percent clay in soil, and regional wet nitrate deposition (Fig. 2; Supporting Information Fig. S3). Lake variables had the highest importance and accounted for 56.4% of combined weighted decrease in Gini index model accuracy while watershed and regional variables accounted for 23.3% and 20.2%, respectively. The top two lake-scale predictors were Chl *a* concentration and maximum depth, with P-limited lakes (Chl *a*: $10.7 \pm 18.5\ \mu\mathrm{g\ L}^{-1}$, depth: 12.7 ± 15.3 m) having lower

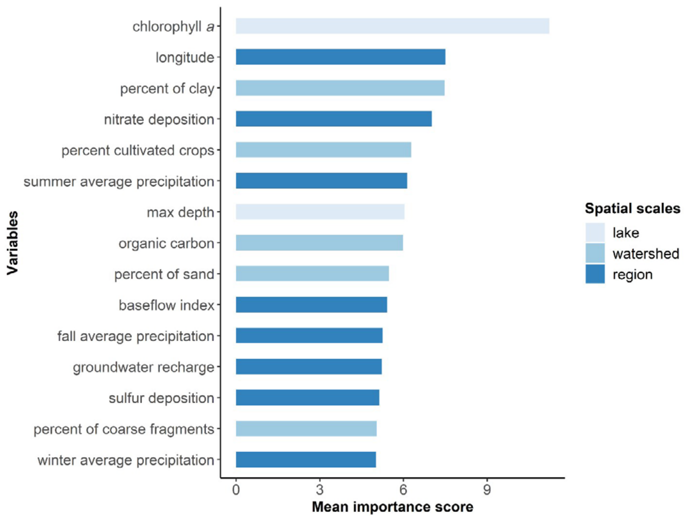

Fig. 2. Mean importance scores of the top 15 predictors of lake nutrient limitation identified by Boruta feature selection. Colors indicate variable spatial scale.

Chl *a* concentrations and greater maximum depth than N-limited (Chl *a*: 34.0 ± 62.8 μg L^{-1}, depth: 9.08 ± 13.2 m) and co-limited (Chl *a*: 32.0 ± 57.7 μg L^{-1}, depth: 9.84 ± 13.8 m) lakes (Fig. 3a,b). At the watershed scale, percent clay in soil and percent cultivated crops were the strongest predictors of nutrient limitation. N-limited lakes (clay: 19.3% ± 6.88%, cultivated crops: 24.9% ± 30.7%) had higher percent clay in soil and percent cultivated crops than P-limited (clay: 14.1% ± 6.93%, cultivated crops: 17.9% ± 24.1%) and co-limited (clay: 17.6% ± 7.08%, cultivated crops 22.9% ± 28.3%) lakes (Fig. 3c,d). Longitude and wet nitrate deposition were the top two predictors at the regional scale. P-limited lakes (longitude: −89.6° ± 12.8°, deposition: 9.14 ± 3.36 kg ha^{-1}) were more common in eastern longitudes and experienced greater wet nitrate deposition than N-limited (longitude: −102° ± 12.9°, deposition: 6.57 ± 3.65 kg ha^{-1}) and co-limited (longitude: −94.0° ± 13.3°, deposition: 8.46 ± 3.50 kg ha^{-1}) lakes (Fig. 3e,f). See Supporting Information Table S4 for summaries of all predictors and Supporting Information Figs. S4–S8 for maps of top predictors.

