Ratios Matter

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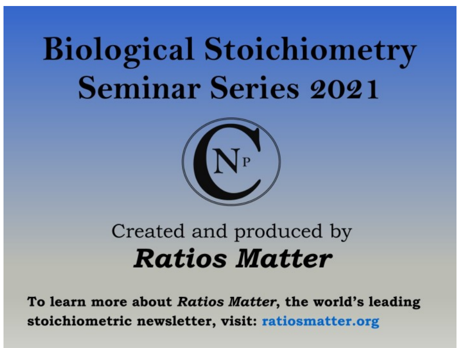
Biological Stoichiometry Seminar Series 2021

Over the past year, you may have turned to Zoom to stay connected with your colleagues. *Ratios Matter* is no different! We launched a new seminar series to create a platform where stoichiometry research can be shared and discussed with like minds. The monthly seminar series has highlighted what draws many of us to the field: the breadth of topics over which stoichiometry is applied. If you missed one, here is a recap of our first four talks.



Kimberley Lemmen (University of Zurich) started the series in May with a talk titled "Evolutionary responses of primary consumers reduce the cost of stoichiometric imbalances." Her work addressed whether or not ecological stoichiometry could help understand evolutionary patterns and trajectories using rotifers as a study organism. She found that even in the absence of standing genetic diversity, heritable responses to stoichiometric food imbalances are possible.

In our June seminar, **Jim Junker (Michigan Technical University)** considered the relative role of biological processes in influencing ecosystem stoichiometric characteristics with a talk titled "Environmental and ecological drivers of organic matter stoichiometry across a geothermally influenced watershed." Jim showed stream flow characteristics are a primary driver of differences in organic matter quantity, composition, and stoichiometry in arctic streams.

Nicole Wagner (Baylor University) gave the seminar in July on the stoichiometry of harmful algal blooms. In her talk, Nicole discussed how biological stoichiometry regulates growth, physiology, and cyanotoxin production in several common HAB producing genera. She found that N:P ratios available to cyanobacteria can dramatically affect multiple aspects of their physiology and toxin production.

In our August seminar, **Cathy Garcia (University of Hawaii)** gave a talk on how genomic markers of nutrient stress improve a stoichiometric phytoplankton trait model. She discussed how combining approaches (genomics and particulate elemental observations) improves our predictions of phytoplankton elemental ratios under nutrient stress among subtropical ocean basins.

All four of these talks are available for viewing on YouTube:
Kimberley Lemmen: https://youtu.be/aj568grg_5I
Jim Junker: https://youtu.be/pxrda2h2yiA
Nicole Wagner: https://youtu.be/xa7rt26WurI
Cathy Garcia: https://youtu.be/UgdVDOB9dWs

The series will continue through February 2022 but maybe longer! For more information about upcoming talks, follow us on Twitter: @ratios_matter. If you are interested in giving a seminar, send us an email at ratiosmatter@gmail.com.

Contributed by Jess Corman

Trivia Time

Welcome to the *Ratios Matter* trivia quiz hosted by the Daphnia's Head virtual pub. If you wish to take part, submit your answers before October 1, 2021 by email to *Ratios Matter* with the subject line "RM Pub Quiz".

You can enter individually or as a team but each entry must be accompanied by a stoichiometry themed team name.

The Questions

1. These freshwater mutualists have been found to kick out their algal symbionts when grown under low light and/or high nutrient conditions.
2. Which zooplankters have been described as "swimming crayons" due to their high C:P content?
3. Give this marine biologist a medal for being one of the first to show super strong connections between relative growth rates and C:P ratios in phytoplankton.
4. These insects have been described as the '*Daphnia of the land*'.
5. Which animal gets its phosphorus by attending sky burials?
6. These animals work very hard increasing productivity by redistributing nutrients. Hint: They have an offaly good name!
7. Stoichiometry takes its name from the ancient Greek word *stoicheion,* what is the original definition of this word?
8. ZNGI's refer to what? And were invented by whom?
9. We all know Justus Von Liebig from his leaky barrel and Law of the Minimum but he was also responsible for inventing this very divisive foodstuff. (We will accept a brand name or a generic one)
10. Where do all the grooviest stoichiometrists go to share ideas?

