Ratios Matter

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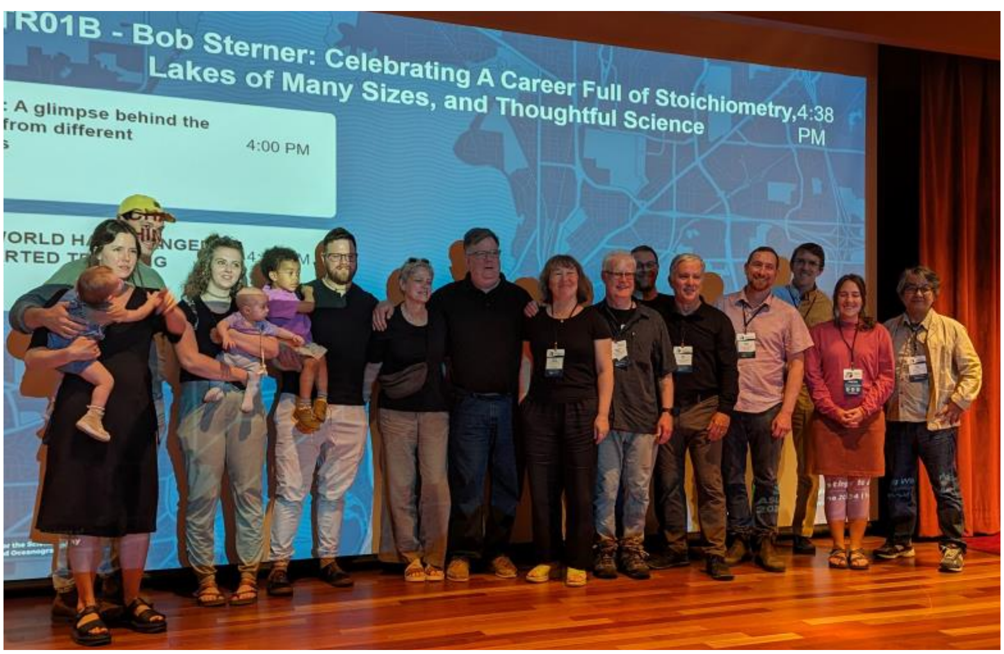
Bob Sterner Retires from Ratio Research

Ecological stoichiometry is synonymous with Bob Sterner. This is partly because he co-wrote the foundational book on the topic, but it goes beyond that. Many of us in the stoichiometry world have benefitted from Bob's deep intellect, his kindness, and his generous spirit. Bob was especially supportive of early career stoichiometrists and encouraged many of us to take leading roles in projects. He was a great mentor, who led by example with his creation of stoichiometric theory, which has given all of us a lifetime of follow-up research opportunities. At the same time, Bob challenged us to do stoichiometry better by sticking to the principles but being flexible and open-minded when needed. These were the stories and recollections brought to the stage at the ASLO 2024 summer meeting in Madison, Wisconsin, during a special session celebrating Bob's stoichiometric career. In one recounting during the session, Jim Hood highlighted how Bob loves a good bivariate plot and the challenge of developing a physiological understanding of why slopes and intercepts act in certain ways. Former students and colleagues also shared their experiences and memories of working with Bob and highlighted his influence on this ecological field.



Bob Sterner takes the stage at 2024 ASLO's special session celebrating his stoichiometric career with family, colleagues and other hanger-ons.

All of us at *Ratios Matter* wish Bob the best during his retirement and hope he has many days on the shores of Lake Superior relaxing...and not chasing emerging cyanobacteria blooms.

Dive into a drop of water and experience the world of plankton! Fight microscopic monsters. Survive environmental challenges. Cooperate with others…but remember, there can only be one winner!

