Ratios Matter

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Stoichiometry Special Sessions – Where is Stoichiometric Research Going?

By Eric Moody and Sarah Collins

Three years have passed since the first Conference on Biological Stoichiometry (COBS) at Trent University, and stoichiometry scientists have continued to convene and present new research at a variety of conferences. For those of us who work in aquatic ecosystems, particularly in North America, the annual meetings of the Society for Freshwater Science (SFS) and the Association for the Sciences of Limnology and Oceanography (ASLO) are popular venues. As interest in stoichiometry has grown, organized special sessions have become a regular feature at these meetings. Popular stoichiometry sessions occurred at the 2018 SFS and ASLO meetings, and provide a slice of the current issues that are at the forefront of stoichiometry research in aquatic systems.

SFS Sessions. The special session at 2018 SFS meeting ("Ecological Stoichiometry as a Bridge Across Disciplinary Boundaries in Freshwater Science," organized by E. Moody, K. MacNeill & R. Nifong) included two blocks of six talks. Interestingly, the talks were clearly separated by- *Continued on page 5.*

GRC 2018 UPDATE

In July, ~140 ecologists met in Biddeford, Maine to discuss unifying ecology using information theory at a Gordon Research Conference. Ecological stoichiometry was well represented in both poster and oral sessions, which considered the importance of elements from molecular to ecosystem level scales. Overall, the conference was thought provoking in attempting to unify various sub-disciplines of ecology to gain a mechanistic view of ecosystems.

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It's always dusty in SW Greenland. Over the last 2 months, researchers from Loughborough University and the University of Nottingham (UK) have been busy collecting dust & water samples and conducting bioassays to examine the role of glacially derived elements in low nutrient Arctic Lakes. According to RM's own Clay Prater, "With >50 different elements found in this dust, we are interested in seeing how dust inputs in this region are used to build lake foodwebs."

Consistent patterns in nutrient limitation in headwater streams across biomes

Ecological stoichiometry can help identify patterns in nutrient limitation that transcend individual ecosystems, but until now, we had little information about detrital resource quality in streams across biomes. Quantifying spatial variation in the quality of this resource is important because detritus fuels the base of the food web in many headwater stream networks.

As part of the Scale, Consumers, and Lotic Ecosystem Rates (SCALER) project, Farrell and colleagues (2018) quantified the C, N, and P content of conditioned coarse and fine benthic organic matter (CBOM and FBOM), and estimated potential nutrient limitation for benthic macroinvertebrate detritivores throughout four stream networks in distinct biomes: tropical montane forest (Luquillo), temperate deciduous forest (Coweeta), tallgrass prairie (Konza), and boreal forest (Caribou Poker Creek).

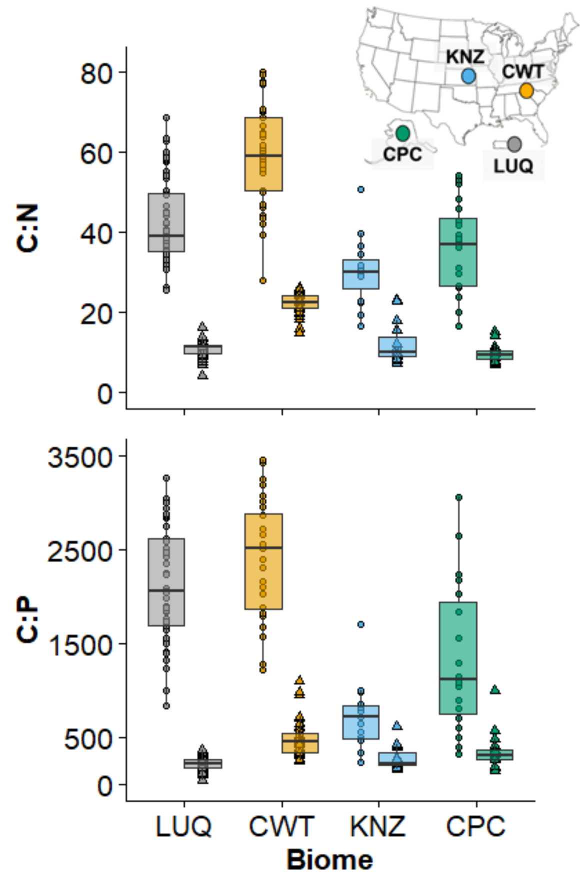


Figure: Cross-biome comparisons indicated highly variable C:N and C:P in CBOM (circles) was substantially reduced in FBOM (triangles).