Winner(s) will receive a certificate of achievement (suitable for framing) and will be announced in the next edition of *Ratios Matter*. We will also be giving out awards for the best team name. Good luck!

Live Fast, DNA Less Hard: The Biochemical Trade-Off Facing Insects with Distinct Metamorphosis Modes

The evolution of insect metamorphosis has given rise to pterygote insects that grow from juveniles to adults through two developmental modes: complete (holometaboly) or partial metamorphosis (hemimetaboly). Research has provided detailed information on the morphological and molecular (mainly hormonal) regulation of insect metamorphosis, but it is unclear how developmental mode relates to the biochemical composition (specifically nucleic acids). This uncertainty is important to resolve because nucleic acid composition determines key differences in life-history traits (e.g. growth rate) and ecological fitness. Holometabolous insects grow almost twice the speed of hemimetabolous ones between moults, so it's possible that they possess more RNA (and higher RNA:DNA ratios) to support this growth, especially in juvenile stages when growth rates are highest.

To help clarify this relationship, Villar-Argaiz et al. (2021) recently analyzed 639 aquatic insects belonging to six holometabolan and six hemimetabolan taxa and examined the genome lengths of 1335 insects from Gregory's genome size database (http://www.genomesize.com). They found significant interactions between body length and metamorphosis mode for RNA content and RNA:DNA ratio. As they predicted, RNA and RNA:DNA ratios were higher in small holometabolans relative to hemimetabolans, but those differences disappeared as the insects became larger. In addition, in both their own data and that of the database, they found lower DNA content in holo- versus hemimetabolans.

Overall, these findings extend the "growth rate-genome size-nutrient limitation" hypothesis (Hessen et al. 2009) to the taxonomical class of insects. This work also suggests that differences in nucleic acid allocation between RNA or DNA may reflect a fundamental evolutionary trade-off of growth at the expense of genome size in holometabolans relative to hemimetabolans. Ultimately, it appears that the importance of nucleic acid allocation goes beyond strictly biochemical questions, and is an important line of evolutionary research.

From the Paper: "*Given the pivotal role that aquatic insects play in freshwater as well as terrestrial food webs, the evolutionary trade-off between RNA and DNA allocation is essential as it influences key life-history traits such as growth rate.* "

Contributed by Charlotte Narr

Villar-Argaiz, M., M.J. López-Rodríguez & J.M. Tierno de Figueroa. Divergent nucleic acid allocation in juvenile insects of different metamorphosis modes. 2021. Scientific Reports 11:10313. https://doi.org/10.1038/s41598-021-89736-w

Evolution's got a hold on stoichiometry

"Only with a leaf can I talk of the forest"
Visar Zhiti, The Condemned Apple: Selected Poetry

The ability of organisms to change their tissue stoichiometry to match their environment is in vogue as research in our field takes an evolutionary bent. One of the central tenets of ecological stoichiometry is that elemental composition and ratios can be somewhat inflexible—at least on ecological times scales—and so create barriers that define organism survival, growth, and reproduction.

The elemental composition of many organisms may not be rapidly evolving, but that does not mean it is independent of evolutionary history. In fact, the evolutionary history of organisms should be a major driver of their elemental concentration and stoichiometry. One taxon where this signal may not be strong is terrestrial plants who have famously flexible leaf stoichiometry, but also have diverse life history strategies and a well-resolved phylogenetic tree. In their recent publication, Sardans et al. gathered data on about 24,000 leaves from plants across the world and across the phylogenetic tree to analyze the influence of evolutionary history and plant environment on their elemental concentration. Their study focused on the concept of a biogeochemical niche, the idea that individual species remain viable within a restricted range of elemental concentrations in their tissues. They suspected that these tissue demands correspond to uptake demand from their environment and so they could help explain where and why each species can grow.