In case you missed it, there is a new card game for teaching about plankton ecology and trait-based ecology! Concepts covered by the game include traits, trade-offs, environmental drivers, ecological strategies, etc. Integration into the classroom involves game-play, followed by reflective questions to discuss the various concepts. Further information about the game, teaching materials, and a free PDF, including options to receive a printed version, can be found at (all materials available by mid-September 2024):

https://nioo.knaw.nl/en/projects/game-of-traits-a-card-game-about-trait-based-ecology

For more information on this game and its use in the classroom, contact: **Dedmer Van de Waal (d.vandewaal@nioo.knaw.nl)**

Stoichiometric Profiles of Individual Microbial Parasites

Nicole Wanger
Oakland University

A new paper from *Ratios Matter*'s own Charlotte Narr, in collaboration with Ed Hall and their colleagues, was recently published in *Ecology and Evolution*. Have you ever wondered how parasites' stoichiometry varies within their hosts? It can be relatively easy to measure stoichiometry on macroparasites by separating the parasite from the host. However, for microbial parasites, it becomes more difficult to separate and measure their stoichiometry. Even if you manage to extract and measure the stoichiometry of microbial parasites, the amount of parasite biomass required for traditional nutrient analyses prevents getting an estimate of the stoichiometric variation within the hosts. Narr and colleagues sought to measure the stoichiometric variation of two parasites, the bacterium, *Pasteuria ramosa,* and the microsporidian, *Hamiltosporidium tvaerminnensis,* within individual hosts of the freshwater invertebrate *Daphnia*. The *Daphnia* were grown for 28 days on a low and high C:P diet, and then the C:N:P of 60-100 individual parasite spores from each host was measured by energy dispersive spectroscopy (EDS). The authors expected the parasites grown in P-limiting conditions to have higher C:P ratios than parasites grown in P-rich conditions. However, the bacteria had a lower C:P when grown in P-limiting conditions compared to P-rich conditions. They also found that variation in parasite C:N and C:P within hosts explained spore load and fecundity in the *Daphnia* better than the mean C:N or C:P of all the parasites within a host.

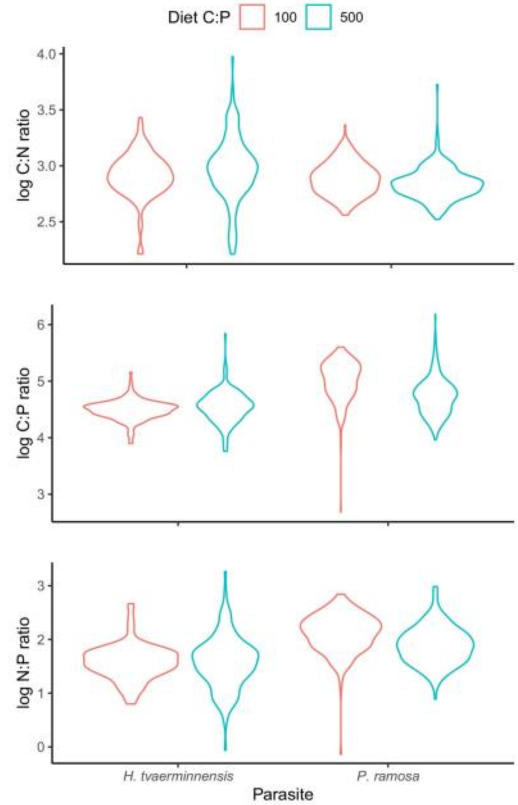


Figure 2 from Narr et al. (2024). Log-transformed stoichiometric ratios of spores from infrapopulations of *Hamiltosporidium tvaerminnensis* and *Pasteuria ramosa* in daphnid hosts raised on diets with C:P ratios of 100 (red) and 500 (blue).

