Ratios Matter

Volume 7 Issue 1 March 2023

Conference on Biological Stoichiometry 2023!

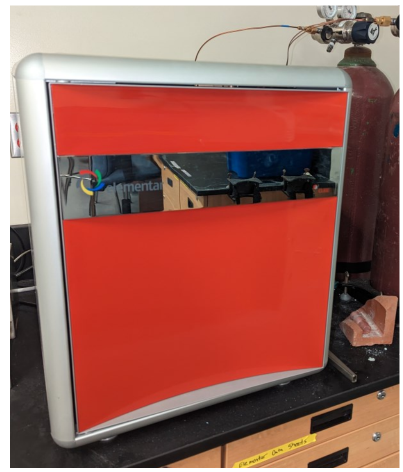
The Conference on Biological Stoichiometry (COBS) is alive and well. The second meeting of COBS will take place between March 20 and 23, 2023 in Lincoln, Nebraska. First, we would like to acknowledge the tremendous contributions by the scientific planning team: Jessica Corman, Paul Frost, Hal Halvorson, Uche Ogbenna, Linnea Rock, and Nicole Wagner. A giant pre-meeting thanks to this group for putting together what will undoubtedly be an exciting and fruitful meeting. COBS 2023 is your chance to be immersed in stoichiometry. The three plenary speakers to be featured are Angélica Gonzáles (Rutgers), Elena Litchman (Carnegie Science), and Shawn Wilder (Oklahoma State). And there is a full slate of oral presentations on a diverse range of stochiometric topics and an equal number of posters to be presented. COBS 2023 will also have workshops, team science, and round tables to more deeply explore the current state of stoichiometric science, consider ways to improve what we are doing, and to think outside the current stoichiometric boxes. COBS 2023 will be ice-breaking with different social events and opportunities to meet young and new stoichiometrists alike. If you are interested in attending, late registration remains open.

Contact Elyse Watson at elyse.watson@unl.edu to inquire about registering late.

More information on COBS 2023 is available at: https://stoichproject.wordpress.com/stoich/cobs_2023/

Unsung Stoichiometric Heroes

***Ratios Matters* would like to dedicate** this issue to the CN machine. The CN machine has demonstrated, over decades, an unvarying pursuit of elemental ratios. Even when leaky or your peaks don't separate, we love you CN machine.



So a big thank you to CN machines around the world for their service to the field of ecological stoichiometry!

Eight Principles of *Stoichism*

Nature: Nature is *rational*.

Law of Mass Balance: The universe is governed by the law of mass balance. Organisms can't actually escape its inexorable force, but they can, uniquely, follow the law deliberately.

Virtue: A life led according to ratio-centric nature is virtuous.

Minimum: Minimum is the root of stoichiometry. From it springs the cardinal concepts: limitation, homeostasis, constraints, and imbalances.

Apathea: Since mass imbalance is irrational, life should be waged as a battle against it. Intense feeling should be avoided.

Limitation: Limitation is neither good nor bad. It is only acceptable if it doesn't interfere with the quest for fitness.

Evil: Mass ratios are not evil.

Duty: Ratios should be sought, not for the sake of pleasure, but for duty.

NSF Funded RCN: **Nitrogen Fixation Across Aquascapes**

AQUATIC
N_2 FIXATION
We have a nitrogen *fixation*

Now recruiting for working group 2:

Stoichiometric drivers and constraints on aquatic nitrogen fixation.

Goal: Develop conceptual and quantitative models of the stoichiometric controls on autotrophic and heterotrophic N_2-fixers from populations to individual ecosystems.

Check out: https://www.aquaticnfixation.com/

Stoichiometric Word Search

R	I	B	O	S	O	M	A	L	R	N	A	T	O
N	I	T	R	O	G	E	N	G	S	T	A	S	E
T	E	R	H	S	E	V	A	E	L	R	F	U	O
I	G	R	E	D	F	I	E	L	D	E	I	R	O
O	H	O	M	E	O	S	T	A	S	I	S	O	M
M	H	D	A	I	N	H	P	A	D	D	E	H	H
Z	N	G	I	E	E	E	C	A	A	G	I	P	O
I	H	I	A	M	I	M	N	I	N	H	T	S	N
G	N	O	R	A	O	G	R	A	A	S	L	O	S
N	O	B	R	A	C	S	L	R	E	R	I	H	A
I	C	R	M	I	A	N	V	A	E	B	A	P	T
Z	S	G	R	H	T	I	O	T	H	E	R	O	O
N	O	I	T	A	T	I	M	I	L	O	C	T	U
R	L	I	E	B	I	G	N	O	R	T	Z	O	Q

How many stoichiometric words, terms, or abbreviations can you find? We've hidden 16 stoichiometry-related words/ abbreviations. Good luck!