Sardans et al.'s efforts demonstrated a dominant effect of evolutionary history on leaf elemental concentration, which they found explains 80% of the variation in their data set. Furthermore, the variation in elemental concentrations across the phylogenetic tree was consistent with evolutionary history so that species in recently divergent genera had elemental concentrations that were more similar than those within genera that diverged further back in history.

In addition to evolutionary history, environmental conditions also played an important role. Mean annual temperature, precipitation, nitrogen deposition, and soil type together explained about 2% variation in leaf stoichiometry once phylogenetic history was considered. Environmental conditions did explain more than 3.8% of the variation in leaf stoichiometry when phylogenetic relationships were ignored. However, the limited explanatory power of environmental conditions after accounting for phylogeny is surprising given our preconception that plant leaf stoichiometry plasticity follows environmental variation.

Sardans et al. proposed a mechanism to explain why leaf stoichiometry may be more variable in some genera. Species that grow in stressful environments with non-elemental limitation (e.g., drought) appeared to have less variation in their elemental concentrations, which suggests a trade-off between optimizing elemental concentrations for the mean environment versus keeping flexible for matching emerging conditions (i.e., ruderals). For those species living in the wet, comfortable, herbivore-free ecosystems of the world, the strong effect of phylogeny on their leaf stoichiometry is a reminder that even the most malleable organisms carry the legacy of their evolutionary past.

From the Paper: *"Shared ancestry explained 60–94% of the total variance in foliar nutrient concentrations and ratios whereas current climate, atmospheric N deposition and soil type together explained 1–7%, consistent with the biogeochemical niche hypothesis which predicts that each species will have a specific need for and use of each bio-element.*"

Contributed by Robert Buchkowski, Jordi Sardans, and Josep Peñuelas

Sardans, et al. 2021. Empirical support for the biogeochemical niche hypothesis in forest trees. Nature Ecology & Evolution 5: 184–194. https://doi.org/10.1038/s41559-020-01348-1

ASLO's 2021 Hutchinson Award

Congratulations to Elena Litchman (Michigan State, USA), who recently received the 2021 G. Evelyn Hutchinson Award from the Association for the Sciences of Limnology and Oceanography (ASLO) for her work on 'trait-based' approaches in the study of plankton ecology. Most of us know Elena for her work on phytoplankton stoichiometry and trying to understand algal growth. According to ASLO, this award is given each year to "a limnologist or oceanographer who has made considerable contributions to knowledge, and whose future work promises a continued legacy of scientific excellence." Well done Elena; this is a decidedly important and well-deserved award. To learn more award this award and Elena's background, visit the ASLO page here:

https://www.aslo.org/aslo-awards/2021-aslo-award-recipients/2021-hutchinson-award-recipient/

ASLO Association for the Sciences of Limnology and Oceanography

Phosphorus starvation of lake phytoplankton

The biogeochemical relationship that lakes have with their key nutrient, phosphorus (P), may be more complicated than originally anticipated. Phytoplankton growth is proportionately related to P levels only over a relatively narrow concentration range, and the C:P ratio of the phytoplankton community rapidly changes depending on the availability of P. This plasticity in phytoplankton community C:P can result in the same biomass production with less P and hinder re-oligotrophication efforts, particularly those focused on deep water oxygen concentrations. We studied a lake that experienced decreasing P concentrations (blue line in Figure 1) due to reduced P inputs. Initially, there was no change in phytoplankton C:P ratios – because P remained in excess and not limiting to algae growth (Phase I in Figure 1). If anything, we found that biomass actually increased in the lake, matching what is known as the 'paradox of re-oligotrophication'. But eventually, the first signs of success of the restoration efforts presented themselves in the increase of the C:P ratio (green line) of the phytoplankton during Phase II. The phytoplankton community has to be economical with its use of P but can maintain its biomass over quite a range of P concentrations. Only when the TP_{mix} (total P after winter mixing) concentration fell below a threshold value did the plankton fully optimize use of P. During Phase III, the community C:P ratio remained steady at a high level and biomass production eventually declined with continuing decreases of TP. It appears that the consumption rate of oxygen in the lake's deep water is decreasing now that Phase III has been reached.