The authors conclude *"that traditional nutrient analyses .... limit the ability to infer the role of the parasite's nutrient content in shaping parasite or host success."*

Narr, C.F., S. Binger, E. Sedlacek, B. Anderson, G. Shoemaker, A. Stanley, M. Stokoski and E. Hall. 2024. Evaluating host diet effects on microparasites by measuring the stoichiometry of infrapopulations one cell at a time. Ecology and Evolution 14: e11645

Revisiting Redfield in the Omics Age:
Trait-based biochemical controls on the elemental stoichiometry of a marine cyanobacterium

Catriona Jones
Purdue University

Phytoplankton elemental stoichiometry is a key driver of ecosystem processes in the oceans, from trophic exchanges to nitrogen fixation. The classic assumption about marine phytoplankton is that their elemental stoichiometry is relatively fixed and adheres to the Redfield Ratio of C:N:P 106:16:1. Field studies in recent years have painted a different picture, with evidence of strong temporal and regional variation in these elemental ratios. Biochemical mechanisms, such as translation, transcription, and macromolecular allocation are suspected to control cellular stoichiometry in marine phytoplankton, but the presence of multiple influential factors can make these effects difficult to tease apart. There are three main hypotheses linking biochemical processes to cellular stoichiometry:

1. *The Nutrient Supply Hypothesis* states that algae are frugal with nutrients under low supplies and will increase nutrient storage under high supplies.
2. *The Translational Compensation Hypothesis* states that P-rich ribosomes are more abundant at low temperatures to compensate for slower translational activity, therefore C:P and N:P ratios are decreased in high-latitude ecosystems.
3. *The Growth Rate Hypothesis* states that cellular growth has specific requirements for P-rich ribosomes and rRNA that can directly affect $C:N:P_{cell}$, resulting in trade-offs with other cell components.

The complication with testing these hypotheses in the field is that each of the hypotheses can explain variation in field observations of elemental stoichiometry equally well due to high latitudinal co-variation in nutrient supply, temperature, and growth rates of marine phytoplankton.

In this paper, Garcia et al. (2024) used controlled laboratory experiments to mimic balanced growth conditions in the ocean and a fully factorial design with two nutritional treatments (N:P = 1.7 and 80 by mol) and three temperature treatments (20, 24, and 28°C). They focused specifically on the proteome to understand trait-based biochemical regulation of cell quotas due to evidence of protein-based mechanisms to manage environmental stress (for example, sulfolipids can replace phospholipids in membranes of cyanobacteria under P-stress, thereby reducing the cellular P quota).

The researchers used the common marine cyanobacterium, *Synechococcus,* which is one of the largest contributors to ocean primary production, in conjunction with peptide mass spectrometry and proteomic analysis to understand trait-based biochemical regulation of cell quotas and elemental stoichiometry.

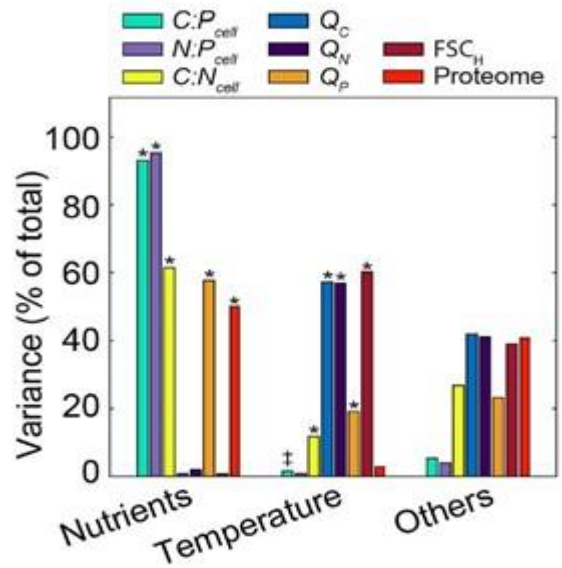


Figure 1 from Garcia et al. (2024). Results from PERMANOVA analysis showing the effect of environmental drivers (nutrients, temperature, and others such as residuals and interactions) on cellular quotas, elemental ratios, and proteome as proportions of whole model variance. *FSC_H = forward scatter (cell size).