Across biomes, CBOM was higher in C and N and higher and more variable in C:N and C:P than FBOM, suggesting that microbial processing results in more tightly constrained elemental composition in FBOM than in CBOM. When they compared CBOM and FBOM stoichiometric ratios to estimated threshold elemental ratios of macroinvertebrates, they found that consumer-resource mismatches could be widespread in headwater streams across biomes. Shredders feeding on CBOM were likely to experience N and/or P limitation, while collector-gatherers feeding on FBOM were likely to experience C limitation. These consistent consumer-resource mismatches reveal potential commonalities in nutrient cycling in headwater streams across biomes.

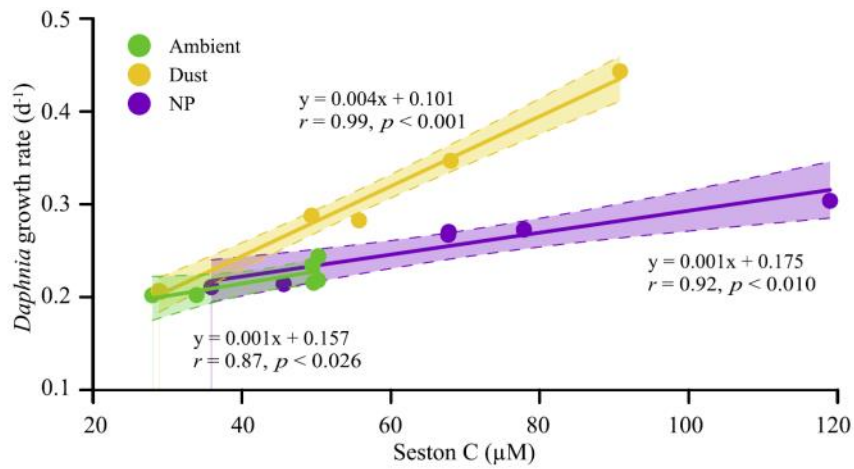
From the paper: "*Our results suggest that differences in basal resource elemental content and stoichiometric ratios have the potential to affect consumer production and ecosystem rates of C, N, and P cycling in relatively consistent ways across diverse biomes*".

Contributed by Kait Farrell and communicated by Charlotte Narr

Farrell, K.J., A.D. Rosemond, J.S. Kominoski, S.M. Bonjour, J. Rüegg, L.E. Koenig, C.L. Baker, M.T. Trentman, & T.K. Harms. 2018. Variation in detrital resource stoichiometry signals differential carbon to nutrient limitation for stream consumers across biomes. Ecosystems, in press. DOI: 10.1007%2Fs10021-018-0247-z.

The sky is falling! Effects of dust deposition on Mediterranean lakes

Despite a long history of studying human-derived impacts of nutrient loading into aquatic systems, our knowledge of a key part of elemental cycles, atmospheric transport and deposition, remains relatively limited. In a recent study by Villar-Argaiz et al. (2018), researchers examined the effects of elevated CO_2, dust-derived elements, and inorganic nutrients on both phytoplankton and zooplankton (*Daphnia*) growth in 3 low nutrient Mediterranean lakes. Elevated CO_2 had little effect on seston quantity (C) or C:P ratios individually, but stimulated seston C when coupled with either dust or N+P enrichment in 2/3 of study lakes. When fed experimental seston cultures, *Daphnia* showed similar responses as phytoplankton and grew faster with CO_2 enrichment only in treatments supplemented with dust-derived or dissolved nutrient enrichment. Seston C:P did not differ significantly across lakes or treatments and stayed moderately low (<350) for a majority of the experiments suggesting that increased daphnid growth was not related to macronutrient food quality. Instead, their increased growth rates were related to higher food quantity, particularly in high dust treatments. As CO_2 levels and the frequency and intensity of dust deposition are expected to continue to increase, these findings underscore the importance of examining the ecological effects of cross-system nutrient transport and their roles in biogeochemical cycling.