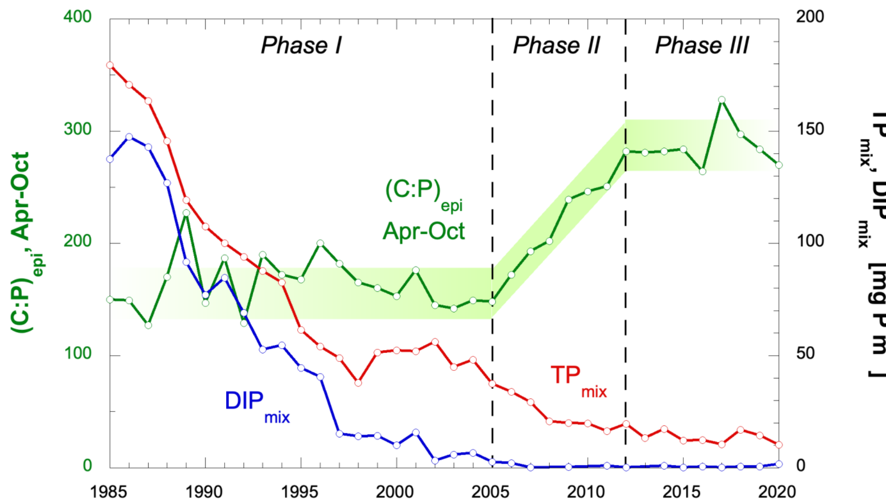


Figure 1. The C:P ratio of the seston in the epilimnion of a lake during the productive summer period (April to October) over three decades of re-oligotrophication. TPmix and DIPmix are concentrations of total phosphorus and dissolved inorganic phosphorus after winter overturn. Modified from Müller et al. (2021)

From the Paper: "*The* $(C{:}P)_{epi}$ *ratio indicates the reduction of productivity prior to classic indicators such as deep-water oxygen depletion.*"

Contributed by Beat Müller and Alfred Wüest

Müller, B., T. Steinsberger, A. Stöckli, and A. Wüest. 2021. Increasing carbon-to-phosphorus ratio (C:P) from seston as a prime indicator for the initiation of lake reoligotrophication. Environ. Sci. Technol. 55: 10.1021/acs.est.0c08526

Ecological Stoichiometry at ESA 2021

The annual meeting of the Ecological Society of America was held this year in virtual form between August 2nd and 6th because of the whole pandemic situation. The virtual meeting still boasted thousands of presentations including a rich slate of diverse stoichiometric topics. These presentations (posters and talks) will remain available on the conference webpage (https://www.esa.org/longbeach/) until July 2022. So if you want to binge watch some ecological stoichiometry from ESA 2021, you can still register to see these talks. Here is a quick rundown of some of what's on the menu.

The impacts of anthropogenically altered biogeochemical cycles on ecosystems was a primary focus of this year's presentations. **Oliver Carroll** discussed the effect of chronic nutrient enrichment on biomass production and temporal stability in grassland ecosystems. **Lindsey Pett** presented findings on the impacts of N and P deposition on aquatic ecosystems contained within Northern pitcher plants across a latitudinal gradient. Using state-of-the-art modeling approaches both **Katrin Fleischer** and **Kara E. Allen** presented the extent to which nutrient limitation may diminish carbon uptake.

The stoichiometry of aquatic and wetland ecosystems was also explored by several of this year's presenters. **Peter J. Flood** presented how alligators act as ecosystem engineers and create nutrient gradients that extend throughout the aquatic food web. The capacity of fire to ease P-limitation in wetlands and its possible application in managing biogeochemical cycling was presented by **Andrea Nocentini**. An investigation of the underappreciated impacts of parasites on nutrient cycling was presented by **J. Trevor Vannatta** who studied how trematodes alter the stoichiometry of their snail hosts. The stoichiometric impacts of changes in hydrology on aquatic communities was presented by both **Marco Fernandez** and **Mingming Ding**, who investigated stoichiometric responses to increases in water flow and water level fluctuations, respectively.

