Ratios Matter

Volume 5 Issue 1 March 2021

Ratios of Logs Matter Too

Yes, it's true. Read enough stoichiometry and you will learn that the elemental composition of logs matter too. If you are a termite or an ambitious decomposer, we're sure you will agree. This is because this large woody debris is known to have distinct elemental ratios in its matter, which matters if you want to make a living from eating it. And as we've recently learned, when doing so, we really should be transforming elemental ratios before statistical analysis. But once you start doing this, it could become quite confusing. Perhaps especially if the wood is commercially harvested. To keep it all straight, you might decide to record all of these transformed elemental ratios in your journal. Do so and you will be logging the logged ratios of logged logs in your log of logs.

Stoich-Comic by Judith Sitters

NOW HIRING!

Postdoctoral Position in Ecological Stoichiometry

A postdoctoral research associate position is available in the laboratory of Dr. Jessica Corman (**ecostoich.weebly.com**) at the University of Nebraska-Lincoln. This position is part of an NSF grant that will combine tools emerging from the data revolution with the ecological stoichiometry framework to advance our understanding of how elemental supplies constrain and are influenced by ecological and evolutionary processes in aquatic ecosystems. More information on this position and how to apply can be found at: **https://ecostoich.weebly.com/stoich_postdoc.html**

Please contact Dr. Jessica Corman (**jcorman3@unl.edu**) to learn more about this opportunity.

Ratios Matter Talks

Ecological Stoichiometry Seminar Series 2021

Do you find yourself frequently thinking about elemental ratios? Are you interested in seeing how others think about and use ecological stoichiometry? Would you like to share your stoichiometric research with an international assemblage of like-minds? If so, we would like to invite you to join us online for a virtual seminar series. We are currently developing the schedule of the inaugural and, possibly, perennial Ecology Stoichiometry Seminar Series 2021.

Who? Anyone and everyone is welcome to join. Send nominations (including self) of potential seminar speakers to ratiosmatter@gmail.com. We would particularly like to showcase young diverse stoichiometrists studying various topics but all offers of seminars are welcome. Please include a c.v. and/or recent publication along with the nomination. Selections will be made by the *Ratios Matter* Editorial Board based on the above criteria.

When? Tentative dates of April through June 2021. Day and time yet to be determined but we will try make something workable for many time zones.

Where? Online through zoom. Links will be distributed through our Twitter feed (@ratios_matter)

Stoichiometric Impacts of Plankton Warfare

Many single-cell organisms have functional traits that provide an advantage over competing organisms in certain environments. One such trait is the production of allelopathic chemicals that can inhibit/suppress competitors' fitness. Whether the allelopathic chemicals excreted are intended to suppress competitors or are a byproduct of an internal fitness advantage (i.e., grazing resistance) remains unknown. Cagle and colleagues examined if unbalanced resource nutrient supply affected how *Prymnesium parvum* allelopathic chemicals are excreted or used for micropredation (i.e., cell to cell contact). The authors grew *P. parvum* for 17 days under balanced N:P and high N:P ratios and measured how toxic the filtrate and whole cells were to *Rhodomonas salina* and *Daphnia magna*. They found that *P. parvum* grown in nutrient replete conditions lysed *R. salina* cells mainly through micropredation contact. However, in P-limited environments, cell lysis occurred through chemical excretion and not micropredation. *P. parvum* was also more toxic to *Daphnia* when grown in P-limited conditions. The authors suggest that in a balanced N:P supply, the chemical is contained internally and used for micropredation. Whereas in P-limited environments, the chemical is excreted, displaying the allelopathic effects.

