Ratios Matter

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Ecological Stoichiometry: Past and Present

It is exciting to see ecological stoichiometry freshly applied to new questions, elements, organisms, and environments. A primary aim of **Ratios Matter** is to highlight this new work and bring attention to these interesting developments in stoichiometric research. One summary in this issue does this with a look at recent work on the multi-elemental stoichiometry of weevil larvae and their acorn hosts. This is a good example of ecological stoichiometry being used in ways not imagined by many of the early papers. **While there is still much to be learned in ecological stoichiometry**, let's not forget where it came from either. In this issue, we include a new column, *Ratios in Review*, which we will use to consider the importance of contributions from stoichiometry's past. Given the emerging diversity in stoichiometric applications, there continues to be a need to think about how earlier stoichiometric concepts apply to new questions and environments. Our hope is to use **Ratios Matter** as one way to continue exploring connections between past and present and to celebrate our stoichiometric successes.

Award of Excellence Bestowed by the Phycological Society of America

Congratulations to Dr. Susan Kilham, who received the Phycological Society of America's Award of Excellence for the extensive impact her research has made on the field of phycology. Kilham's collaborative and dynamic research on diatoms brought resource ratio theory to the forefront of community ecology and provided the medium that inspired many experiments in ecological stoichiometry over decades. Over forty years into her career, Kilham continues to dig into some of the most pressing and complex issues in ecology using an impressive breadth of techniques to examine, for one example, interactions between climate, disease, and foodwebs in the tropics. For more information on this award, click **here**.

Editorial Board

Excellence Professorship Awarded by the Prof. Dr. Werner-Petersen-Foundation

We congratulate Dr. Elena Litchman, who was awarded an Excellence Professorship award by the Prof. Dr. Werner-Petersen-foundation (based in Kiel, Germany) for her innovative work in plankton ecology. Litchman's work has examined responses, including stoichiometric ones, of planktonic ecosystems to environmental gradients (e.g., temperature, nutrients, and light). Her trait-based approach is helping generate predictions about how ecosystem structure and function will change with the projected warmer waters of the future. This award will facilitate collaboration between Litchman and researchers at GEOMAR institute in Kiel.

Stoich-Comic by Judith Sitters

Comictary on Anderson et al. (2016) Frontiers in Microbiology. See Ratios Matter 2017 Issue 2 for more details.

Ratios in Review

Phytoplankton stoichiometry and temperature effects

Classic studies by G-Yull Rhee and Ivan J. Gotham on phytoplankton responses to nutrient stress have long been recognized as central to ecological stoichiometry. One of these papers is now particularly of interest for climate change research due to its focus on interactions between temperature and nutrient limitation (Rhee and Gotham (R&G) 1981). Since its publication, this study has been cited 201 times including by ~31 explicitly stoichiometry related publications. Interestingly, R&G (1981) is increasingly being cited with more citations during the past decade (2006-2016; 7.2/year; Fig. 1) than in the decade after its publication (1981-1991: 6.6/year). This is remarkable for a paper published >35 years ago.

In R&G (1981), we find a detailed study of the physiological responses to temperature of a freshwater diatom (*Asterionella*) and a green alga (*Scenedesmus*) in N- and P-limited turbidostats (pre-defined cell density) and chemostats (pre-defined dilution rate). Although the paper primarily examines the effect of low suboptimal temperatures on algae, its results powerfully demonstrate how higher temperatures affect phytoplankton nutrient physiology. For instance, minimal nutrient quota decreased with increasing temperature, which the paper links to declines in cellular protein and RNA demands. While cellular C:nutrient ratios also seemed to increase, high experimental variation prevented a conclusion about the stoichiometric effects of elevated temperature.

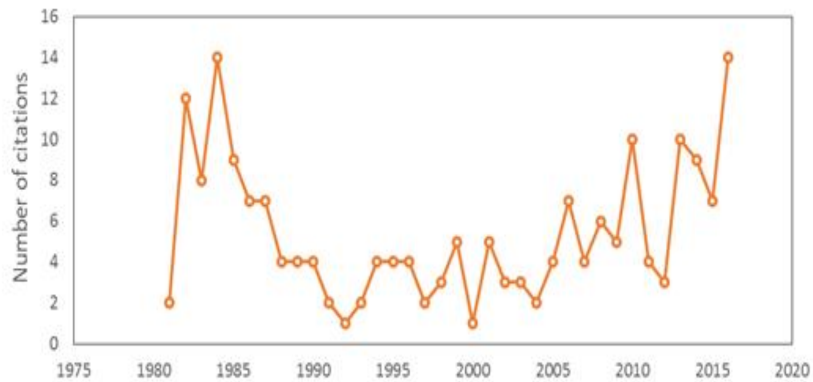


Figure 1. Web of Science results showing the number of citations for Rhee and Gotham 1981 (b), over the period 1981-2016.

