Ratios Matter

VOLUME 1 ISSUE 2 APRIL 2017

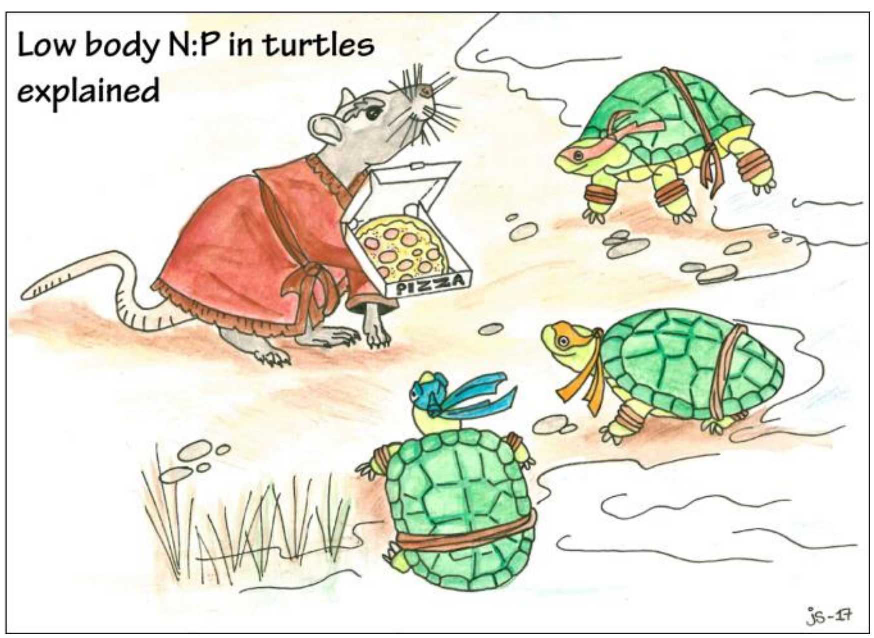
Ratios Matter– Take 2!

We here at *Ratios Matter* are very excited to share the 2nd issue of our newsletter with you. There was a very positive response to our first issue and we thank everyone who sent supportive comments. Our goal is to provide a means to collect and distribute information on ecological stoichiometry to like-minded researchers. **We hope to do so primarily by telling the story of ecological stoichiometry: Where did it come from? What is happening now? And where is it going?** In this issue, we share several paper summaries, which will be a regular feature of *Ratios Matter*. You will also find a new type of article (Profiles in Stoichiometry: 9 Questions) that will feature a short interview of a stoichiometrist. We hope to continue to innovate *Ratios Matter* with new types of articles and interesting stories about ecological stoichiometry. Going forward, we would like to become a platform for sharing new ideas and concepts relevant to emerging (or established) issues in ecological stoichiometry. If you have something you would like to see in *Ratios Matter*, contact us at ratiosmatter@gmail.com with a short description of your submission idea.

On the lighter side, ***Ratios Matter*** **presents:**

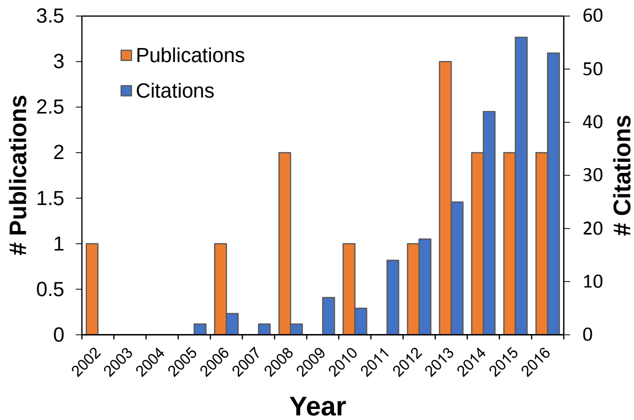
Stoich-Comic

by Judith Sitters



Comictary on Sterrett et al. (2015) Freshwater Biology. See Ratios Matter 2017 Issue 1 for more details.

A Growing Body of Stoichiometric Parasite-tations



Results from a Web of Science search for parasite stoichiometry papers. Shown are the number of articles and citations of those publications since Smith (2002). Search used the key words ("ecological stoichiometry" OR "biological stoichiometry") AND ("parasite" OR "disease").