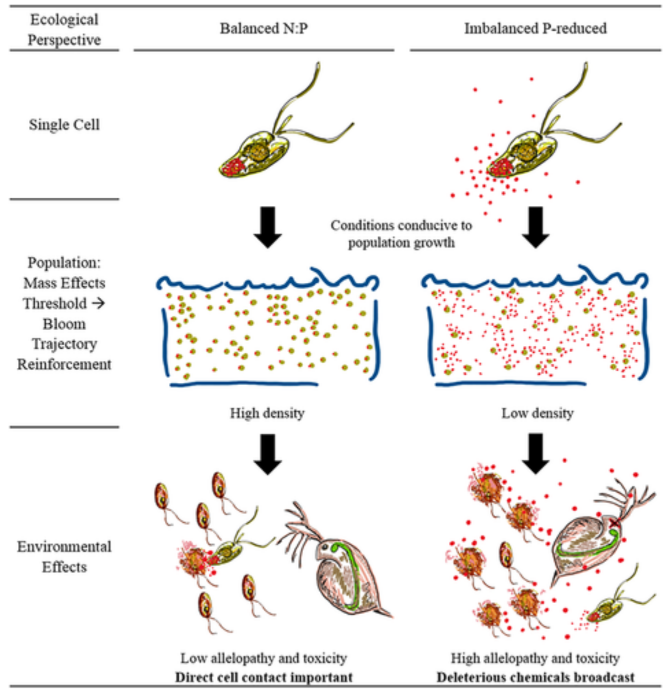


Figure 6 from the paper "Conceptual model summarizing how differences in N:P stoichiometry of aquatic systems may influence bloom dynamics of ambient *Prymnesium parvum* populations. Imbalanced P stoichiometry (skewed away from the Redfield ratio) leads to high ambient concentrations of deleterious chemicals at lower *P. parvum* population density. This allows for mass effects of the chemicals to occur and reinforces a bloom trajectory at lower population density, which may ultimately lead to greater and more widespread environmental consequences."

From the Paper: In P-limited conditions, "*wide spread allelopathic effects may occur if the population density reaches a threshold but these effects do not determine the evolutionary selection of chemical production.*"

Contributed by Nicole Wagner

Cagle, S.E., D.L. Roelke, and R.W. Muhl. 2021. Allelopathy and micropredation paradigms reconcile with system stoichiometry. Ecosphere 12:e03372

Ratios in Review

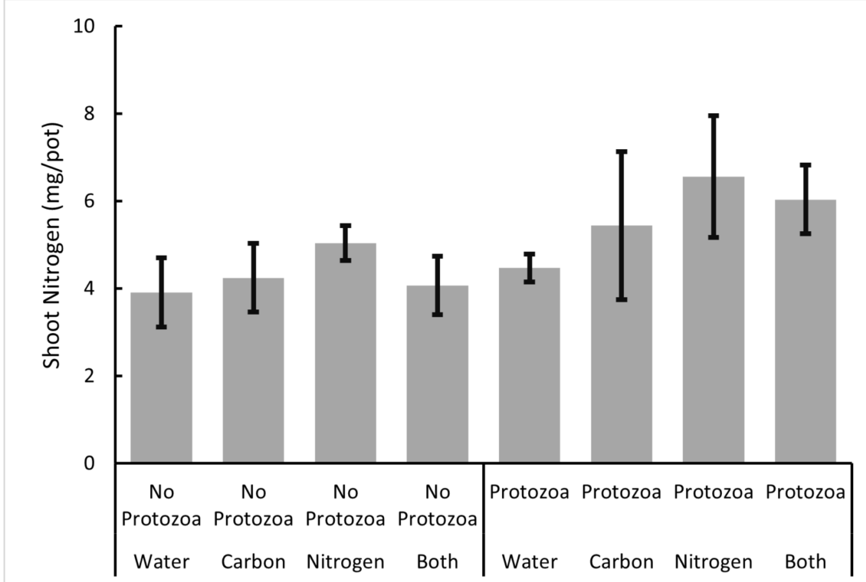
Soil stoichiometry on the ground level

I sometimes wonder why our field of ecological stoichiometry has its origins in lakes instead of in the soil. Perhaps these are the jealous musings of a terrestrial ecologist. However, it is true that soil science has a long history of stoichiometric ideas that are not always recorded in our annals. In fact, it was Dr. Marianne Clarholm's 1985 paper on the "Interactions of bacteria, protozoa and plants leading to mineralization of soil-nitrogen" that helped inspire me to pursue stoichiometric research. Today, Dr. Clarholm's paper, and other soil papers of that era, live on in soil ecology but are absent from the more general stoichiometric literature built on its lentic foundation.

Dr. Clarholm studied the response of soil mesocosms after the addition of inorganic nitrogen, organic carbon, and both. Her innovative experiment demonstrated one of the central tenets of our field—that the cycling of nutrients is impacted by the *interaction between biotic communities and relative nutrient supply*.