Finally, the presentation of **Peter A. Wilfahrt** is worth tuning into as he discusses the emergent understanding gained of nutrient cycling on grassland ecosystems during the last decade of the Nutrient Network experiment.

Contributed by Kimberley Lemmen

Selected Abstracts of Interest

S. Beier	Dominance of eutrophic generalist species after microbial community coalescence events
K. Dynarski	Patterns of foliar nutrient stoichiometry and intraspecific flexibility across the United States
B. Currey -	Woody plant expansion drives ecosystem-level redistribution of carbon, nitrogen, and phosphor orus in the Northern Great Plains
J. Edwards	Linking ectomycorrhizal communities to ecosystem function and soil biogeochemical cycling
A. Swain	Leaf contours delineate genetic control of leaf shape and predict ecological traits of trees
K. Lemmen	Direct and indirect effects of phosphorus limitation on the functional response of the microzooplankton consumer *Brachionus calyciflorus*
J. Lucas	Anthropogenic and climatic variables interact to disrupt soil communities and their function
K. Rocci	Elucidating relationships of mineral-associated and particulate organic matter stocks, distribution, and stoichiometry across contrasting grassland ecosystems

Extraterrestrial Stoichiometry
C:N:P ratios that are out of this world!

One the most fascinating discoveries in the history of our field was A.C. Redfield's observation that life on Earth has relatively narrow requirements of C, N, and P and that these requirements in-turn shape the biogeochemistry of these elements. However, there is no reason that this insight is unique to our planet as the chemical nature of these three elements makes them indispensable to biology. This observation suggests that stoichiometric theory could be leveraged towards another great human endeavor – the search for life on other planets. Until recently, this search has been limited to measuring atmospheric C and N composition of planets, as direct measurements of planetary P outside of our own solar system were not possible. In a new paper, Hinkel et al. (2020) report the first stoichiometric estimates of C, N, P, and Si concentrations in nearby stars as a proxy for elemental concentrations of their surrounding planets and report these values along-side direct abundance measurements in the Earth and Mars to gain a better understanding of solar stoichiometry and its potential for aiding in the search for extraterrestrial life.

