Ratios Matter

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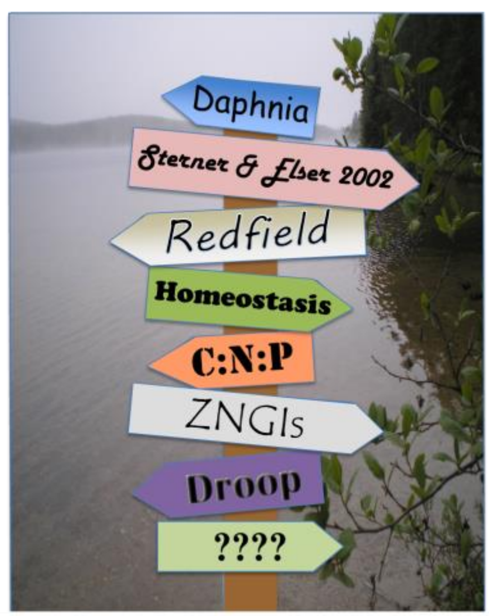
Collaborations in Stoichiometry

This issue of *Ratios Matter* is focused on the role of collaborations in ecological stoichiometry. By definition, stoichiometry seeks to understand how biological processes and ecological interactions are affected by mass balance dynamics. While we might all imagine collaborations with chemical stoichiometrists, most of the integrative work is done between ecologists/biogeochemists (within and outside of ES realms), biochemisty types, and analytical chemists (e.g., how do I measure this element?). We have collected some reflections on collaborative experiences in past studies of ecological stoichiometry (pages 4-8). One part of this is to acknowledge the valuable contributions of colleagues in other fields, who sometimes have to be convinced to test our 'stoichiometric' hypotheses but whose expertise has been invaluable in pushing the boundaries of ES. We also hope this issue can provide inspiration to any stoichiometrist, who may have thought at one time or another, "I wonder if stoichiometry is at play in that dynamic/process" but lacked the knowledge or tools to answer the question. In other words, we are hoping you turn your wildest stoichiometry daydreams into reality.

Stoichiometric Survey



Over the past eight issues, *Ratios Matter* has highlighted interesting applications and advances in the field of ecological stoichiometry. While the stoichiometry of turtles, wine making, and Mediterranean dust were among our favorite topics from the past two years, we aren't sure these represent the future of stoichiometry. But we are curious about what you think. What do you see as the future of ecological stoichiometry? We ask that you take a few minutes to complete this anonymous poll and to encourage your stoichiometric colleagues to do the same. We will present a summary of your responses in *Ratios Matter's* first issue of 2019. Take the survey now by clicking here: **Stoichiometry Survey**