The authors found support for all three of the proposed hypotheses, but their findings suggest a hierarchical environmental control on cellular stoichiometry. The strongest control was found to be nutrient availability, with most of the observed variation in $C:N:P_{cell}$ explained by nutrient supplies. This, in turn, prompted trade-offs between nutrient acquisition and ribosomal proteins, which provides support for the Growth Rate and Nutrient Supply hypotheses. However, there was also evidence for the Translational Compensation Hypothesis, but this was only observed in P-limited treatments. Additionally, nutrient-supply effects on $C:N_{cell}$ showed a weaker, more temperature-dependent relationship. Together, these findings indicate that the regulation of marine C:N ratios, in particular, is complex and multi-faceted and likely depends on multiple, latitudinally varying drivers.

Finally, the authors acknowledge that there is more work to be done expanding this research, with particular focus on including multiple strains and species to scale these results to a community level and understanding the potential role of external factors such as biodiversity shifts in addition to biochemical regulation.

From the paper: *"…shifts in biodiversity may contribute to C:N:P variability in the surface ocean beyond the physiological mechanisms described here. Hence, the combined field and experimental data suggest complex effects on C:N:P in marine ecosystems that incorporate current hypotheses and evolving theories."*

Garcia, N.S., M. Du, M. Guindani, M.R. McIlvin, D.M. Moran, M.A. Saito and A.C. Martiny. 2024. Proteome trait regulation of marine *Synechococcus* elemental stoichiometry under global change. Isme Journal 18: Article wrae046

Stoichiometry in the Classroom: New teaching module focuses on fish nutrient recycling

Chip Small
University of St. Thomas, Minnesota

Carissa Ganong (Missouri Western State University) and I recently published a stoichiometry teaching module titled: *How do tropical fish, rainforest canopies, and volcanic groundwater inputs affect stream phosphorus cycling* (https://www.learngala.com/cases/fish-forests-phosphorus)? These teaching materials are based on research that I conducted 15 years ago as part of my dissertation research (Ecology 92: 386-397). This module was developed through the NSF-funded Online Content for Experiential Learning of Tropical Systems (OCELOTS) project. Below, I answered questions from *Ratios Matter* editors about this new resource and my experience teaching the next generation of stoichiometric researchers.

How did you get started with teaching stoichiometry?
My first job out of college was teaching high school chemistry, so I had to learn how to teach 10th graders to balance chemical equations, calculate yields, etc. I remember having my students work out stoichiometry problems with hot dogs (which often come in packs of 10) and hot dog buns (which come in packs of 8 for some reason).

And then you transitioned into ecology research?
I started my Ph.D. program just after the Sterner and Elser book came out. I was really excited about working in tropical streams and Mike Vanni had just published an amazing study from Venezuela on how fish and amphibian species body N:P ratio affects N:P recycling rates. I wanted to expand on this idea in our study streams in Costa Rica. We didn't have as large a range of body N:P in the fish assemblage, but we did have a range of diets represented (with fish specializing in feeding on periphyton, aquatic insects, and terrestrial insects). And we had study streams with high-P groundwater inputs, which resulted in the entire aquatic food web being P-enriched.

Is this the study that the new teaching module is based on?
Yes! Students get to walk through the process of making hypotheses about fish nutrient recycling rates based on fish diet and body N:P, and testing those hypotheses using the data we collected. They then apply this information to show why one fish species, which makes up only 20% of the fish community biomass, nonetheless accounts for 90% of the fish-derived P recycling.

What level of students is the teaching module designed for?
The target audience is upper-level undergraduates in an ecology or aquatic biology course. I actually beta-tested it in an introductory environmental science course. It can still work for students with less of a science background—you just want to take a little more time to make sure that all students are on the same page with interpreting the graphs. The module was designed to be a stand-alone 2-hour lab activity, but instructors have a lot of flexibility. You could pull out just a few key points to incorporate into another lecture. We've also included some questions that could be developed into mini-research projects if you wanted to use this project as a jumping-off point to have students explore some of these topics in more detail.