If you find:

0-5 words, Go buy a copy of Sterner and Elser (2002)

6-10 words, You're not entirely imbalanced

11-13 words, Is Redfield your middle name?

14-16 words, Stoichiometric Genius!

NSF Research Coordination Network Virtual Seminar to Explore Patterns and Controls of Plant Stoichiometric Flexibility

Ecosystem stoichiometry is a key driver of global biogeochemical cycling and influences the ways carbon (C) and nutrient cycles respond to global change. Multiple lines of evidence show that ecosystem stoichiometry is shifting globally due to several factors, including rising atmospheric carbon dioxide (CO_2), nitrogen (N) deposition, and climate change (McNeil et al. 2007; Fleischer et al. 2013; Du et al. 2019; Wang et al. 2021, Mason et al. 2022). While stoichiometric flexibility may be a key determinant of future C and nutrient cycling in terrestrial ecosystems, it remains uncertain whether plants exhibit sufficient stoichiometric flexibility to maintain growth despite growing imbalances in C, N and phosphorus (P) availability that are anticipated with environmental change. Accordingly, an improved understanding of stoichiometric flexibility would significantly advance our understanding and capacity to forecast terrestrial ecosystem responses to change.

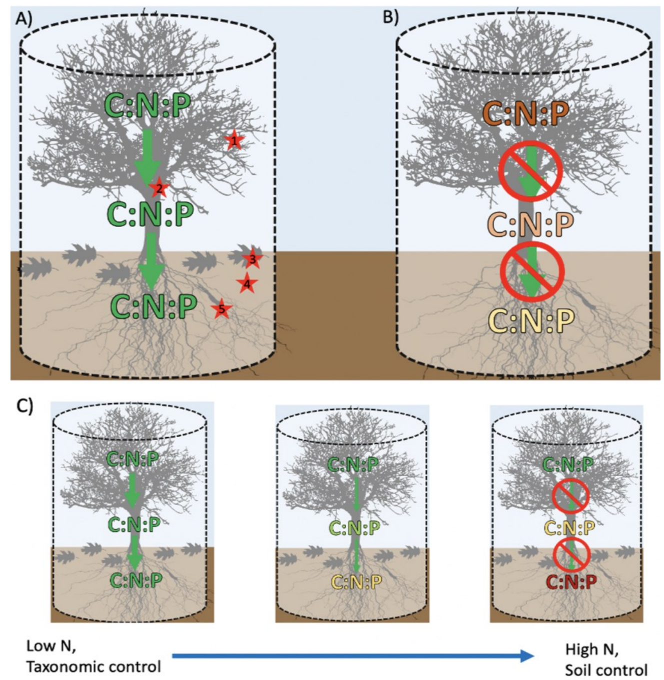


Figure 1. Working hypotheses for the stoichiometric observatories to explore ecosystem stoichiometric flexibility. Stoichiometric ratios may be coupled across *vertical cores* (A), including: (1) foliage, (2) wood, (3) litter, (4) soil and microbial biomass, and (5) roots, possibly because of a footprint of foliage and litter stoichiometries on other ecosystem components. Alternatively, stoichiometry may be decoupled across the profile (B) if root-driven processes or varying stoichiometry across the profile produce divergent C:N:P patterns in aboveground versus belowground systems. Over broad spatial scales, we can test drivers of stoichiometric flexibility and connectivity, such as soil N availability and taxonomic diversity (C), across the vertical core.

In part, uncertainty about stoichiometric controls over ecosystem processes stems from a poor understanding of how C:N:P ratios are coupled across space, such as within individual plants, among species, and across ecosystems, as well as over time. To address this uncertainty, the Investigating Nutrient Cycles in Terrestrial Ecosystems (INCyTE) Network is proposing a distributed experiment to develop a set of *stoichiometric observatories* that will explore how ecosystem stoichiometry is coupled vertically, from tree canopies into soil, as well as how those relationships vary across environmental gradients. Data collected by participants will contribute to a global and community accessible stoichiometry database.