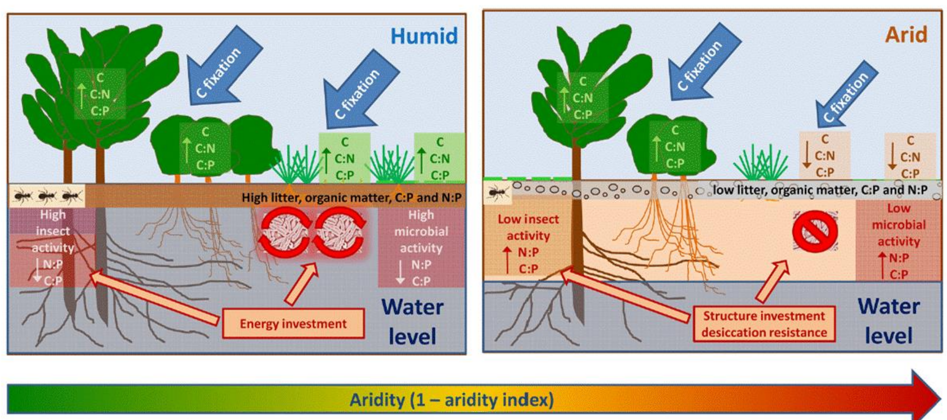
WANTED: Associate Editors

***Ratios Matter* is currently accepting applications** for two open AE positions on our editorial board. Applicants should have an interest in ecological stoichiometry and newsletters, and some experience writing science. In other words, little experience is needed and all interested parties are encouraged to apply. Positions are for 2 years with the possibility of renewal at the end of the initial appointment. To apply, send a cover letter, a c.v. and a writing sample (e.g., manuscript, proposal, essay, blogpost, etc.) to: ratiosmatter@gmail.com. Applications should be sent before **January 1, 2019** to receive full consideration. Inquires and questions should be sent to Paul Frost, Editor-in-Chief (paulfrost@trentu.ca) or *Ratios Matter* (ratiosmatter@gmail.com).

Ecological Stoichiometry in a Drier World

Many areas of Earth are expected to become increasingly arid in the coming decades. As these dryland areas expand, the biogeochemical importance of biological processes may decline and elemental fluxes due to weathering may increase. This shift may profoundly affect elemental cycles by decoupling the cycling of C and N from P in soils. How would aridity-driven shifts affect C:N:P stoichiometry in terrestrial foodwebs? In particular, how will these changes affect the elemental composition of microbes, insects, and plants that access and use soil for nutrition?

To find out, Delgado-Baquerizo and colleagues (2018) measured C, N, and P concentrations of soils, autotrophs, and heterotrophs across an aridity gradient in Australia. As they expected, plant communities showed different connections to aridity than insects and microbes. Increasing aridity decreased the soil C pools and C:N and C:P ratios in mosses and short grasses. In contrast and unexpectedly, C:N:P composition of shrubs or trees was not related to aridity. This lack of relationship was likely because larger vascular plants have adaptive root systems that provide some buffer against reductions in water availability due to their ability to access water stored deep below surface soils. Conversely, this study found that increased aridity was matched with higher C:P and N:P ratios in microbes and ants, which was attributed to increased body C due to slower growth and more investment in structures that reduce the vulnerability to desiccation.



Possible changes in C, N, and P cycling due to increased aridity. Reprinted by permission from Springer, Ecosystems. See citation below.

This study shows that future arid ecosystems are likely to experience significant changes in foodweb stoichiometry due to changes in both producers and consumers. While Delgado-Baquerizo et al. (2018) didn't measure soil organic matter decomposition and mineralization rates, they note that aridity may also influence these processes through its effect on litter quality and microbial stoichiometry. Ultimately, herbivores benefit from higher quality vegetation; that is if both they and the vegetation they depend on can find enough water.

From the paper: *"More than impacting ecosystem functioning in the medium term (years to centuries), increases in aridity could promote evolutionary long-term changes in the stoichiometry of soil microbes, insects, and short plants."*

Contributed by Charlotte Narr and Paul Frost

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

Ecological stoichiometry within the Nutrient Network

by Judith Sitters (Vrije Universiteit Brussel, Belgium)

Two of the most pervasive human impacts on grasslands are the alteration of global nutrient budgets, through fertilization and changes in the abundance and identity of grazing herbivores. The Nutrient Network, or NutNet (**nutnet.org**), consists of globally coordinated experiments to quantify the impacts of these human activities on ecosystem processes in grasslands. The experiments are relatively simple: at each site, plots receive nitrogen (N), phosphorus (P), and potassium (K) plus micronutrients (µ) in a full factorial and randomized manner, including an unfertilized control. In addition, two plots are fenced to exclude aboveground mammalian herbivores; one plot receives a full nutrient combination (NPKµ) while the other one is used as an ambient nutrient control plot. Each site consists of at least three blocks with 10 plots of 5 m x 5 m. Recently, I joined NutNet and helped set up the **first Dutch site** and it now includes over 100 sites in 25 countries on 6 continents.