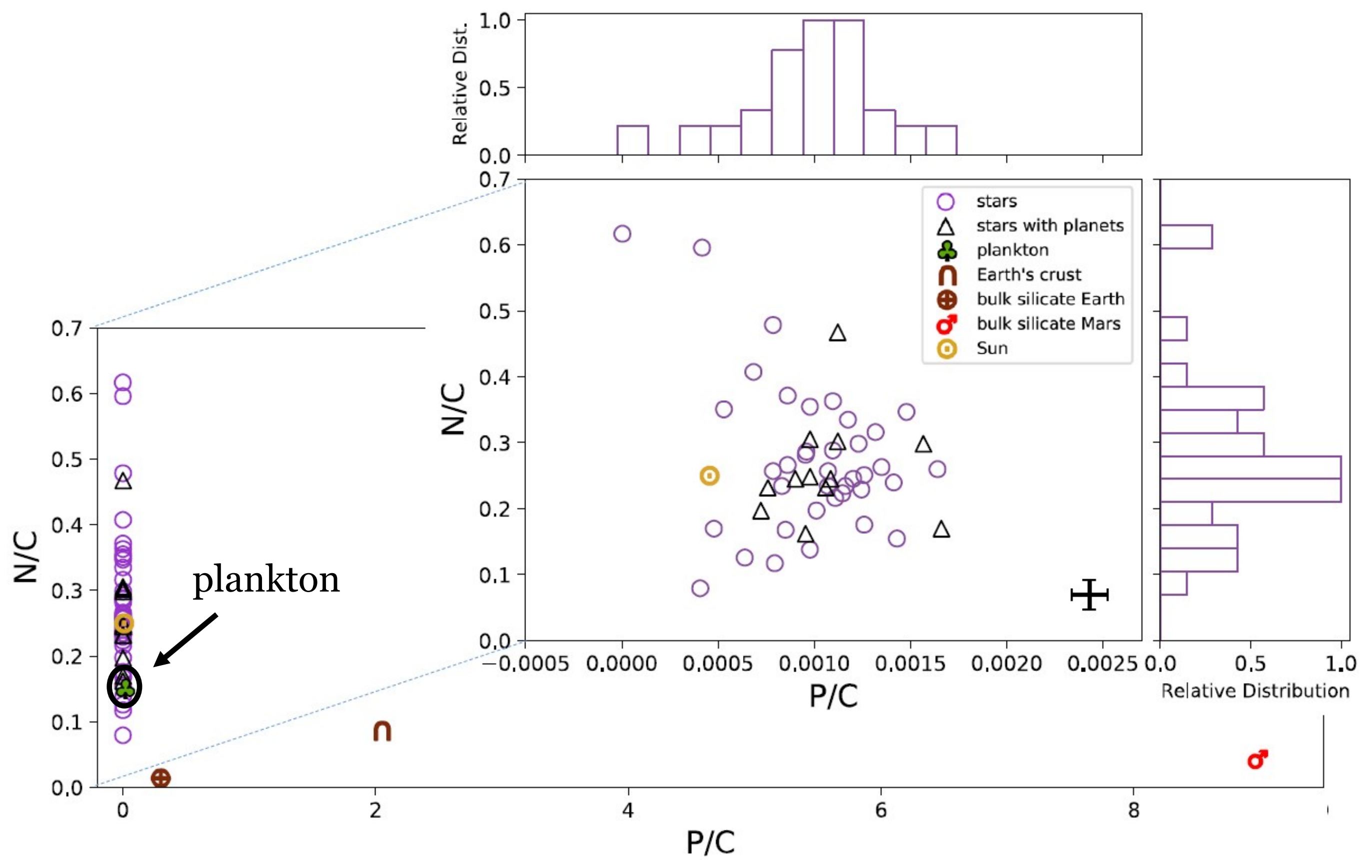


Figure 1. Molar elemental ratios of stars, Mars and Earth crust, and phytoplankton. Representative estimate error is shown on the bottom right of the inset panel, and histograms depict the relative distribution of elemental ratios. Modified from Hinkel et al. (2020).

Relative to all other measured stars, molar C:N ratios are similar to and C:P ratios are lower in our Sun, which suggests that it is stoichiometrically P-rich compared to other stars (Table 1). For Earth and Mars, C:N ratios are much higher compared to stars whereas C:P ratios are much lower. While there appears to be much more P on these two planets, this element shows a strong relationship with Si concentrations, which could mean that much of the P on Earth and Mars is biologically unavailable and tightly bound to silicates. Phytoplankton C:N ratios were found to be quite similar to the ratios of Earth and Mars, while C:P ratios were higher in plankton (Table 1), suggesting that P-limitation could still be common even on relatively P-rich planets.

Table 1. Molar C, N, Si ratios normalized to P for plankton, Earth and Mars, and stars. Reproduced from Hinkel et al. 2020.

	C	N	Si	P	Reference
Plankton	106.0	16.0	15.0	1	Redfield (1958)
Earth Crust	0.49	0.04	291.16	1	Mason and Moore (1982)
Bulk Silicate Earth	3.44	0.05	2573.35	1	McDonough (2003)
Bulk Silicate Mars	0.11	0.005	443.89	1	Yoshizaki & McDonough (2020)
Sun	2233.93	564.82	132.88	1	Lodders et al. (2009)
Hypatia Catalog Star (average)	3814.33	1010.77	235.79	1	Hinkel et al. (2014)

Potentially more important is the discovery that N:P ratios are constrained in the small subset of planet hosting stars where C, N, P data are available (n=12; Figure 1). These ratios are similar to our own Sun, which indicates that the stoichiometric conditions necessary for supporting life could be common in our universe. However, as P concentration measurements have only been made for 1% of all stars, including planet hosting stars, technological advancements in extrasolar planetary P measurements and close collaborations between stoichiometrists and astronomers are essential to fully extend our stoichiometric understanding to boldly go where no ratio has gone before!