Do you have any tips for teaching ecological stoichiometry to undergraduates?
I've found that students can grasp the basic concepts quickly because they've had some experience with this from chemistry, but we're applying these ideas in ways that they haven't thought about before. One resource I like to use with my students is an article that Bob Sterner, Jim Hood, and I wrote on The Conservation of Mass for the Nature Education Knowledge Project. That article has some fun examples of stoichiometry at the organismal and ecosystem levels. I'll also mention that we included an instructor's teaching guide with the new module, which includes some teaching tips, as well as some suggested questions for assessment and optional extension activities.

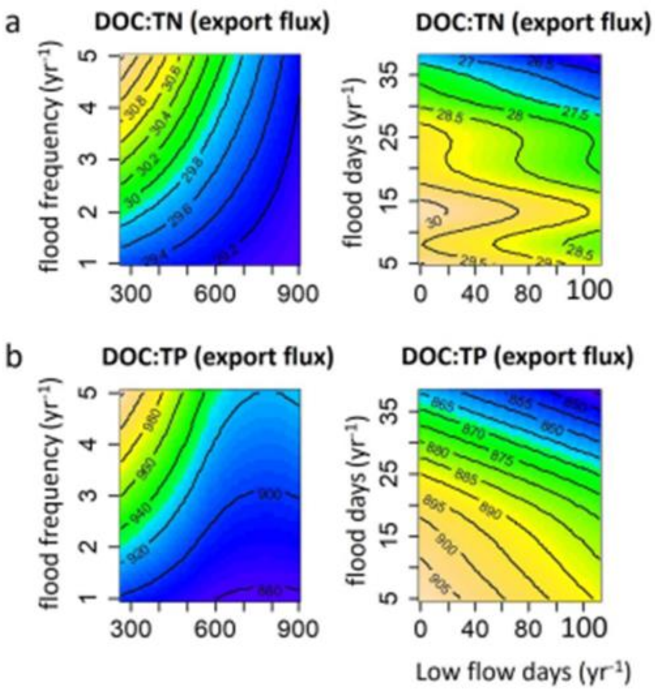
Chip Small and Pedro Torres collecting fish for this study at La Selva Biological Station, Costa Rica, in 2007.

Flow regimes and seasonality are critical to shaping organic carbon: nutrient stoichiometry in aquatic ecosystems

Brittany Perrotta
USA

Christina Fasching
Philipps-University Marburg, Germany

Christina Fasching and co-authors recently published a new study in Water Resources Research that used a 37-year dataset to understand how flow regimes and seasonality affect watershed scale stoichiometry within two lake watersheds (meaning two lakes including their ten inflow and two outflow streams) in the southern Boreal Shield (Ontario, Canada). They found that extreme events, such as floods and droughts, can significantly alter DOC:TN:TP stoichiometry in streams and change the retention behavior of lakes. For example, slightly higher than average baseflows (10%–20% higher) initially increased the amount of DOC exported from the watershed compared to N and P. DOC export was notably lower during low flows and flood events, leading to increased relative contributions of TN and TP in recipient streams and lakes. While the lakes generally retained DOC and TP, longer periods of low flow stimulated TN removal, but larger floods on an annual scale lowered the lake's ability to retain DOC and TP. The authors also show that seasonality played an important role in shaping watershed scale stoichiometry.



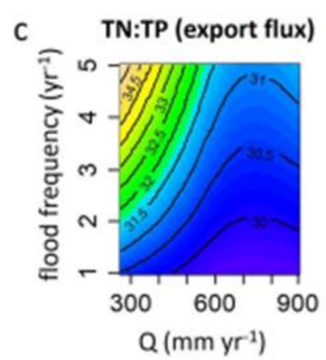


Figure 4 from Fasching et al. (2024). General Additive Models (GAMs) of the stoichiometry (a) DOC:TN, (b) DOC:TP and (c) TN:TP, in grams) of yearly (1979–2014) export fluxes for the ten inflows. The color scale indicates the range of the stoichiometric ratios, with yellow indicating increased values that are specific to individual subplots (see contour line values for exact numbers).