For a host infected by parasites, shifts in its mass balance may mean the difference between life, death, or complete loss of reproduction. These elemental conflicts make host-parasite stoichiometry an exciting landscape for the ecological stoichiometrist. Val Smith was among the first to highlight how ecological stoichiometry could be used to explain patterns in disease (Smith 2002). Building on this call to study parasite stoichiometry, there has been a steady stream of publications (~1-3/year) that have explicitly used ecological stoichiometry to test fundamental hypotheses about parasitism and disease. These studies have largely worked to uncover the drivers and consequences of nutrient x disease interactions using tractable parasite-host systems. In 8 out of the 14 studies since Smith's review, the host organism was either a *Daphnia* or snail and usually included rigorous combinations of experimental and observational work. While the effects of a host's diet quality on its responses to parasites or on parasite success remain difficult to predict, we have learned a great deal about the potential range and magnitude of these effects. The relevance of this work is clearly demonstrated by the increasing rate at which these studies are being cited in the broader disciplines of ecology, parasitology, and even oncology.

Contributed by Charlotte Narr

Notable Publications in Disease Stoichiometry

Aalto, S.L., E. Decaestecker and K. Pulkkinen. 2015. A three-way perspective of stoichiometric changes on host–parasite interactions. Trends in Parasitology 31: 333-340.

Kareva, I. 2013. Biological stoichiometry in tumor micro-environments. PLoS ONE 8:e51844.

Mischler, J., P.T.J. Johnson, V.J. McKenzie and A. R. Townsend. 2016. Parasite infection alters nitrogen cycling at the ecosystem scale. Journal of Animal Ecology 85: 817-828.

Smith, V.H. 2002. Effects of resource supplies on the structure and function of microbial communities. Antonie van Leeuwenhoek International Journal of General and Molecular Microbiology 81: 99-106.

Editorial Board

Stoichiometric Effects of Warming

Warming has strong effects on organism metabolism. A community's response to increased temperature depends not only on such direct species-specific temperature effects, but also on indirect effects related to bottom-up and top-down processes. In a recent paper, Velthuis and co-workers (2017) investigated how warming affected a freshwater plankton food web with a mesocosm experiment. They analyzed phytoplankton community dynamics, seston stoichiometry, fungal parasitism, and grazing in mesocosms exposed to ambient versus high temperatures (+4°C). They observed that community dynamics changed in response to warming. Seston C:P and N:P ratios were both lower, phytoplankton biomass decreased, and parasite dynamics differed in the artificially warmed mesocosms. Surprisingly, earlier bloom termination and lower phytoplankton biomass in the warm treatment may have resulted from increased fungal infection due to elemental constraints on parasite development in the unwarmed scenario. At the same time, in warm mesocosms, grazer phenology generated a temporal advancement of the top-down control with greater nutrient recycling by heterotrophs and reduced seston C:P and N:P ratios.