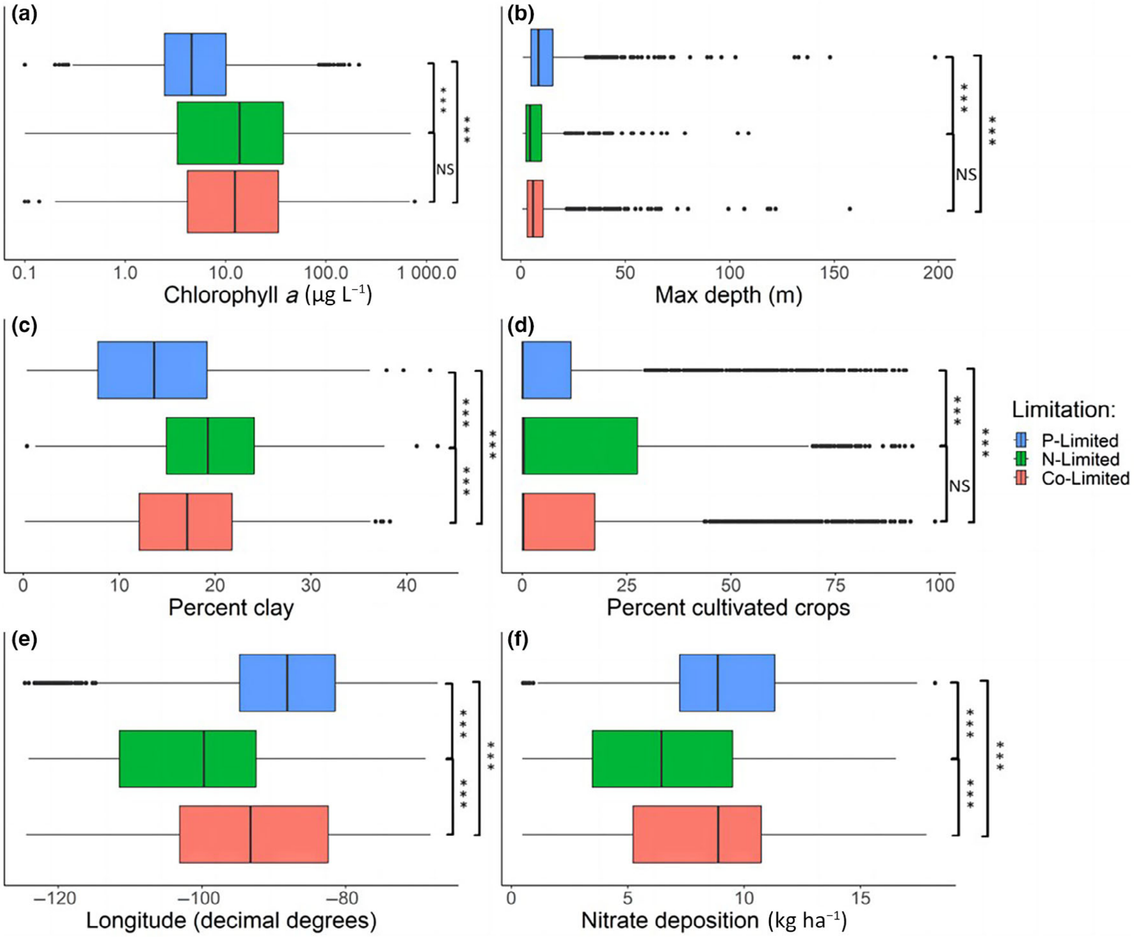

Fig. 3. Comparison of P- (blue), N- (green), and co-limited (pink) lakes across the top two predictors of nutrient limitation at lake (**a**, **b**), watershed (**c**, **d**), and regional (**e**, **f**) scales. The bolded lines in the boxes represent the median values of variables. Pairwise comparisons were based on Tukey's contrasts. NS, nonsignificant difference; ***$p < 0.001$.

Nutrient–chlorophyll relationships

Nutrient–chlorophyll relationships varied across P-, N-, and co-limited lakes and were related to interactions between TN and TP (GLMM, $p < 0.001$). Slopes of TP–chlorophyll relationships were greater in P-limited lakes and slopes of TN–chlorophyll relationships were greater in N-limited lakes (Fig. 4). Conversely, these respective relationships were weaker in N-limited and P-limited lakes, indicating that primary limiting nutrient concentrations were generally more strongly correlated with Chl *a* concentrations. Specifically, in N-limited lakes, there was a strong positive relationship between Chl *a* and TN concentrations (GLMM, slope ≧1.71, $p < 0.001$), with increasing slopes as TP concentrations increased providing evidence of TN : TP interaction (Fig. 4a,d). Additionally, despite N-limitation, we observed a positive relationship between Chl *a* and TP concentrations (GLMM, slope ≧0.38, $p < 0.001$), with increasing slopes as TN concentrations increased (Fig. 4a). We also encountered interactions between TN and TP in P-limited lakes (Fig. 4b,e). Whereas there were significant, positive relationships between Chl *a* and both TP and TN concentrations in P-limited lakes (GLMM, TP slope ≧1.53, TN slope ≧0.47, $p < 0.001$), TP had greater slopes, indicating stronger effects on Chl *a* concentrations. We did not find significant interactions between TN and TP in co-limited