Relationships between seston C and *Daphnia* growth rate under different nutrient additions. Figure 7 from Villar-Argaiz et al. (2018) reproduced with permission provided by the Copyright Clearance Center to M. Villar-Argaiz.

From the paper: *"Dust aerosols not only exert a major radiative effect on the Earth's energy balance, but also constitute major vectors for nutrient transfer (e.g., iron [Fe], P or N) between distant worldwide regions, affecting the productivity of ecosystems."*

Contributed by Clay Prater

Villar-Argaiz, M., M.J. Cabrerizo, J.M. González-Olalla, M.S. Valiñas, S. Rajic & P. Carrillo. 2018. Growth impacts of Saharan dust, mineral nutrients, and CO_2 on a planktonic herbivore in southern Mediterranean lakes. Science of The Total Environment 639: 118-128.

-those that focused on the organismal scale and those which focused on the ecosystem scale. Organismal talks typically included the influence of diet and environment on growth rates (E. Moody), excretion rates (B. Perrotta), and body stoichiometry (R. Sherman). On the other hand, ecosystem talks focused on nutrient limitation of primary production (C. Chamberlin; L. Collis), the impact of extreme events on ecosystem stoichiometry (J. Corman) and the stoichiometric coupling of nutrient cycling (T. Scott; K. MacNeill).

ASLO Sessions. The 2018 ASLO special session ("Ecological Stoichoimetry Across Scales," organized by C. Godwin, S. Thompson, R. Maranger, S. Jones, J. Cotner & T. Scott) was organized similarly to the SFS session. Two blocks and two posters covered a wide range of issues related to organismal and ecosystem scale stoichiometry. The session began with a number of talks about organisms ranging from microbes to fish (e.g., T. Scott, E. Herstoff, R. El-Sabaawi). The end of the first day concluded with a number of whole-ecosystem talks focused on cycles of multiple nutrients (e.g., J. Walsh) and the influence of stoichiometry on biogeochemical cycles (e.g., S. Thompson). The second session included broad scale talks, bookended by two synthesis presentations: I. Creed's tutorial presentation on coupled biogeochemical cycles and implications for northern food webs and R. Maranger's synthesis of C:N:P stoichiometry through the freshwater pipe (Maranger, Jones & Cotner 2018).

Conclusions. Organismal and ecosystem scale-focused talks clearly relate to each other as consumers can modify the stoichiometry of nutrient supply while variation in ecosystem functions alters the quality and quantity of food available to consumers. Although the discussion across scales in both recent special sessions suggests that this topic is of interest, few individual presentations looked directly across scales. However, the SFS talk from C. Atkinson provided an exception in thinking directly about stoichiometric impacts across scales, which is a topic we hopefully hear more about in the future.

These sessions and other recent synthetic work in the literature are leading to new insights about how organisms (particularly animals) and ecosystems function separately, and we see linkages between these functions as an area that is ripe for exciting synthesis. The SFS session reflected a strong focus on elemental variation in animals, while the ASLO session reflected a stronger balance of talks across taxa, including autotrophic and heterotrophic microbes. While some have thought about variation in whole microbial community responses by measuring primary production, little is being done with individual taxa in the way we are with animals. We look forward to future opportunities to discuss stoichiometry research at conferences, new synthetic papers that consider stoichiometry across scales, and future initiatives to employ ecological stoichiometry to study ecological function across scales.

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Profiles in Stoichiometry

9 Questions for Mehdi Cherif

Tell us about your scientific background and how you became interested in ecology. It might sound a little bit cliché, but ecology was my interest since childhood. While I have been attracted to other fields like physics and mathematics, I have remained mostly faithful to my first interest. Thankfully, working on food web models offers me the opportunity to combine all at once! During my Bachelor's at the University of Lyon in France, I knew that my career would be in research. I still remember vividly a talk given by a PhD student working on the Siberian marmot and really enjoyed a two-month summer internship in the Alps, working on the European globeflower. Then stoichiometry came during my graduate studies and I still work on stoichiometry as associate professor at the University of Umeå in Sweden.