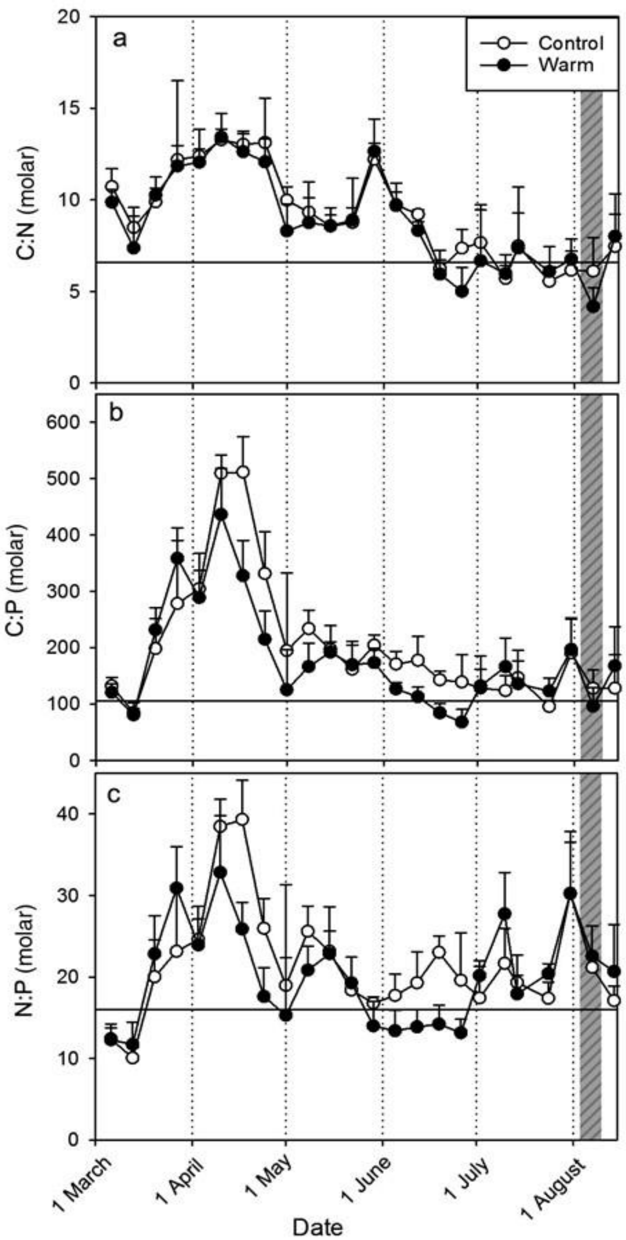


Figure 3 from Velthuis et al. (2017) showing changes in seston C:N, C:P, and N:P ratios in mesocosms over the course of their experiment. Heatwave indicated by gray bar and black lines show Redfield ratio.

From the paper: "Our findings indicate that warming advances top-down control and reduces phytoplankton biomass, thereby demonstrating how bottom-up and top-down related processes can shape future phytoplankton dynamics."

This paper demonstrates that the effects of warming on communities may be complicated. Increased temperatures may change key processes that directly or indirectly shape phytoplankton dynamics and modify elemental mismatches between consumers and their food.

Contributed by Cecilia Laspoumaderes

Velthuis, M., L.N. de Senerpont Domis, T. Frenken, S. Stephan, G. Kazanjian, R. Aben, S. Hilt, S. Kosten, E. van Donk, and D.B. Van de Waal. 2017. Warming advances top-down control and reduces producer biomass in a freshwater plankton community. Ecosphere (1):e01651. 10.1002/ecs2.1651

Profiles in Stoichiometry
9 Questions for Orpheus Butler

Tell us about your scientific background and how you became interested in ecology. I'm a graduate student at Griffith University in Brisbane, Australia, where I also did undergraduate studies in environmental science with a focus on chemistry and soil science. In the first year of my studies, I participated in an ecological field course in Malaysian Borneo. That was my first real experience in ecological research and it definitely got me interested!

Do you remember when you first heard about ecological stoichiometry? Yes - about four years ago, it was during a discussion about a potential undergraduate project with my supervisor, Prof. Chengrong Chen (Griffith University, Brisbane, Australia); he introduced me to the ES concept and the idea that fire could modify an ecosystem's stoichiometry, and both really resonated with me.

What is your current research on ecological stoichiometry? My PhD project is focused on how forest fire alters the stoichiometry of different ecosystem components (soil, leaf litter, etc.), and how these changes (or lack thereof) are related to changes in the function or composition of plant, microbial and invertebrate communities. There is increasing evidence that fire tends to shift the balance of C, N and P in soil toward P, and a long term absence of fire can lead to P-limitation and even ecosystem decline. This is really interesting in Australia because we have a lot of fires as well as very low P soils, so the evolution and ecology of fire-tolerant or fire-dependent flora might be underpinned by stoichiometry in some way.

Do you view ecological stoichiometry as its own research field? Why or why not? At the moment I'm approaching ES as a way of thinking about different things, but I'm sure it could be a field on its own as long as it didn't become an echo chamber. I certainly think there could be more dedicated spaces for people interested in stoichiometry to exchange ideas. That said, science is probably fragmented enough already, and I think that one of the strengths of ES is its integrative approach and its potential utility in many different areas of ecology and biology.