R&G (1981) is a good example of a paper that should not escape our attention simply because it was published ahead of its time. This paper set the stage for future work in ecological stoichiometry and global change by linking elements to algal function across a range of temperatures. In particular, it showed the importance of interactive effects of nutrient and temperature on phytoplankton physiology, which may be a common result of global change. As studies increasingly focus on how climate change affects phytoplankton, we should certainly follow the path blazed by R&G (1981) in examining interactive effects on organisms.

From the paper: ""For the simultaneous stresses of nutrient limitation and suboptimal temperature, the combined effect is greater than the sum of the individual effects"

Contributed by Dedmer Van de Waal and Paul Frost

Rhee G.-Y. & Gotham I.J. (1981) The effect of environmental factors on phytoplankton growth: Temperature and the interactions of temperature with nutrient limitation. Limnology and Oceanography 26: 635-648.

High Intraspecific Variation in *Daphnia* to Dietary P-limitation

***Daphnia* is a central study organism** in stoichiometric research with much work on examining contrasts between daphnid species and with other zooplankton taxa. To expand our knowledge of variation in *Daphnia* responses to P supply, a recent paper by Prater et al. (2017) examined changes in body P, mass-specific growth rate, and P use efficiency of many unique genotypes of 2 daphnid species, which were caught in the field and grown across P gradients in the lab. *Daphnia* responses to food quality varied widely within each species. While growth and P-use responses differed due to genetic differences among clones, changes in daphnid P content were mostly plastic and were only weakly related to growth. By sampling natural populations and analyzing them in common garden environments, this work sheds new light on how *Daphnia* respond to environmental variation and demonstrates the ecological and evolutionary consequences of these changes.

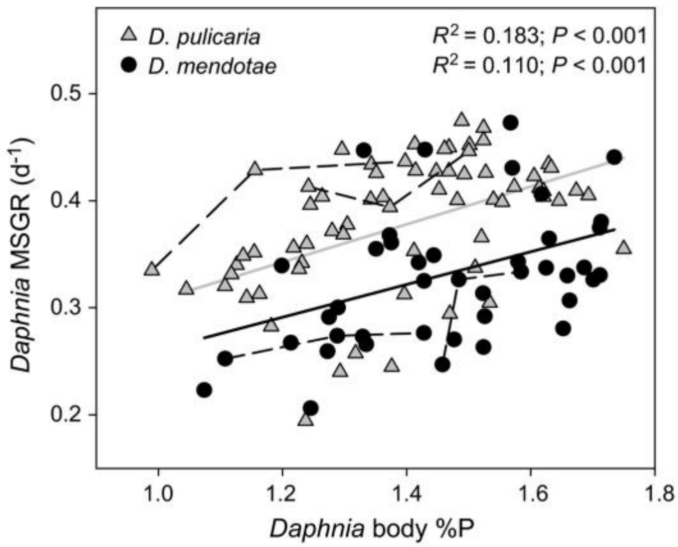


Figure 3 from Prater et al. (2017) showing relationships between growth and body P in two daphnid species. Dotted lines show responses of selected individual clones. Reproduced with permission.

From the paper: "These observations indicate that consumer elemental variation might be more common than previously acknowledged by stoichiometric theory and could represent a form of adaptive phenotypic response to dietary nutrient heterogeneity in natural environments."

Contributed by Eric Moody

Prater C., Wagner N.D., & Frost P.C. 2017. Interactive effects of genotype and food quality on consumer growth rate and elemental content. Ecology 98: 1399-1408.

Speaking of *Daphnia*

Stoichiometry in the classroom. In February 2017, Jim Hood delivered a guest lecture on consumer stoichiometry to undergraduates at Trent University enrolled in Biological Stoichiometry.

Do you have a photo or story to share about teaching ecological stoichiometry? Send it to us and we will include it in an upcoming issue of *Ratios Matter.*

Workshop in Stoichiometric Ecotoxicology

The United States' National Institute for Mathematical and Biological Synthesis is accepting applications for its Investigative Workshop, "Stoichiometric Ecotoxicology," to be held January 17-19, 2018 at NIMBioS at the University of Tennessee, Knoxville (USA).