Over the past few years, the theory of ecological stoichiometry has gotten more attention in this network. In 2013, the working group **sToichFun** was set up by Prof. Helmut Hillebrand, who explained: '*The group was initialized to see whether stoichiometric constraints of resource use could explain the shape of the relationships between potential productivity (available resources), biodiversity and realized productivity. We used NutNet data as several participants were also Nutnet PIs, and so the data became part of the larger meta-analysis by Lewandowska and others*'. This **meta-analysis**, which included 40 NutNet sites, was published in 2016 and showed a significant relationship between resource availability and realized productivity, but no significant effect of resource availability or imbalances on diversity; grassland diversity is thus not tightly coupled to soil nutrients.

A second working group was initialized in 2016 named '**sToichNutNet**' to specifically use ecological stoichiometry within NutNet as a promising mechanistic approach for developing a predictive understanding of community and ecosystem consequences of global changes. A paper published in 2018 by **Anderson and others** showed that both herbivory and eutrophication mediated plant nutrient responses in 18 NutNet sites; herbivores dampened the positive effects of fertilization on plant nutrient pools through their consumption, especially in drier sites.

These papers clearly show that the NutNet data have great potential for stoichiometric applications, which should definitely be examined further! Or as Helmut puts it: '*I think multi-element resource use efficiency will become a key aspect of future research focusing on how biodiversity mediates the transfer of available resources into biomass production. Here, data from NutNet on both soils and plants could make an interesting contribution.*'

Collaborative Stoichiometry: Weaving webs to understand bromeliads and spiders

by Angélica González (Rutgers University, USA)

Collaboration is central to my group's work on the stoichiometry of terrestrial communities and ecosystems. This has involved working with researchers from South America, North America and Europe, who share common interests in stoichiometry and ecology. One example is my participation in the Bromeliad Working Group, which is an international team of ecologists that use tank bromeliads (i.e., phytotelmata) to test general ecological theory, including ecological stoichiometry principles. Rainwater collects in the leaves of tank bromeliads to form compartments, which capture leaf litter and create unique aquatic habitats. This supports the development of invertebrate food webs and provides highly-replicated but miniature ecosystems to study. By sampling >850 aquatic invertebrates from 71 species inhabiting tank bromeliads from five distant localities across Central and South America (Costa Rica, Puerto Rico, French Guiana, and two locations in Brazil) we showed that among species differences in elemental composition depend on evolutionary relationships and trophic grouping, whereas differences among individuals within a species depend on body size. Further, as these patterns were largely consistent across sites, these findings suggest the existence of general mechanisms underlying the elemental content of invertebrates. For more on these results, see **González et al. (2018) Ecological mechanisms and phylogeny shape invertebrate stoichiometry: a test using detritus-based communities across Central and South America.**

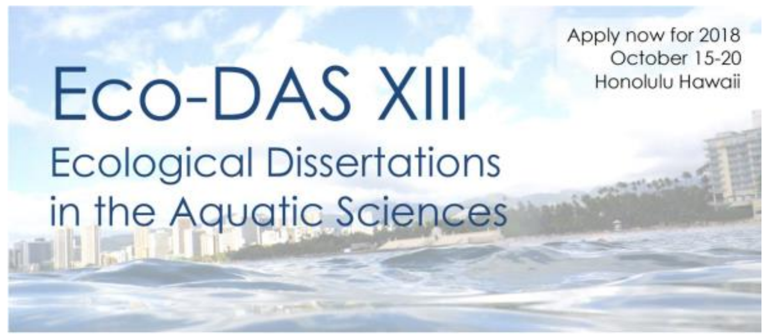
Tank bromeliad. Looks like vegetation but inside is a diverse detritivorous foodweb.