What is your favorite stoichiometry paper and why? I'm going to say Orians & Milewski (2007)*. It might not be a stoichiometry paper in a strict sense, but stoichiometry is definitely part of the paper's story. It's a paper that has really stimulated my thinking during the last few years and laid a lot of groundwork for research into the evolutionary and ecological implications of fire-stoichiometry interactions.

*Orians, G.H. and A.V. Milewski. 2007. Ecology of Australia: The effects of nutrient-poor soils and intense fires. Biol. Rev. Camb. Philos. Soc. 82:393-423.

9 Questions Continued

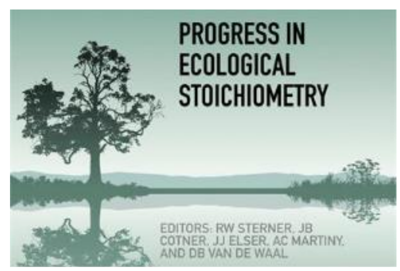
Where do you see ecological stoichiometry progressing in the next 10 years? I think it's been happening for a while, but hopefully it will continue to integrate well with other key ecological and biological theories. It would also be interesting to see what sort of patterns and processes are influenced by the stoichiometry of nutrients like K, Na, Fe, Mo, etc. based on biochemical fundamentals and how stoichiometry has influenced human history and evolution (paleoanthropological stoichiometry?).

What is your view of P:N:C ratios vs C:N:P ratios? I don't mind either way, but I'm quite used to C:N:P ratios and will probably continue to use them unless advised otherwise. In some ways showing the proportion of the minor element relative to the major element does make sense though, particularly if the minor element is limiting.

What is your favorite element? Probably molybdenum. It has some really interesting biogeochemistry and its availability might have constrained eukaryotic evolution for millions of years. 'Molybdenum' is also a great word (look at the symmetry!) and it could be worth 266 points in scrabble when covering two triple word scores.

Has ecological stoichiometry changed what you eat for lunch? It probably has to an extent – now that I have an appreciation for how the balance of global C, N and P cycles have been distorted by human activities I try to increase the N:P of my lunch. Koalas seem to have the right idea, but I've found that eucalyptus leaves taste horrible.

Progress on *Progress in Ecological Stoichiometry*



In the 15+ years since Sterner and Elser's *Ecological Stoichiometry* was published, hundreds of papers on ecological stoichiometry have appeared, on topics ranging from the cellular regulation of elements to the role of elemental ratios in ecosystems and global biogeochemical cycles. Building on this, the Frontiers Research Topic '*Progress in Ecological Stoichiometry*' was initiated as a collaborative effort to publish a collection of papers on emerging topics in ecological stoichiometry. This Research Topic is well on its way now with 8 papers published and another 25 manuscripts currently under consideration. Being an open access journal, all papers appearing in *Progress in Ecological Stoichiometry* will be freely available to everyone everywhere!

Access the Research Topic page on the Frontiers website to see the most recent papers published by clicking here.

Selected papers that have recently been published include:

J Sitters, E Bakker, M Veldhuis, C Veen, H Olde Venterink & M Vanni The stoichiometry of nutrient release by terrestrial herbivores and its ecosystem consequences

EK Moody, AT Rugenski, JL Sabo, BL Turner & JJ Elser Does the growth rate hypothesis apply across temperatures? Variation in the growth rate and body phosphorus of Neotropical benthic grazers

M Velthuis, E van Deelen, E van Donk, P Zhang & ES Bakker Impact of temperature and nutrients on carbon:nutrient tissue stoichiometry of submerged aquatic plants: an experiment and meta-analysis

The Ecology and Evolution of Stoichiometric Phenotypes

Although intra-specific variation in consumer stoichiometry has become better appreciated over the past decade, little is known about how natural selection acting on this variation shapes the evolution of consumer phenotypes. To stimulate this work, a recent paper by Leal et al. (2017) reviews much of what we currently know regarding sources of stoichiometric trait variation and presents a conceptual framework for linking variation in these traits to consumer fitness. The authors provide a clear guide for using reaction norm approaches to better understand how genes, plasticity, and ontogeny jointly influence consumer stoichiometric trait expression. Then, they outline how consumer elemental composition might be related to fitness and suggest ways to quantify selection effects on juveniles and adults using either stage-specific fitness proxies (i.e., growth and reproduction) or homeostasis as a single value fitness function. Finally, they highlight some outstanding questions and discuss how consumer stoichiometric evolution might feedback to influence ecological processes and ecosystem-level dynamics in nature.