The overarching goal of the stoichiometric observatories is to explore C:N:P relationships among ecosystem compartments, as well as assess environmental drivers of stoichiometric flexibility (Fig. 1). Within these larger goals, **the specific concepts, questions, and methodology guiding observatory establishment will be collaboratively developed through an INCyTE seminar series in the spring of 2023.** We will review knowledge gaps and hypotheses on the theme of stoichiometric flexibility, discuss how to design and implement a successful distributed experiment, and generate protocols for consistent sampling across forests. **Anyone interested in participating in a network of distributed stoichiometric observatories is encouraged to register for the INCyTE Network at the link below.** Please join us this spring for these exciting discussions about stoichiometric flexibility!

Contributed by Emma Hauser (University of Montana)
Communicated by Francis Brearley

WEEKLY SEMINAR MEETINGS ON ZOOM

Every Wednesday, 9-10:30 am US MST
March 1-April 5, 2023

For more information or to register for seminar updates, please visit the INCyTE Research Coordination Network website (https://www.umt.edu/incyte/default.php). You can also email questions to emma.hauser@umt.edu or cory.cleveland@umontana.edu

References

Du, C., X. Wang, M. Zhang, J. Jing & Y. Gao. 2019. Effects of elevated CO_2 on plant C-N-P stoichiometry in terrestrial ecosystems: a meta-analysis. Science of the Total Environment 650: 697-708.

Fleischer, K., K.T. Rebel, et al. 2013. The contribution of nitrogen deposition to the photosynthetic capacity of forests. Global Biogeochemical Cycles 27: 187–199.

Mason, R.E., J.M. Craine, et al. 2022. Evidence, causes, and consequences of declining nitrogen availability in terrestrial ecosystems. Science 376: eabh3767.

McNeil B.E., J.M. Read & C.T. Driscoll. 2007. Foliar nitrogen responses to elevated atmospheric nitrogen deposition in nine temperate forest canopy species. Environmental Science & Technology 41: 5191–5197.

Wang, C., Y. Sun, H.Y. Chen & H. Ruan. 2021. Effects of elevated CO_2 on the C: N stoichiometry of plants, soils, and microorganisms in terrestrial ecosystems. Catena 201: 105219.

IN CASE YOU MISSED IT

How does resource stoichiometry impact host-parasite coevolution?

Nutrient limitation can lead to changes in body stoichiometry in populations over time and influence species interactions. Larsen and colleagues (2019) hypothesized that these shifts result in eco-evolutionary feedbacks that alter the stability of antagonistic species interactions. They tested their hypothesis by coevolving populations of the cyanobacterium, *Synechococcus,* with its lytic phage parasite in N- and P-limited environments. To determine how nutrient limitation influenced the mode of coevolution between these two species, the researchers conducted a time-shift experiment in each environment.

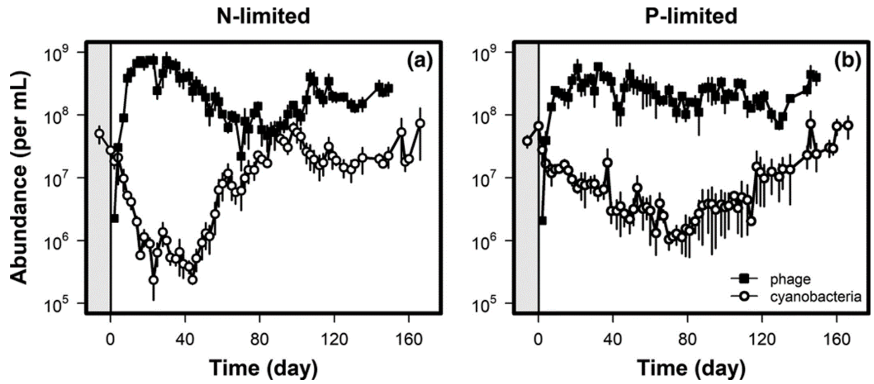


Figure 1 Microbial community dynamics were affected by nutrient stoichiometry. *Synechococcus* and phage densities were tracked in replicate (n = 3) chemostats receiving nitrogen (N)- (a) or phosphorus (P)-limited (b) media. Vertical lines at day 0 indicate time of phage amendment. Data are represented as mean +/- SEM. Reproduced from Larson et al. (2019) Ecology Letters 22: 1009-1018 with permission.