Specifically, she demonstrated that the presence of soil protozoa changed the response of bacteria and plants to nutrient addition. She writes: "*Additions of C to the plants grown in soil with protozoa, resulted in a significant 18 % increase of N in the shoots, while the N contents did not vary significantly without grazers. An addition of N alone resulted in significantly higher N contents of the shoots both with and without protozoa. If the N additions were made together with C, the plants were only able to utilize the N when grazers were present*" (see Figure 1). This series of observations could be re-written with a stoichiometric view focused on the C:N ratio of soil bacteria. We can understand why plants responded to carbon addition only when protozoa were present by considering bacterial nitrogen requirements. Added carbon promoted bacterial growth, which primed them to mine nitrogen from the soil organic matter pool. This was all well and good for bacteria in the absence of their predators. When protozoa were present, they consumed the bacteria releasing the nitrogen back into the soil—effectively allowing added carbon to be converted through microbial biomass to plant-available nitrogen. The magnitude of this exchange can be predicted using the bacterial C:N ratio.

Figure 1. The amount of nitrogen found in wheat shoots after the addition of water only, carbon, nitrogen, or both in the presence and absence of protozoa. When both carbon and nitrogen were added, plants only gained extra shoot nitrogen in the presence of protozoa. Data from Table 1 in Clarholm (1985).



Today, we have comprehensive frameworks to play out such stoichiometric games between plants, decomposers, and their predators but the earliest ideas in soil stoichiometry were developed with experiments reminiscent of the pioneering ones in aquatic ecosystems between prey, predators, and recycling elements.

Interestingly, stoichiometric ratios are conspicuously absent from these early results. The C:N ratio makes one appearance in the discussion of Dr. Clarholm's paper as a means of calculating how much microbial nitrogen might have come from autoclaved microbes using her data on the microbial carbon pool. It seems that ratios were a means of converting between different elements rather than a framework for understanding why elements moved the way they do. In fact, root-to-shoot ratios play a larger role in these early soil nutrient papers than do elemental ratios.

The power of ecological stoichiometry to me is demonstrated by how soil science has used elemental ratios to build upon the pioneering work of Dr. Clarholm and her contemporaries. Instead of discussing elements in turn, as our early work on soil food webs did, ratios have provided a means of predicting the rate of exchange from added carbon to plant-available nitrogen that protozoa promote.

Contributed by Rob Buchkowski

Clarholm, M. 1985. Interactions of bacteria, protozoa and plants leading to mineralization of soil-nitrogen. Soil Biology & Biochemistry 17:181–187

What Drives the Stoichiometry of Poop?

I have been collecting poop (hereafter, dung) of mammalian herbivores for 10 years now and can recognize dung of at least 30 African and European species by sight. These herbivores play an important role in nutrient cycling and availability through the deposition of their dung and urine. And not all dung is created equal! Dung N:P ratios vary among herbivore species and can range from 2 to 20 (Sitters and Olde Venterink 2021a), thereby supplying plants with a more N- or P-limited resource. Indeed, this variation in dung N:P supply is large enough to affect plant competitive interactions and plant community composition (Valdes-Correcher et al. 2019; Sitters and Olde Venterink 2021b). But the factors driving dung stoichiometry of terrestrial vertebrate herbivores remains poorly understood compared to, for example, aquatic herbivores.

Sterner and Elser (2002) predicted that food and body N:P would be important determinants of excreted N:P. For vertebrates, body size in turn is an important driver of body N:P – the larger an animal, the more P-rich bones it contains, the lower body N:P and the higher excreted N:P (assuming food N:P is more or less constant). Studies on relationships between body size – as a proxy for body N:P – and dung N:P for terrestrial vertebrate herbivores are extremely limited. However, a recent study in PNAS gave some of the first empirical evidence that this relationship might hold true for South African ungulate herbivores feeding on nutrient-rich grazing lawns (le Roux et al. 2020; orange points and line in Fig. 1).