A commonly studied fish, the stickleback, stained pink to show primary P deposits. Photo taken by D.W. Schmid.

From the Paper: "Overall, stoichiometric traits are a useful focal point for studying both interactions and feedbacks between phenotypic evolution and ecosystem processes."

Contributed by Clay Prater

Leal, M.C., O. Seehausen and B. Matthews. 2017. The ecology and evolution of stoichiometric phenotypes. Trends in Ecology and Evolution 32: 108-117.

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Stoichiometry of Oceanic Detritivores

Microbivory can be a beneficial nutritional strategy

More than half of global primary production becomes detritus yet relatively little attention is paid to understanding how the myriad of detritivorous invertebrates can prosper when consuming this seemingly innutritious resource. Detritus is typically rich in energy (carbon) but poor in the micronutrients (e.g., fatty acids, amino acids) that are essential to life. Micronutrient-limited detritivores may overcome nutritional constraints by consuming the detritus-associated community of nutrient-rich microorganisms (e.g., bacteria, flagellates, ciliates), rather than the detritus itself. But this strategy is costly in terms of energy acquisition owing to metabolic losses throughout the microbial food chain. In this paper, we developed a new stoichiometric model to explore the trade-off between these opposing ends of the nutritional spectrum and show that 'microbivory' can be an effective trophic strategy.

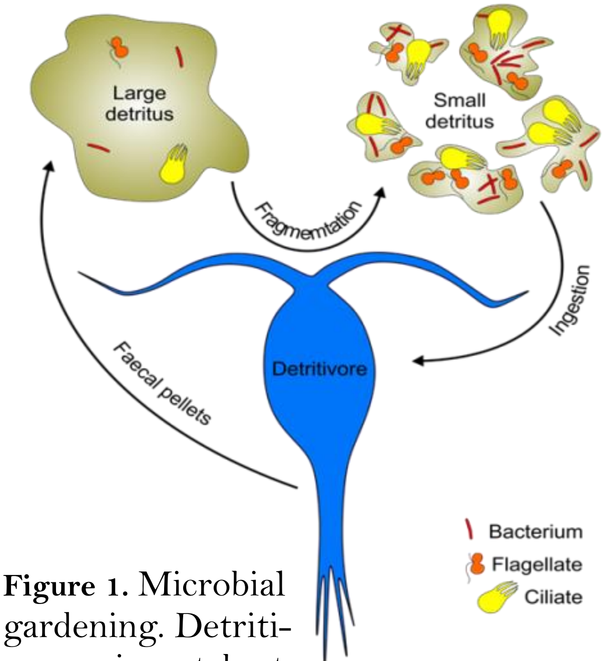

Figure 1. Microbial gardening. Detritivorous invertebrates may increase the nutritional content of detritus by fragmenting it, thereby stimulating growth of the microbial community. Reproduced from Mayor et al. (2014) BioEssays 36:1132-1137 under the Creative Commons Attribution License.

Indeed, it seems at least plausible that detritivores could benefit from stimulating microbial production via the fragmentation of detrital matter, so-called 'microbial gardening' (Figure 1). Nevertheless, 'microbivory' is only beneficial when the physiological requirements for micronutrients outweigh those for energy – and at present we know very little about this balance. We hope that our recent work, and that of our predecessors, will provide the impetus for more research into the nutritional requirements of detritivorous invertebrates, which are "among the least known organisms in terms of elemental concentrations and stoichiometric relationships" (Danger et al., 2016. Fungal Ecology 19:100-111).

From the paper: "We suggest that better understanding the ecology and physiology of detritivorous invertebrates is urgently required if we are to develop mechanistic biogeochemical models"

Special contribution by Dan Mayor and Tom Anderson of the National Oceanography Centre (United Kingdom)

Anderson, T.R., D.W. Pond and D.J. Mayor. 2016. The role of microbes in the nutrition of detritivorous invertebrates: A stoichiometric analysis. Frontiers in Microbiology 7:2113.