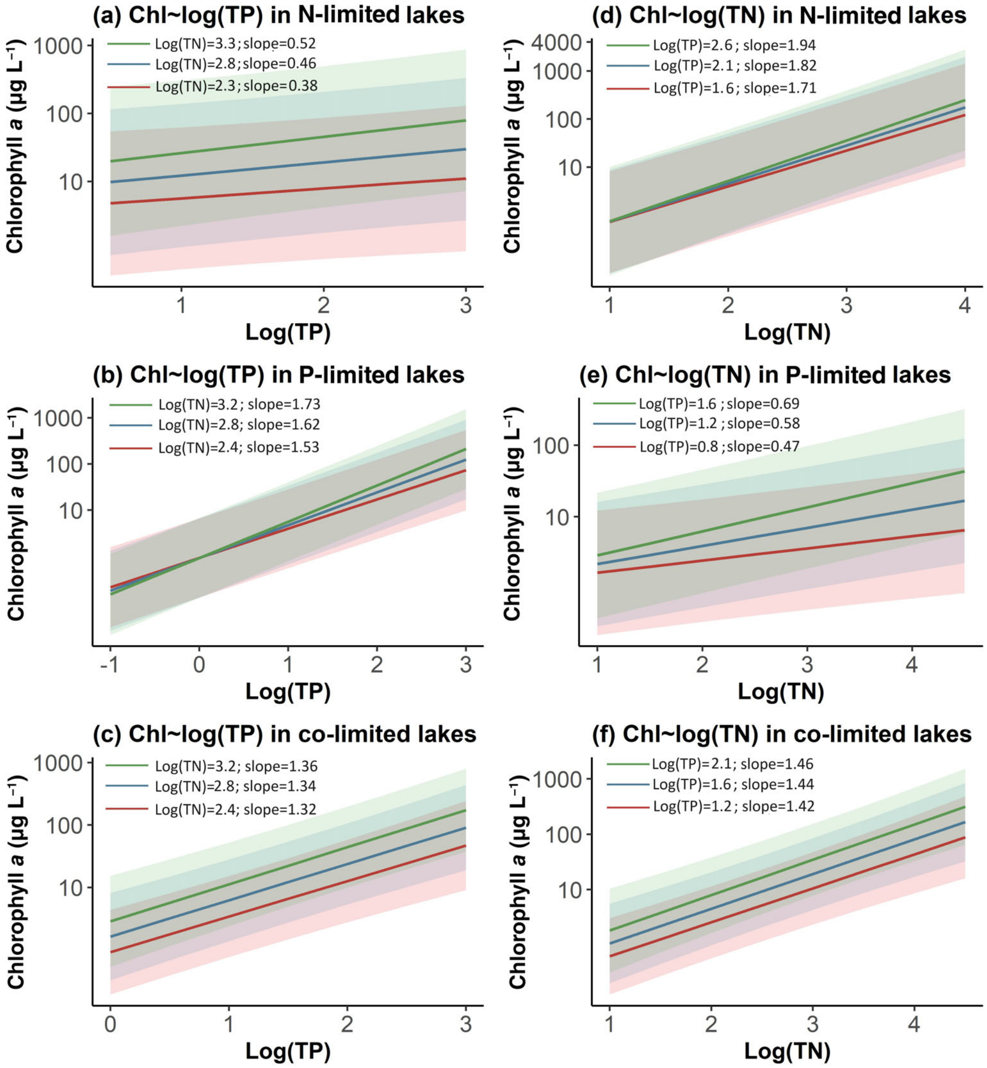

Fig. 4. Relationships between Chl *a* (μg L^{-1}) and log$_{10}$-transformed TN or TP concentrations, taking into account different levels of the other nutrient. Plots (**a**–**c**) Chl *a* and log$_{10}$(TP) relationships in N-, P-, and co-limited lakes; and lines with different colors are the prediction lines at mean–SD (standard deviation), mean, and mean + SD of log$_{10}$(TN). Plots (**d**–**f**) Chl *a* and log$_{10}$(TN) relationships in N-, P-, and co-limited lakes; and lines with different colors are the prediction lines at mean–SD, mean, and mean + SD of log$_{10}$(TP). Shadow areas represent 95% confidence intervals. The mean ± SD values of log$_{10}$(TN) in plots (**a**–**c**) are 2.81 ± 0.49, 2.80 ± 0.35, and 2.82 ± 0.43, respectively. The mean ± SD values of log$_{10}$(TP) in plots (**d**–**f**) are 2.09 ± 0.50, 1.17 ± 0.38, and 1.64 ± 0.44, respectively.

lakes (GLMM, $p = 0.460$; Fig. 4c,f). In summary, nutrient–chlorophyll relationships were consistently positive across P-, N-, and co-limited lakes. Relationships were generally stronger for whichever nutrient was primarily limiting and both nutrients interactively increased Chl *a* concentrations in both N- and P-limited lakes.