Continued from previous page. Spring floods decreased DOC:TN, but warmer summer air temperatures and prolonged low flow periods were related to lower TN:TP and DOC:TP concentration ratios. The research of Fasching et al. (2024) demonstrates the value of expanding analyses beyond individual nutrients and extending sampling timelines, as DOC:TN:TP patterns may only become evident over extended time spans. While similar concentration and export trends of DOC, TN and TP individually may be observed with discharge, the study shows that extreme events can significantly alter DOC:TN:TP stoichiometry. Overall, their results suggest that alterations in flow regime—the frequency, magnitude, and timing of flow events–can markedly influence the fluxes and retention of aquatic carbon and nutrients to downstream ecosystems across the continuum from inland to marine environments.

From the paper: *"Our results underscore that using a stoichiometric approach significantly enhances our ability to monitor water quality and their biogeochemical im-pacts beyond single extreme events, thereby enabling predictions regarding potential alterations in the biogeochemistry of lake ecosystems caused by current and future events."*

Fasching, C., K.S. Boodoo, H. Yao, J.A. Rusak and M.A. Xenopoulos. 2024. Role of lakes, flood, and low flow events in modifying catchment-scale DOC: TN: TP stoichiometry and export. Water Resources Research 60: e2023WR034839.

AI Art of Ecological Stoichiometry

Inspired by similar artwork displayed by Jim Cotner in his recent ASLO talk and with dead space to fill, we asked Google Gemini to draw something stoichiometric for us. We used key words from the Sterner and Elser (2002) Ecological Stoichiometry book and choose one of several intriguing, interesting, and inspiring (?) options.

*If you have real art that you want to be featured, send it our way!

Patterns in Lake Nutrient Limitation: Elemental, but not simple

Linnea Rock
University of Wyoming

Charlotte Narr
Southern Illinois University

Nutrient limitation of lakes influences the health of the entire ecosystem including primary productivity, biodiversity, and biogeochemistry. So, which has a greater impact on lake productivity, N or P? A new study published in Environmental Science and Technology by Rock and Collins (2024) weighs in on the age-old question using data from the U.S. Environmental Protection Agency's National Lakes Assessment. The result: it depends, and it's changing over time. The study revealed regional variation in broad-scale nutrient limitation, with N correlating more strongly with productivity in the Western regions and P more influential in the East (See Fig. 2 on next page).

To look beyond these broad trends and consider nutrient limitation at the lake-by-lake scale, Rock and Collins (2024) used limitation tipping points specific to each ecoregion. They found that nutrient limitation was spatiotemporally variable, and a majority of lakes (84% in 2017) were co-limited by N and P or other confounding factors. The prevalence of co-limitation actually increased over a decade from 2007 to 2017, underscoring the complexity of nutrient dynamics in lakes. Furthermore, co-limited lakes were more commonly mesotrophic or eutrophic, suggesting there may be fluctuations between insufficient and excess nutrients.

Nutrient management strategies are essential for preserving the health and functionality of lakes. This study highlights the necessity for combined nutrient management strategies to mitigate eutrophication effectively. Moreover, understanding nutrient dynamics requires consideration of both broad-scale patterns and localized conditions due to the significant spatiotemporal variability in nutrient limitation.