Objectives: Accurately assessing the risks of contaminants requires more than an understanding of the effects of contaminants on individual organisms, but requires further understanding of complex ecological interactions, elemental cycling, and interactive effects of natural and contaminant stressors. The development of ecotoxicological models over the last few decades have significantly contributed to interpreting how contaminants impact organisms and cycle through food webs. Existing modeling efforts take a variety of approaches to predict the effects of diverse chemical contaminants on organismal growth and survival; however, current models do not consider dynamical interactive effects of contaminant stressors and stoichiometric constraints, such as nutrient/light availability and food quality. This investigative workshop will provide a forum for discussions of incorporating multiple essential elements and contaminants in ecotoxicological models. The discussions and breakout sessions throughout the workshop will shed light on nutrient and chemical contaminant cycling and will ultimately help improve toxicological risk assessment protocols. Objectives for the workshop include:

- Discussing the importance of linking Ecological Stoichiometry with Ecotoxicology and summarizing the current state of the synthesis of these two theories
- Formulating a series of empirically testable and robust models of individual and population dynamics subject to stoichiometric constraints and contaminant stressors
- Identifying future directions for models to be used in practice for ecological risk assessments and determining areas where empirical data are lacking in order to parameterize, test, and improve the models

Co-Organizers: Angela Peace (Texas Tech) and Paul Frost (Trent)

For more information about the workshop and a link to the online application form, go to **http://www.nimbios.org/workshops/WS_ecotox**. Participation in NIMBioS workshops is by application only. Individuals with a strong interest in the topic are encouraged to apply. If needed, financial support for travel, meals, and lodging is available for workshop attendees. The due date for applications is September 25, 2017.

NIMBioS (**http://www.nimbios.org**) brings together researchers from around the world to collaborate across disciplinary boundaries to investigate solutions to basic and applied problems in the life sciences. NIMBioS is sponsored by the U.S. National Science Foundation, with additional support from The University of Tennessee, Knoxville.

Stoichiometry of Parasitic Weevil Larvae and Their Acorn Hosts

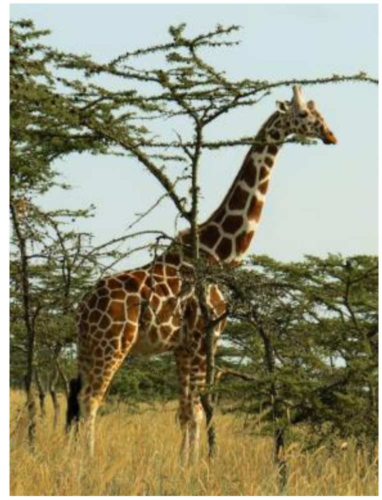
Determining the origins of elemental differences between organisms and trophic levels is a central focus of stoichiometric research. In a recent paper by Ji et al. (2017) this concept was extended to examine ionomic variation (13 elements) in a host-parasite (acorn/weevil) system located in the Yunnan province of southwestern China. The authors documented significant differences in elemental composition between two acorn species (P, K, Mg, & Mn) and weevils (P, Ca, Mg, Fe, Mn, Al, & Na) growing in high and low nutrient soils and showed that stoichiometric variation in these organisms was largely driven by variable soil elemental supplies. However, despite finding evidence of elemental plasticity in certain elements (P, Ca, & Fe) and elemental ratios (C:P & Ca:P), nutrient stoichiometry of both hosts and parasites was relatively constrained across the study. This suggests that while organisms were capable of making minor adjustments to their elemental composition when faced with resource imbalances, major differences in ionomic composition between sites were likely driven by longer-term adaptive responses to soil nutrient supplies rather than elemental plasticity.

From the Paper: "These findings highlight the importance of both environmental influence in elemental stoichiometry and composition and physiological regulations of nutritional needs in organisms."

Contributed by Chunjiang Liu, Huawei Ji, & Clay Prater

Ji H., B. Du & C Liu. 2017. Elemental stoichiometry and compositions of weevil larvae and two acorn hosts under natural phosphorus variation. Scientific Reports 7, 45810

Getting the Lay of the Land: Assessing the Stoichiometric Impact of Mammalian Herbivores on Soils and Plants



Research on the stoichiometric impact of herbivores on autotrophs (e.g., consumer-driven nutrient recycling) has been strongly focused on aquatic ecosystems. New research has applied these concepts to terrestrial ecosystems by examining the stoichiometric impact of large mammalian herbivores on soils and plants (Sitters and Olde Venterink 2015, Sitters et al. 2017a). These herbivores can change the N:P stoichiometry of soils, mainly through dung deposition and plant consumption, which then alters plant nutrient limitation and community composition. I studied several of these processes in the African savanna. For example, I found large interspecific variation in C:N:P stoichiometry of dung among a wide range of African mammalian herbivores, which in turn impacted the release rates of N and P during dung decomposition (Sitters et al. 2014). The effects of this variable N:P ratio in dung on competitive interactions between plants is currently being investigated using dung of both African and European herbivore species in several mesocosm experiments. I've also documented these effects of large herbivores in Arctic tundra ecosystems where the effect of reindeer on soil N and P depended on habitat fertility (i.e., plant C:N:P stoichiometry) and where reindeer promoted P limitation of plants (Sitters et al. 2017b). Altogether this research shows ecological stoichiometry to be a highly relevant and very promising approach to understanding the herbivore-mediated effects on terrestrial ecosystems (Sitters et al. 2017b).