From the Paper: "*In the truest sense, it is absolutely vital to understand planetary bulk composition, internal structure, mineralogy, and atmosphere in order to fully assess whether a planet is habitable.*"

Communicated by Clay Prater

Hinkel, N.R., H.E. Hartnett, and P.A. Young. 2020. The influence of stellar phosphorus on our understanding of of exoplanets and biology. The Astrophysical Journal Letters 900:L38 DOI: 10.3847/2041-8213/abb3cb

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Selected Recent Stoichiometry Publications

Beck, W.S., A.T. Rugenski and N.L Poff (2021) Limiting nutrients drive mountain stream ecosystem processes along an elevation gradient. Freshwater Science 40: 368-381. https://doi.org/10.1086/714441

Balseiro, E., C. Laspoumaderes, F. Smufer, et al. (2021) Short term fluctuating temperature alleviates *Daphnia* stoichiometric constraints. Scientific Reports 11: 12383. https://doi.org/10.1038/s41598-021-91959-w

Frenken, T., R. Paseka, A.L. González, L. Asik, et al. (2021) Changing elemental cycles, stoichiometric mismatches, and consequences for pathogens of primary producers. Oikos 130: 1046-1055. https://doi.org/10.1111/oik.08253

Ipek, Y. and P.D. Jeyasingh (2021) Growth and ionomic responses of a freshwater cyanobacterium to supplies of nitrogen and iron. Harmful Algae 108:102078. https://doi.org/10.1016/j.hal.2021.102078.

Knapp, D.D., L.L. Smith, and C.L. Atkinson (2021) Larval anurans follow predictions of stoichiometric theory: implications for nutrient storage in wetlands. Ecosphere 12. doi:10.1002/ecs2.3466

Le Mézo, K. Priscilla and E.D. Galbraith (2021) The fecal iron pump: Global impact of animals on the iron stoichiometry of marine sinking particles. Limnology and Oceanography 66.1: 201-213. https://doi.org/10.1002/lno.11597

Lind, P.R., F.S. Osburn, A.R. Dzialowski, et al. (2021) Variation in iron and its potential relevance to phytoplankton ecology in Oklahoma reservoirs. Hydrobiologia 848: 2731–2744. https://doi.org/10.1007/s10750-021-04592-z

Lürig, M.D. and B. Matthews (2021) Dietary-based developmental plasticity affects juvenile survival in an aquatic detritivore. Proceedings of the Royal Society B: Biological Sciences 288:20203136.

McCain, J.S.P., A. Tagliabue, E. Susko, et al. (2021) Cellular costs underpin micronutrient limitation in phytoplankton. Science Advances 7:eabg6501. http://foi.org/10.1126/sciadv.abg6501

Wymore, A., P.J. Johnes, S. Bernal, J. Brookshire, et al. (2021) Gradients of Anthropogenic Nutrient Enrichment Alter N Composition and DOM Stoichiometry in Freshwater Ecosystems. Global Biogeochemical Cycles 35: 1-11. https://doi.org/10.1029/2021GB006953

Xu, M., Y. Zhu, S. Zhang, et al. (2021) Global scaling the leaf nitrogen and phosphorus resorption of woody species: Revisiting some commonly held views. Science of The Total Environment 788:147807.

Zhou, L. and S.A.J. Declerck (2021) A critical assessment of the stoichiometric knife-edge: no evidence for artifacts caused by the experimental P-supplementation of algae. Aquatic Ecology. https://doi.org/10.1007/s10452-021-09867-0