I am also involved in a study looking at predator-prey elemental imbalances using web-building spiders with an international team of scientists from USA, Ecuador and Canada. We recently found that web architecture partially affects prey richness and community composition and that prey specialization by some web-building spiders seems to have resulted in large elemental imbalances. In addition, we found larger P imbalances (compared to N imbalances) between spiders and their prey, which suggest that P limitation of web-building spiders may be of similar magnitude to N-limitation described for other predators. See **Ludwig et al. (2018) Caught in the web: Spider web architecture affects prey specialization and spider–prey stoichiometric relationships.**

Eco-Stoichiometry at Eco-DAS XIII

by Keeley MacNeill, Whitney Beck, Jim Junker, Lillian Aoki, Kait Farrell, Kelly Hondula, Dustin Kincaid, Amber Rock, Simon Stewart, Seth Thompson, & Tanner Williamson

What does an invert person who works in Ohio mesocosms have in common with a stream algae person who works in Ecuador, a guy who studies ooze in potholes, and a data scientist focusing on wetlands? Stoichiometry!



The 13th Eco-DAS (Ecological Dissertations in the Aquatic Sciences) convened last month in Hawaii under the leadership of Dr. Paul Kemp, editor of L&O Methods. The symposium is a gathering for early career (i.e., within a year of PhD defense) water scientists from all over the world and with a variety of backgrounds to share their science, think deeply about current water issues, and develop collaborative manuscripts to address them. This year's cohort had a strong representation of stoichiometrists with experience from a variety of freshwater and marine systems, allowing us to create unique collaborations addressing some of the most exciting issues in stoichiometry.

Three key themes emerged out of our discussions on the next most important steps for stoichiometry. The first main theme we discussed is better utilizing big data to synthesize and identify drivers of C:N:P stoichiometry across aquatic systems and across local to continental scales. Secondly, we discussed the importance and paucity of non-CNP elements in current literature and the utility of including additional elements into the stoichiometric framework. Third, we discussed the need to better integrate temperature and nutrient interactions in aquatic studies, particularly because of predicted changes for both of these factors. Our collaborative groups consisted of oceanographers, limnologists, and stream ecologists with expertise working with big data, large experimental set-ups and multiple trophic levels, from detritus and algae through top-consumers.

Connecting with early career scientists with such a diversity of experience in person for a week provides a unique opportunity to build and pursue such collaborative projects. This experience established a rapport that will continue through future collaborations, and we highly encourage aquatic scientists who will defend in about two years to pursue this wonderful bi-annual opportunity!

From elements to function: Unifying ecological stoichiometry and trait-based ecology

by Cédric Meunier (Alfred-Wegener-Institut, Helmholtz Centre for Polar and Marine Research, Germany)

Mankind has long recognized the importance of interdisciplinarity and collaborative work. From the construction of Roman roads to managing global change associated issues, the realization that key challenges cannot be solved by individuals has repeatedly brought specialists from different fields together. Despite its necessity, collaborative work is not without obstacles and, even within a given discipline, cooperation requires a certain structure to be successfully conducted. Such structure can be provided by frameworks articulating different disciplines around one central concept, as is the case for biological stoichiometry and trait-based ecology. These two widely used frameworks in ecology owe their success, at least partly, to their ability to unify disparate fields and to connect processes ranging from the cellular to the ecosystem level.

Hoping to strengthen collaborative work, Elena Litchman and I organized a workshop to synthesize and explore promising connections between biological stoichiometry and trait-based ecology. This workshop was part of the Conference on Biological Stoichiometry (CoBS), which was held at Trent University (Canada) in 2015. The workshop aimed to foster collaborations between scientists of different fields (freshwater, marine, and terrestrial ecologists) by highlighting how complex ecological questions can be answered using a multifaceted approach. The workshop was structured to have: 1) a short introductory presentation, 2) break out group sessions of small groups (organized to be experience and expertise diverse) to discuss selected topics such as applications or challenges to their study systems, 3) group intermixing to explore commonalities and differences in discussion, and 4) general discussion and Q&A involving the entire audience. This workshop yielded a **paper** published in 2017 in *Frontiers in Environmental Science* as part of the special issue *on "Progress in Ecological Stoichiometry".* A key result in this manuscript is that coupling functional traits to the stoichiometry of organisms allows a more general understanding of ecological interactions which can, for example, help predict the ecosystem consequences of global change. This successful collaborative experience shows that linking and applying multiple frameworks allows crosstalk between various scientific disciplines, fostering the exchange of comparable efforts in understanding the complexity of ecosystem structure and functioning.