Time-shift experiments challenge naïve hosts (hosts unexposed to parasites) or hosts from one generation against coevolving parasites from the past, present, or future. The success of these challenges can then be expressed as a network, and network metrics can be calculated to help describe the coevolutionary process. For example, if contemporary hosts are more resistant to past parasites and contemporary parasites can more easily infect past hosts (i.e., if the network exhibited a high degree of nestedness), this would indicate arms-race dynamics between the host and parasite. High levels of network modularity, on the other hand, would indicate that coevolution is occurring through negative frequency dependent selection. An effect of nutrient limitation on any network characteristic would indicate that nutrient limitation can, indeed, influence the stability of antagonistic species interactions.

The authors found evidence that nutrient limitation can influence the coevolution of antagonistic interactions. Naïve bacteria raised in N-limited conditions were more susceptible to infection than those raised in P-limited conditions, and N-limited communities were less stable than P-limited ones (Figure 1). The networks produced from both N- and P-limited time-shift experiments were highly nested, suggesting arms-race dynamics were an important mode of coevolution under both conditions. However, networks from P-limited experiments showed a higher level of modularity indicative of negative frequency-dependent selection. The authors suggest that these differences reflect the effect of differential nutrient limitation on defense and virulence.

From the Paper: *"We demonstrated that nutrient stoichiometry [affects] the evolutionary dynamics of microbial communities likely through differences in the expansions and contraction of virus host-ranges under N- vs. P-limited conditions."*

Contributed by Scott Binger and Charlotte Narr

Larsen, M.L., S.W. Wilhelm and J.T. Lennon. 2019. Nutrient stoichiometry shapes microbial coevolution. Ecology Letters 22: 1009-1018. https://doi.org/10.1111/ele.13252

Using ionomics to test whether evolution can mitigate elemental imbalances.

There are ~20 biogenic elements of life that are separated by building blocking (C, N, P), balancing ions (Mg, Na, K), and co-factors within enzymes that perform catalytic functions (Fe, Zn, Mn). With all the known interconnectedness of elements, it should be no surprise that altering one element can affect the composition of others. Ecological stoichiometry has demonstrated the use of elements and ratios to predict growth, population dynamics, ecosystem function, and eco-evo feedbacks. Most past work considered the consequences of a limiting element but had little concern for changes to the remaining ~19 elements.

A new study by Jeyasignh and others (2023) examined how the ionome adapts to different nutrient limitations (C, N, P, Fe, and Mn) in the pathogenic bacterium, *Serratia marcescens*. Briefly, they evolved an ancestral strain of the bacterium under nutrient-replete and nutrient -limited conditions for ~ 285 generations. They measured the ancestral and descendant strains for growth, yield, and ionomic composition. The descendant strains in N-, Fe- and Mn- limited conditions had slower growth rates compared to the ancestral strains. Whereas descendant strains in C-, N-, and P-limited treatments had lower yields compared to the ancestral strains. The elemental imbalances between the ancestral nutrient-limited strains and descendant strains differed by elemental limitation. For example, the ancestral Mn-limited strain had a lower iron quota compared to the nutrient-replete strain. However, the Mn-limited descendant strain was able to balance iron quotas (See figure above), suggesting an ability to substitute metal co-factors within enzymes. Overall, the authors found the quotas of elements involved in catalytic centers are more variable and likely to evolve in concert with elements involved in biomass (C, N, P).