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Selected Recent Stoichiometry Publications

Bi, R., S. Ismar, U. Sommer, and M. Zhao. 2017. Environmental dependence of the correlations between stoichiometric and fatty acid-based indicators of phytoplankton nutritional quality. Limnol. Oceanogr. 62: 334–347. doi:10.1002/lno.10429

Carrillo, Y., C. Bell, A. Koyama, A. Canarini, C.M. Boot, M. Wallenstein, and E. Pendall. In Press. Plant traits, stoichiometry and microbes as drivers of decomposition in the rhizosphere in a temperate grassland. J. Ecol. doi:10.1111/ijlh.12426

Cunningham, B.R., and S.G. John. In press. The effect of iron limitation on cyanobacteria major nutrient and trace element stoichiometry. Limnol. Oceanogr. doi:10.1002/lno.10484

Henneron, L., M. Chauvat, F. Archaux, and others. In press. Plant interactions as biotic drivers of plasticity in leaf litter traits and decomposability of Quercus petraea. Ecol. Monogr. doi:10.1002/ecm.1252

Hessen, D.O., O.T. Hafslund, T. Andersen, C. Broch, N.K. Shala, and M.W. Wojewodzic. 2017. Changes in stoichiometry, cellular RNA, and alkaline phosphatase activity of *Chlamydomonas* in response to temperature and nutrients. Front. Microbiol. 8: 1–8. doi:10.3389/fmicb.2017.00018

Mariotte, P., A. Canarini, and F.A. Dijkstra. In press. Stoichiometric N:P flexibility and mycorrhizal symbiosis favor plant resistance against drought. J. Ecol. doi:10.1111/ijlh.12426

Piper, L.R., W.F. Cross, and B.L. McGlynn. 2017. Colimitation and the coupling of N and P uptake kinetics in oligotrophic mountain streams. Biogeochemistry 132: 165–184. doi:10.1007/s10533-017-0294-0

Prater, C., N.D. Wagner, and P.C. Frost. In press. Interactive effects of genotype and diet and food quality on consumer growth rate and elemental content. Ecology doi:10.1002/ecy.1795

Sileshi, G.W., N. Nhamo, P.L. Mafongoya, and J. Tanimu. 2016. Stoichiometry of animal manure and implications for nutrient cycling and agriculture in sub-Saharan Africa. Nutr. Cycl. Agroecosystems 107: 91–105. doi:10.1007/s10705-016-9817-7

Stephens, J.P., A.B. Stoler, J.P. Sckrabulis, A.J. Fetzer, K.A. Berven, S.D. Tiegs, and T.R. Raffel. 2017. Ontogenetic changes in sensitivity to nutrient limitation of tadpole growth. Oecologia 183: 1–11. doi:10.1007/s00442-016-3746-7

Thomas, M.K., M. Aranguren-Gassis, C.T. Kremer, M.R. Gould, K. Anderson, C.A. Klausmeier, and E. Litchman. In press. Temperature-nutrient interactions exacerbate sensitivity to warming in phytoplankton. Glob. Chang. Biol. doi:10.1534/g3.113.006437

Vance, D., S.H. Little, G.F. de Souza, S. Khatiwala, M.C. Lohan, and R. Middag. 2017. Silicon and zinc biogeochemical cycles coupled through the Southern Ocean. Nat. Geosci. 10: 202–207. doi:10.1038/ngeo2890

Wagner, N.D., Z. Yang, A.B. Scott, and P.C. Frost. 2017. Effects of algal food quality on free amino acid metabolism of Daphnia. Aquat. Sci. 79: 127–137. doi:10.1007/s00027-016-0484-1

Wang, X., X. Ma, and Y. Yan. 2017. Effects of soil C:N:P stoichiometry on biomass allocation in the alpine and arid steppe systems. Ecol. Evol. 7: 1354–1362. doi:10.1002/ece3.2710

Yang, X., Z. Huang, K. Zhang, and J.H.C. Cornelissen. In press. Taxonomic effect on plant base concentrations and stoichiometry at the tips of the phylogeny prevails over environmental effect along a large scale gradient. Oikos doi:10.1111/oik.02629