No bones about it, South America is a great place to study phosphorus

by Manuel Villar-Argaiz (University of Granada, Spain)

It seems so long ago when my ecology professor rephrased Dr. Ramón Margalef's hypothesis that the South American continent did not have large ungulates like elephants or giraffes due to the lack of phosphorus as an essential element for their bony skeletons. Those words remained at the back of my mind until the opportunity came up to collaborate with limnologists Drs. Esteban Balseiro and Beatriz Modenutti in San Carlos de Bariloche, Argentina. Little phosphorus in the rocks would also mean little phosphorus in the water. Just as I expected, lakes in this part of the world had higher C:P ratios in seston compared to lakes at similar latitudes in the northern hemisphere. Although this is not direct evidence for the absence of large ungulates, it revealed the large continental differences in the elemental imbalances among food webs. During my pleasant stay in the Andes, I also experienced how elemental imbalances extend to the entire food web. After two weeks eating the most delicious *bifes de chorizo on Earth,* I had to resume a strictly herbivore diet to rebalance my own nutrition.

Periphyton stoichiometry and land-use

by Andrea Kirkwood (UOIT, Canada)

As part of a larger study led by doctoral student, Sarah MacKay, the Kirkwood Lab at the University of Ontario Institute of Technology (UOIT) is collaborating with Ratios Matter's own Paul Frost (Trent University) to measure stoichiometric responses of periphyton to variation in land-use type and water quality. The first year (2016) focused on periphyton accrual on artificial substrates, which were deployed at 14 creeks representing distinct land-use types (agriculture, urban, natural). In the second year (2017), focus shifted to measure established periphyton communities from natural substrates at the same creek sites and their associated macroinvertebrate communities. For the periphyton accrual study, we were examining if stoichiometry of colonizing algae varies with land-use. The second study focuses on periphyton stoichiometry as a metric for macroinvertebrate food quality, and the role that land-use and associated water quality has on periphyton C:N:P. Overall, we want to determine if land-use type influences not just the bioavailability of nitrogen and phosphorus, but also the elemental ratios in periphyton, which has important implications for the aquatic foodweb.

Artificial substrates pulled out of White Creek, a tributary of Lake Simcoe, after a 3-week deployment. Circles were scraped and collected for later stoichiometry, taxonomy, and biomass analyses. Source: S. MacKay (June, 2016).

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Selected Recent Stoichiometry Publications

Barnes, C.L., D. Hawlena and S.M. Wilder. 2018. Predators buffer the effects of variation in prey nutrient content for nutrient deposition. Oikos In Press: 1–8. doi:10.1111/oik.05685

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Iannino, A., A.T. L. Vosshage, M. Weitere and P. Fink. 2018. High nutrient availability leads to weaker top-down control of stream periphyton: Compensatory feeding in *Ancylus fluviatilis.* Freshw. Biol. In Press: 1–9. doi:10.1111/fwb.13192

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Yan, Z., X. Li, D. Tian, W. Han, X. Hou, H. Shen, Y. Guo, and J. Fang. 2018. Nutrient addition affects scaling relationship of leaf nitrogen to phosphorus in *Arabidopsis thaliana*. Funct. Ecol. In Press: 1–10. doi:10.1111/1365-2435.13219

Zhang, P., R.F. Van Den Berg, C.H.A. Van Leeuwen, B.A. Blonk and E.S. Bakker. 2018. Aquatic omnivores shift their trophic position towards increased plant consumption as plant stoichiometry becomes more similar to their body stoichiometry. PLoS One 13: e0204116.