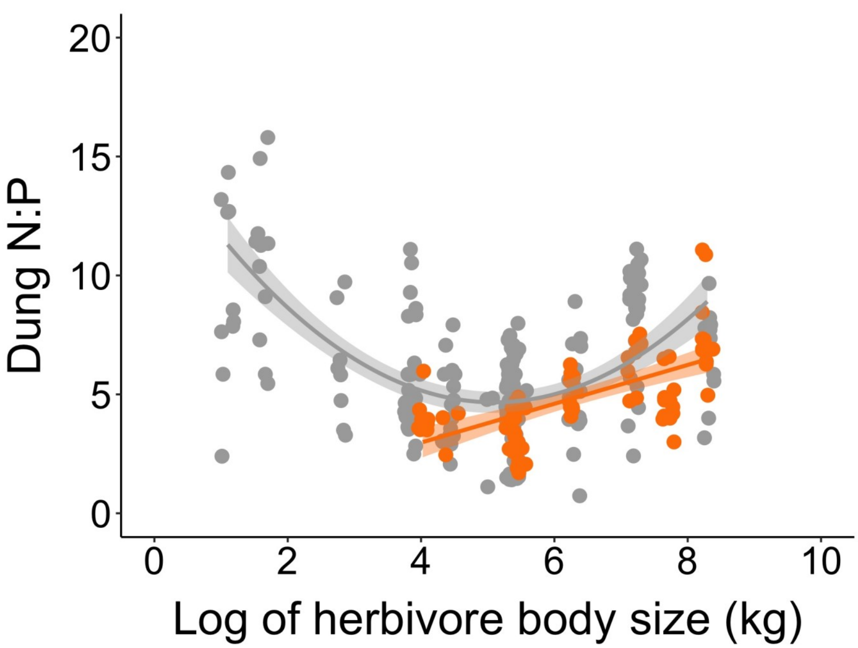


Figure 1. Dung N:P ratio in relation to herbivore body size at Hluhluwe-iMfolozi Park, South Africa (orange points) and Saadani National Park, Tanzania (grey points). Data are used with permission from le Roux et al.(2020) and Sitters and Olde Venterink (2021a).

Sterner and Elsers' complete prediction, however, included a quadratic relationship between body size and excreted N:P; higher N:P excretion at both large and small body sizes, the former driven by high P investment in bones, the latter by high metabolic P requirement due to faster growth rates. Indeed, in my own dataset from a Tanzanian savanna such a quadratic pattern could be found, likely as a result of including species with smaller body sizes compared to the data from le Roux et al. (grey points and line in Fig. 1).

And what role does diet N:P play as another factor that simultaneously operates to drive the stoichiometry of herbivore dung? Smaller herbivores are, for example, known to feed more selectively on N-richer food than larger ones, suggesting that variation in dung N:P is likely also driven by dietary N differences.

To get to the bottom of what drives the stoichiometry of dung from African herbivores we have combined forces together with le Roux et al. – and some 30 other researchers – to build a more comprehensive database. So far, we have data on dung nutrients from 60 herbivore species, ranging in body size from rabbits to elephants, from 11 countries in Africa. Feel free to contact me if you might have data to contribute (for now, we are focusing on African herbivores) and would like to be part of this project!

Contributed by Judith Sitters

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Freshwater Management and Stoichiometry?

State and federal agencies don't always consider N:P ratios in policy development, but a new study by Westphal and colleagues suggests that studying the regulatory drivers of shifting N:P ratios in large rivers is an important part of quantifying how policy influences biology. Over the past decades, nutrient loads to many large rivers have been reduced by mitigation efforts targeting both point (e.g. inputs from industrial or domestic wastewater) and diffuse sources (e.g. runoff from agriculture). Understanding how the timing of these mitigation efforts influenced river N:P ratios might improve the timing of future nutrient management efforts. In Germany, efforts to limit point sources reduced P inputs as early as the 70s, but efforts targeted at non-point sources weren't widespread until the late 80s. Westphal and colleagues suspected that these asynchronous mitigation measures may have shifted the N:P ratio (and the limiting nutrient) of the Rhur River in Germany over time.

To test their hypothesis, the group quantified the effects of mitigation measures on N and P in the Rhur River over a rural-urban land use gradient for more than 3 decades. They calculated annual average concentration-discharge relationships at 3 sites to determine if export patterns were driven by dilution (which would indicate a point source), mobilization (indicating a diffuse source), or neither (also indicating a diffuse source). To assess how these trends shaped nutrient ratios and the identity of the limiting nutrient over time and space, they compared weekly total phosphorus and dissolved inorganic nitrogen and annual median N:P ratios at each site.