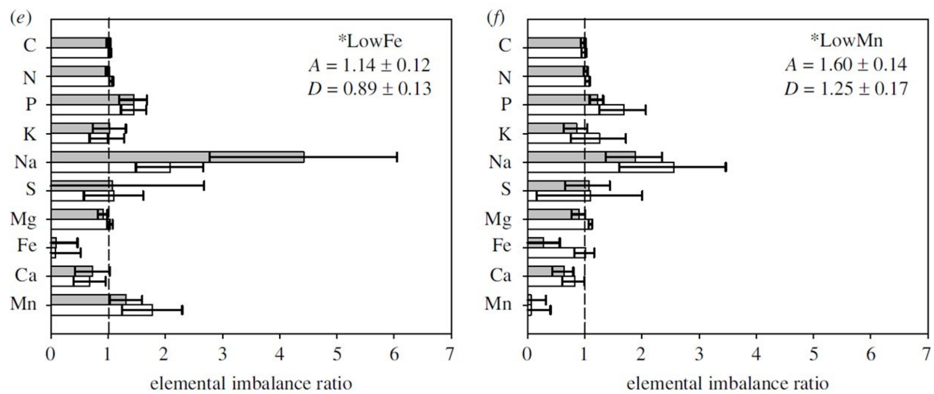


Figure 3. Ionomic elemental imbalance ratios in each of the six treatments: (d) Low Fe, (f) Low Mn with the ancestor strain in grey and descendant strain in white. Univariate imbalances for individual elements are expressed as concentration ratios relative to ancestral optimally growing phenotypes where 1 is perfectly balanced (dashed vertical line), less than 1 is nutrient limited and greater than 1 is nutrient surplus.

From the paper: "*... measuring one or a small subset of elements to understand any biological process is bound to ignore a substantial proportion of underlying mechanisms. Observations in this study indicate that adaptation to limitation of a particular element involves readjustment of multiple other elements*"

Contributed by Nicole Wagner

Jeyasingh, P.D., R.E. Sherman, C. Prater, K. Pulkkinen, and T. Ketola. 2023. Adaptation to a limiting element involves mitigation of multiple elemental imbalances. J. R. Soc. Interface 20:20220472. http://doi.org/10.1098/rsif.2022.0472

'A Very Stable Genus'

Stoichiometric homeostasis across trophic levels in response to eutrophication and warming

Stoichiometric homeostasis is a central concept in ecological stoichiometry. The ability of an organism to regulate its body elemental composition to variable nutritional supplies is central to the development of elemental imbalances and their effects on foodwebs. This organismal buffering of internal stoichiometry against variation in resource stoichiometry is generally agreed to vary among broad taxonomic groups (e.g., vascular plants are more stoichiometrically homeostatic than algae) and trophic level (e.g., consumers are more stoichiometrically stable than producers). In the face of global change that is dramatically changing the environment, it is important for us to understand how environmental stress percolates through the foodweb. The effects of temperature and nutrient enrichment, two primary agents of global change, could be modified by the differential elemental homeostasis exhibited among taxonomic groups and trophic levels.

In this paper, Feng et al. (2023) stocked 48 mesocosms with a freshwater foodweb comprised of two macrophytes (*Vallisneria denseserrulata* and *Hydrilla verticillata*), snails (*Bellamya aeruginosa*), shrimps (*Macrobrachium nipponense*) and carp (*Carassius carassius*). In addition, mesocosms had sediments containing established benthic communities. These foodwebs were exposed to different combinations of three stressors; eutrophication (increased N and P), periodic warming (heatwaves fluctuating between 0 and 6°C above ambient), constant warming (+3°C warmer), and glyphosate-based herbicide. Treatments were applied to the mesocosms for a period of 12 weeks after which the experimental organisms were collected and dried for elemental analysis. Stoichiometric ratios of C:N, C:P, and N:P were measured for each species in addition to $\delta^{15}N$ stable isotope ratios to determine trophic position. Stoichiometric stability (S) was calculated as the degree of variance in each variable relative to its mean (μ/σ).