Discussion

Our analysis of 3342 lakes across the conterminous US is one of the largest studies of nutrient limitation of primary productivity in lakes. We showed that US lakes are predominantly P-limited or co-limited, but with some distinct regional patterns. Notably, two of the three regions with majority P-limitation (Northeast and Upper Midwest) have many of the longest-running, most well-known US lake monitoring programs (e.g., North Temperate Lakes Long-Term Ecological Research program; Magnuson et al. 1997). Although such programs have provided foundational knowledge for limnology, it is possible that some principles, such as the prevalence of P-limitation, cannot be consistently applied to lakes in fundamentally different environmental contexts. Moreover, our finding that nutrient–chlorophyll relationships were generally stronger for the primary limiting nutrient has substantial implications for lake eutrophication management because of the wide geographic variability in P-, N-, and co-limitation across the United States. We not only found that all regions contained a mix of P-, N-, and co-limited lakes, but also that the plurality of lakes in 11 of 16 regions are co-limited and only 3 regions had a majority of lakes limited by one nutrient. These findings are corroborated by regional-scale studies that also found high prevalence of co-limitation but also mixes of P-, N-, and co-limitation (Bratt et al. 2020; Lewis et al. 2020; Volponi et al. 2023). Taken together, there is increasing evidence that eutrophication management should consider N and P jointly in most, if not all regions.

A strength of our broad-scale approach is the ability to demonstrate that lake nutrient limitation is related to a combination of environmental context at lake, watershed, and regional scales. Our finding that Chl *a* concentration was the best predictor of nutrient limitation is consistent with past broad-scale studies showing the importance of trophic state (e.g., Liang et al. 2020). This has important implications in a global change context for lakes at risk of eutrophication (Gilarranz et al. 2022). We also found that lake maximum depth is a strong predictor of nutrient limitation (consistent with Zhao et al. 2023), but it may be just as noteworthy which variables were unimportant, such as lake area and natural lake vs. reservoir status (Fig. 2; Supporting Information S1). Interestingly, longitude was an important predictor of limitation with a greater prevalence of P-limitation and N-limitation in the eastern and western US, respectively. This could reflect legacies of intensive agriculture and urbanization in the eastern US, but even remote mountain lakes in the western US can shift from N- to P-limitation due to atmospheric N deposition (Elser et al. 2009*b*). However, soil properties, nitrate deposition, precipitation, hydrology, and agriculture were also important regional predictors and many of these have spatial patterns related to longitude (Lapierre et al. 2018). Teasing apart complex, interacting mechanisms across scales is beyond the scope of this paper, but is an important future step. Although our 3342 lakes are distributed across many wide ecological gradients, different drivers of nutrient limitation may still be more important in other ecological contexts (e.g., very high or low latitudes) and our findings of a mix of N-, P-, and co-limited lakes across all regions caution against overgeneralizing patterns and drivers of lake nutrient limitation. Nevertheless, we expect our finding of the combined importance of lake, watershed, and regional context in lake nutrient limitation to apply across diverse ecological settings.

Broad-scale studies such as ours can provide us with the knowledge to apply to a broad range of ecological contexts and can complement fine-scaled studies limited in the generalizability of their findings. However, broad-scale approaches are limited in other ways. For example, TN : TP ratios represent a coarse metric of nutrient limitation and our results only indicate general patterns of how nutrients may influence primary productivity. There are no practical ways to assess important processes such as nutrient bioavailability or denitrification vs. N fixation rates at the macroscale (e.g., Elser et al. 2009*a*; Bergström et al. 2020). Moreover, our study focused on lakes ≥ 4 ha (smaller lakes are rarely sampled; Shuvo et al. 2023) from May to September, but nutrient limitation can vary seasonally, particularly in small, shallow lakes (Maberly et al. 2020). Many lakes throughout our study are biologically active outside May–September, including during winter and particularly at lower latitudes (Hampton et al. 2017). Therefore, a productive path forward is to work toward connecting mechanistic insights from finer-scaled studies to broad-scale patterns of lake nutrient limitation across wide environmental gradients.

Although the long-standing nutrient limitation “debate” in limnology may never be fully resolved, our results support a more balanced view of nutrient limitation that recognizes the critical role of both nutrients, as others have previously argued (e.g., Sterner 2008; Conley et al. 2009; Harpole et al. 2011; Paerl et al. 2020), and we add evidence that nutrient limitation varies geographically according to a combination of lake, watershed, and regional context. Our study uncovered a mix of P-, N-, and co-limitation in all regions of the conterminous US, but with considerable variability across and within regions. As large, public limnological databases are increasingly coming online (e.g., Canadian Lake Pulse Network, Huot et al. 2019; European Multi-Lake Survey, Mantzouki et al. 2018; US NLA, Pollard et al. 2018, China lake dataset, Zhang 2019; LAGOS-US LIMNO, Shuvo et al. 2023) limnologists now have remarkable capacity to study nutrient limitation in lakes across unprecedented spatial and temporal scales and across wide ecological gradients, particularly when coupled with multiscale environmental context (LAGOS-US, Cheruvelil et al. 2021; HydroLAKES, Messager et al. 2016). Considering the ever-increasing global change stressors on lakes, perhaps our best bet for informing lake eutrophication management is to invest our growing wealth of data toward a growing wealth of knowledge.

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