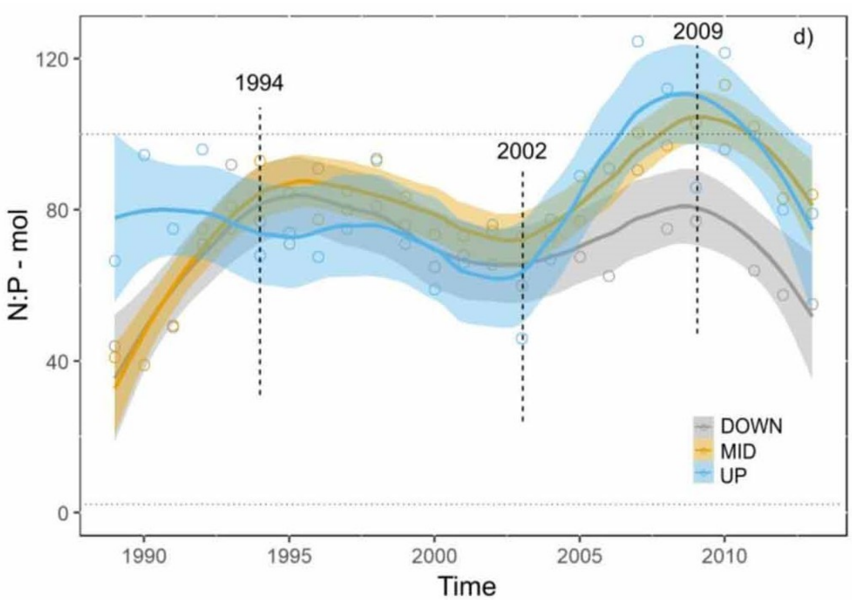

Figure 1. Long term development of annual median molar N:P ratios over time from up [rural] to downstream [urban]. [skipped some content] The dashed horizontal lines indicate molar N:P ratios of 1:1 and 100:1. Dashed vertical lines indicated years of a trend change.

These analyses indicated that asynchronous management of point and nonpoint N and P sources produced asynchronous reductions in N and P and a shifting river N:P ratio over time (Fig. 1). They found that upgrades in wastewater treatment plant technology caused by national policy changes from the 1970s to 1990s led to quick declines of 86-97% in both total phosphorus and ammonium. However, improved agricultural land use practices and N efficiency took 4 to 9 years before producing a reduction in nitrate of 31-44%.

The initial reduction in P from point sources followed by reductions in N from diffuse sources caused N:P ratios to increase at the beginning of the study period and decline towards the end of it. In urban areas (grey line in Figure 1), increasing P inputs may have offset this trend, but at rural sites (blue and orange lines in Figure 1), both the N:P ratios and the likelihood of P limitation has increased over time. These patterns drive Westphal and colleagues to suggest that stoichiometric-based freshwater management may be a useful tool for policy makers, especially in areas where land use is rapidly changing.

From the paper: "*Synchronous N and P reduction measures will be of particular benefit for those regions that experience rapid economic growth without adequate environmental protection, leading to significant degradation of water quality in freshwaters, and which will soon address these problems with more stringent environmental lessons.*"

Contributed by Charlotte Narr

Westphal, K., A. Mussolff, D. Graeber, and D. Borchardt. 2002. Controls of point and diffuse sources lowered riverine nutrient concentrations asynchronously, thereby warmping molar N:P ratios. Environmental Research Letters 15: 104009

Ratios Matter Reads

Do you love to read? Have you run out of books in lockdown?

Never fear, Ratios Matter Reads is back, bringing you all the latest in stoichiometric literature!

In this issue, we are pleased to announce the release of *Phosphorus: Past and Future* by Jim Elser and Phil Haygarth. To find out more about the book and where to order your copy, click here and visit the

Sustainable Phosphorus Alliance

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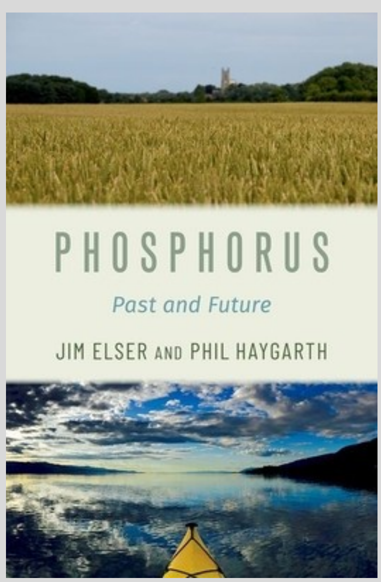
Phosphorus 15 P 30.974

HOSPHORUS: AST AND FUTURE

BY JIM ELSER AND PHIL HAYGARTH



ABOUT THE BOOK

"Phosphorus has always seemed to be eclipsed by C and N and in this book, we try to pull some of the attention back to P" – Phil Haygarth

"Like a good parent, a good stoichiometrist should love all bio-elements equally. But let's be honest. Phosphorus is the best, isn't it? It certainly deserves its own book." – Jim Elser

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Selected Recent Stoichiometry Publications

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