Do you remember when you first heard about ecological stoichiometry? Yes, that was some time ago now! I was a recent graduate, looking for an interesting research project to work on in Paris. I remember entering the office of Dr. Gérard Lacroix, who was the first to utter some esoteric words to me: "ecological stoichiometry", "homeostasis", "N:P ratios". To say I was intrigued is an understatement! Soon, I started learning more about such things like phosphorus-craving *Daphnia* and bacteria, and the head-spinning consumer-driven nutrient recycling!

What is your current research on stoichiometry? I've worked on and read about many mathematical models based on the stoichiometry theory. I've always been unhappy with the assumption that species and trophic level can be treated as homogenous bags of elements. One feature that distinguish populations from collections of individuals is their ordered division into stages that most often differ in their stoichiometry. Instead of just complaining about this unrealistic assumption, I finally decided to take the issue seriously and strive to come with a reasonable stoichiometric model of stage-structured populations.

Do you view ecological stoichiometry as its own research field? Why or why not? As much as it saddens me, my answer is a resounding no! Those who read my recent contribution to the Frontiers Research topic on ecological stoichiometry might already have a clue as to why. Ecological stoichiometry needs the other fields of genetics, evolution, population biology, etc., in order to make true its wish of unifying scales from genes to the biosphere. Stoichiometry is too important to keep it for ourselves! Is there a field in ecology that wouldn't benefit from a bit of stoichiometry?

What is your favorite stoichiometry paper and why? That's a tough question! My first impulse would be to say that it's always the next coming, groundbreaking article that is the best. Concretely, I'd say that one of the most influential papers on my early thinking (and which I still greatly appreciate) is Cebrian (1999)*. The paper is not consciously stoichiometric, but provides such a broad view on the importance of elemental content at the level of ecosystems!

Where do you see ecological stoichiometry progressing in the next 10 years? And do you see elements beyond CNP becoming more of a focus? I think (and hope!) that it will move towards closing some of the gaps that exist in the theory as of now: how exactly do stoichiometric constraints affect the dynamics of populations and the composition of communities? How did the differences in stoichiometry evolve? And of course, what about those other elements besides C, N and P that make biomass? I also see the field moving towards more relevance in terms of management and conservation.

What is your favorite element? There are the mighty C, N and P of course… But I have a soft spot for Fe (although I haven't worked on this one yet!). It does its best to reach the podium, and I have the feeling that it has yet to reveal all of its capacities! We know it plays an important role in infections and diseases. Given how ecologically relevant are pathogens and parasites, shouldn't we keep an eye on iron?

*__Cebrian, J.__ 1999. Patterns in the fate of production in plant communities. American Naturalist 154:449-468.

DID YOU KNOW?

While comprising only about 6% of witnessed falls, iron meteorites are probably the most famous type of space debris. These meteorites are primarily composed of Fe-Ni alloys, which yields a much higher %Ni content that other Earth-origin iron based metals. So if you are considering purchasing a meteorite, be sure to check its Fe:Ni ratio and make sure its low!

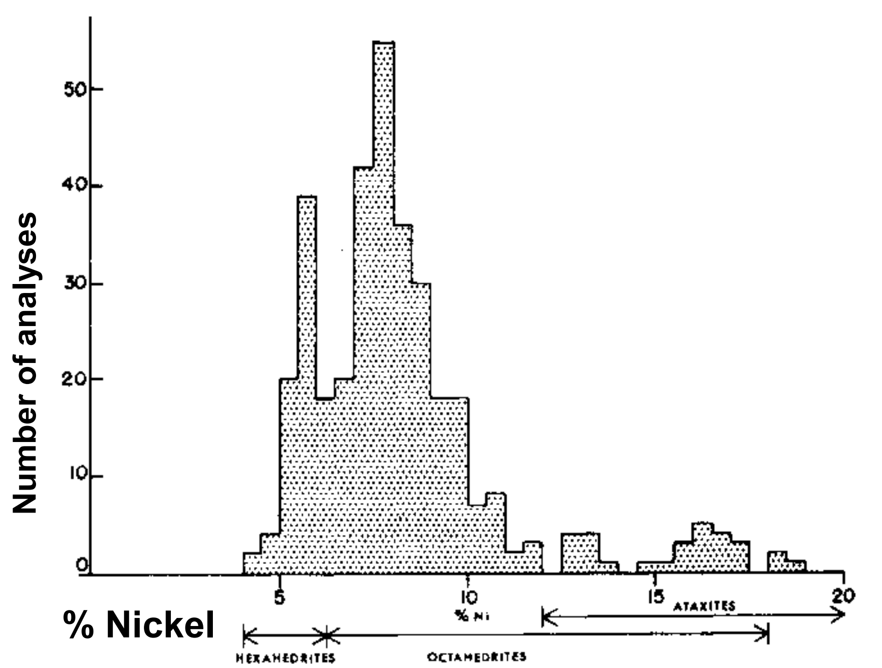

FIG. 14. The frequency of distribution of nickel content in analyses of iron meteorites.