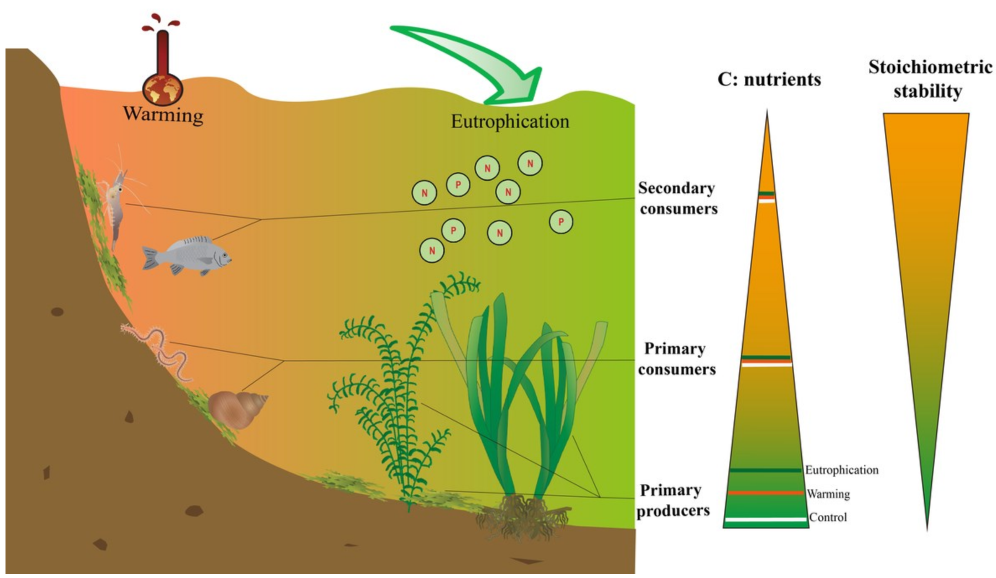


Figure 1. Graphical representation of foodwebs and their stoichiometric responses to global change drivers as examined in Feng et al. (2023)

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Feng et al. (2023) found that herbicide exposure had no significant effects on stoichiometric traits. In contrast, eutrophication and warming both had effects on stoichiometric traits and these were strongest in the lower trophic levels. Eutrophication significantly reduced C:nutrient ratios in primary producers while warming had weaker, antagonistic effects to the eutrophication treatments. Producer stoichiometry was also more strongly affected by periodic warming than by constant warming. By far the strongest predictor of variability in stoichiometric traits was trophic level, with η^2 effect sizes of 0.5-0.8 on C:N, C:P, N:P for trophic position compared to η^2 effect sizes of <0.2 on C:N, C:P, N:P for the three environmental drivers. These results indicate that environmental stressors have the potential to increase elemental imbalances between producers and consumers.

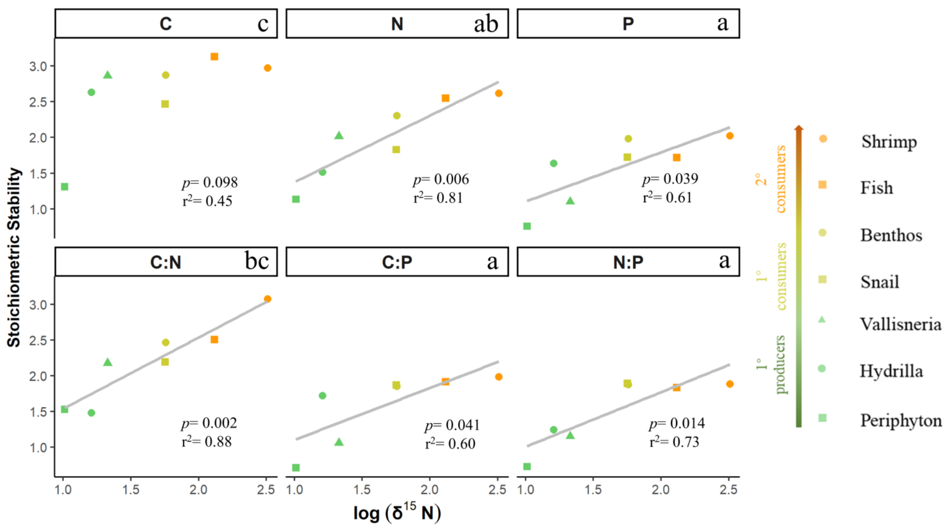

Fig. 2. The relationship between stoichiometric stability (S) and trophic level ($\delta^{15}N$) for each organism/organismal group included in the experiment.

From the paper: *"Our results demonstrate that warming and eutrophication might substantially alter the stoichiometric traits of lower trophic levels, thus impairing the nutrient transfer to higher trophic level, which might further change the structure of food webs and functions of the ecosystems."*

Contributed by Catriona Jones

Feng, M., H. Cheng, P. Zhang, K. Wang, T. Wang, H. Zhang, H. Wang, L. Zhou, J. Xu, and M. Zhang. 2023. Stoichiometric stability of aquatic organisms increases with trophic level under warming and eutrophication. Science of the Total Environment 858