From the Paper: *"Our study showed how patterns can aggregate across subcontinental scales yet still demonstrate considerable variation when more deeply examined within ecoregions. 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."*

Rock, L.A. and S.M. Collins. 2024. A broad-scale look at nutrient limitation and a shift toward co-limitation in United States lakes. *Environmen-*

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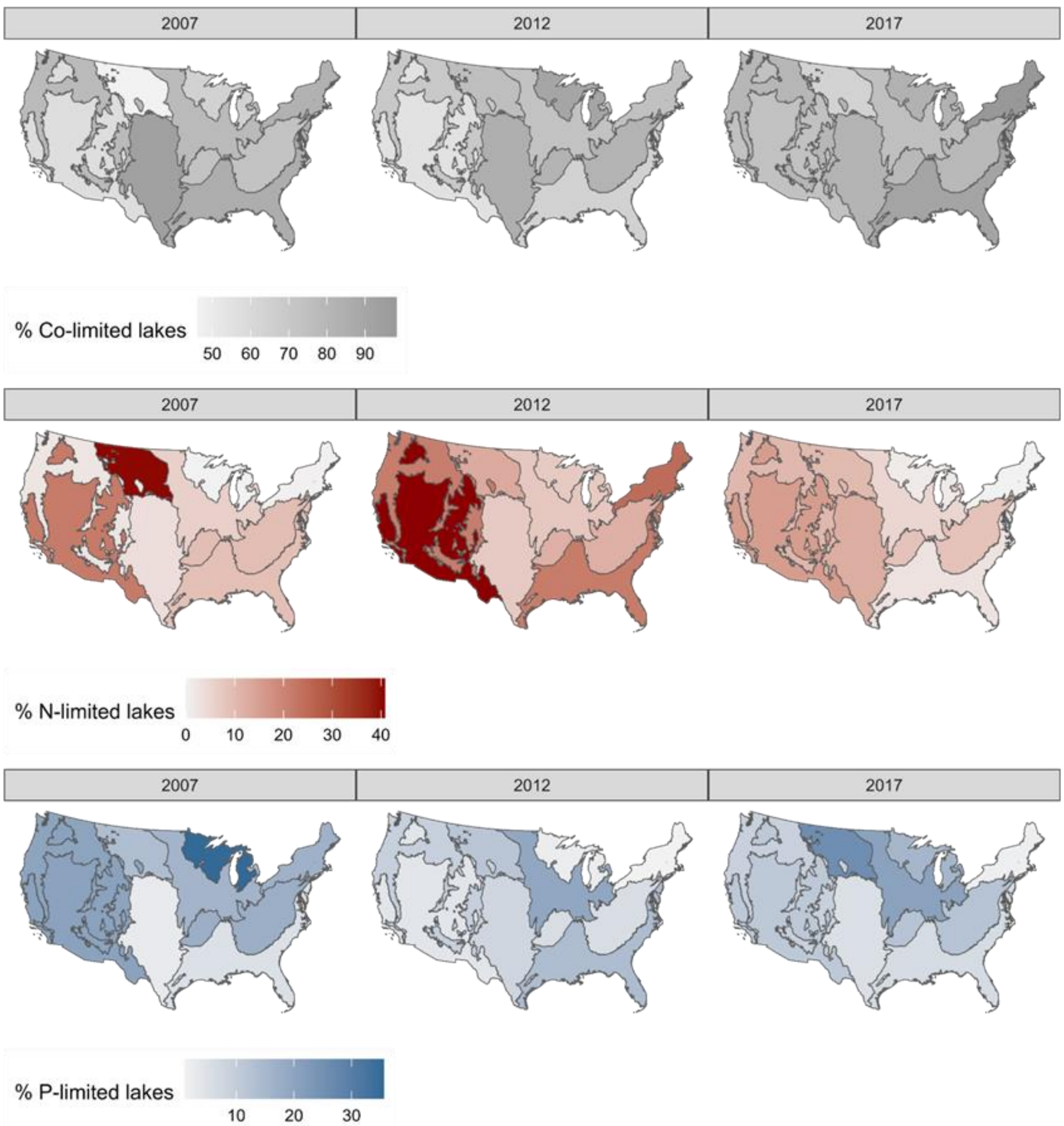

Figure 2 from Rock and Collins (2024). Spatial and temporal variability of nutrient limitation mapped across nine ecoregions of the U.S. Percent of lakes that are co- (gray), N-(red), and P- (blue) limited are displayed within each ecoregion and year.