Source including modified figure: Mason, B. 1967. Meteorites. American Scientist 55: 429-455.

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Selected Recent Stoichiometry Publications

Branco, P., M. Egas, J.J. Elser and J. Huisman. 2018. Eco-Evolutionary dynamics of ecological stoichiometry in plankton communities. Am. Nat. 192: E1–E20. doi:10.1086/697472

Delgado-Baquerizo, M., D.J. Eldridge, F.T. Maestre, V. Ochoa, B. Gozalo, P.B. Reich and B. K. Singh. 2018. Aridity decouples C:N:P stoichiometry across multiple trophic levels in terrestrial ecosystems. Ecosystems 21: 459–468. doi:10.1007/s10021-017-0161-9

Dittberner, H., N. Ohlmann and C. Acquisti. 2018. Stoichio-Metagenomics of ocean waters: A molecular evolution approach to trace the dynamics of nitrogen conservation in natural communities. Front. Microbiol. 9: 1590. doi:10.3389/FMICB.2018.01590

Filipiak, M. 2018. Nutrient dynamics in decomposing dead wood in the context of wood eater requirements: The ecological stoichiomtry of Saproxylophagous Insects. In: Ulyshen M. (eds) Saproxylic Insects. Zoological Monographs 1: 429-469. Springer, Cham.

Jiang, Y., M. Song, S. Zhang, Z. Cai and Y. Lei. 2018. Unravelling community assemblages through multi-element stoichiometry in plant leaves and roots across primary successional stages in a glacier retreat area. Plant Soil 428: 291–305. doi:10.1007/s11104-018-3683-9

Ludwig, L., M.A. Barbour, J. Guevara, L. Avilés and A.L. González. 2018. Caught in the web: Spider web architecture affects prey specialization and spider-prey stoichiometric relationships. Ecol. Evol. 8: 6449–6462. doi:10.1002/ece3.4028

Mathews, L., C.L. Faithfull, P.H. Lenz and C.E. Nelson. 2018. The effects of food stoichiometry and temperature on copepods are mediated by ontogeny. Oecologia In Press: 1–10. doi:10.1007/s00442-018-4183-6

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Moreno, A.R. and A.C. Martiny. 2018. Ecological stoichiometry of Ocean plankton. Ann. Rev. Mar. Sci. 10: 43–69. doi:10.1146/annurev-marine-121916-063126

Sanders, A.J. and B.W. Taylor. 2018. Using ecological stoichiometry to understand and predict infectious diseases. Oikos In Press: 1–11. doi:10.1111/oik.02629

Stark, S., H. Ylänne and A. Tolvanen. 2018. Long-term warming alters soil and enzymatic N:P stoichiometry in subarctic tundra. Soil Biol. Biochem. 124: 184–188. doi:10.1016/j.soilbio.2018.06.016

Trierweiler, A.M., K. Winter and L.O. Hedin. 2018. Rising CO_2 accelerates phosphorus and molybdenum limitation of N_2-fixation in young tropical trees. Plant Soil 429: 363–373. doi:10.1007/s11104-018-3685-7

Wang, H., Z. Lu and A. Raghavan. 2018. Weak dynamical threshold for the “strict homeostasis” assumption in ecological stoichiometry. Ecol. Modell. 384: 233–240. doi:10.1016/j.ecolmodel.2018.06.027

Wen, J., H. Ji, N. Sun, H. Tao, B. Du, D. Hui and C. Liu. 2018. Imbalanced plant stoichiometry at contrasting geologic-derived phosphorus sites in subtropics: the role of microelements and plant functional group. Plant Soil In Press: 1–13.