Contributed by Judith Sitters

Sitters J, Maechler M, Edwards PJ, Suter W, Olde Venterink H. 2014. Interactions between C:N:P stoichiometry and soil macrofauna control dung decomposition of savanna herbivores. Functional Ecology 28: 776-786.

Sitters J, Olde Venterink H. 2015. The need for a novel integrative theory on feedbacks between herbivores, plants and soil nutrient cycling. Plant and Soil 396: 421-426.

Sitters J, Bakker ES, Veldhuis MP, Veen GF, Olde Venterink H, Vanni MJ. 2017a.The stoichiometry of nutrient release by terrestrial herbivores and its ecosystem consequences. Frontiers in Earth Science 5:32. doi: 10.3389/feart.2017.00032.

Sitters J, te Beest M, Cherif M, Giesler R, Olofsson J. 2017b. Interactive effects between reindeer and habitat fertility drive soil nutrient availabilities in arctic tundra. Ecosystems. doi: 10.1007/s10021-017-0108-1.

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Selected Recent Stoichiometry Publications

Bracken, M.E.S. 2017. Stoichiometric mismatch between consumers and resources mediates the growth of rocky intertidal suspension feeders. Front. Microbiol. 8:1-10. doi:10.3389/fmicb.2017.01297

Chen, M., M. Fan and Y. Kuang. 2017. Global dynamics in a stoichiometric food chain model with two limiting nutrients. Math. Biosci. 289: 9-19. doi:10.1016/j.mbs.2017.04.004

Collins, S.M., S.K. Oliver, J.-F. Lapierre, E.H. Stanley, J.R. Jones, T. Wagner and P.A. Soranno. 2017. Lake nutrient stoichiometry is less predictable than nutrient concentrations at regional and sub-continental scales. Ecol. Appl. 27:1529-1540. doi:10.1002/eap.1545

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

Durston, D.J. and R.W. El-Sabaawi. In press. Bony traits and genetics drive intraspecifc variation in vertebrate elemental composition. Funct. Ecol. doi:10.1111/1365-2435.1291

Goos, J.M., R.D. Cothran and P.D. Jeyasingh. In press. Within-population variation in the chemistry of life: the stoichiometry of sexual dimorphism in multiple dimensions. Evol. Ecol. doi:10.1007/s10682-017-9900-9

Jeyasingh, P.D., J.M. Goos, S.K. Thompson, C.M. Godwin and J.B. Cotner. 2017. Ecological stoichiometry beyond Redfield: An ionomic perspective on elemental homeostasis. Front. Microbiol. 8:1-7. doi:10.3389/fmicb.2017.00722

Jochum, M., A.D. Barnes, D. Ott, B. Lang, B. Klarner, A. Farajallah, S. Scheu and U. Brose. 2017. Decreasing stoichiometric resource quality drives compensatory feeding across trophic levels in tropical litter invertebrate communities. Am. Nat. 190:131-143. doi:10.1086/691790

Luhring, T.M., J.P. DeLong and R.D. Semlitsch. 2017. Stoichiometry and life-history interact to determine the magnitude of cross-ecosystem element and biomass fluxes. Front. Microbiol. 8:1-11. doi:10.3389/fmicb.2017.00814

Mas-Martí, E., I. Sanpera-Calbet and I. Muñoz. 2017. Bottom-up effects of streambed drying on consumer performance through changes in resource quality. Aquat. Sci. 79:719-731. doi:10.1007/s00027-017-0531-6

Moody, E.K., A.T. Rugenski, J.L. Sabo, B.L. Turner and J.J. Elser. 2017. Does the growth rate hypothesis apply across temperatures? Variation in the growth rate and body phosphorus of neotropical benthic grazers. Front. Environ. Sci. 5:1-11. doi:10.3389/fenvs.2017.00014

Teurlincx, S., M. Velthuis, D. Seroka, L. Govaert, E. van Donk, D.B. Van de Waal and S.A.J. Declerck. 2017. Species sorting and stoichiometric plasticity control community C:P ratio of first-order aquatic consumers. Ecol. Lett. 20:751-760. doi:10.1111/ele.12773

Thrane, J.E., D.O. Hessen and T. Andersen. 2017. Plasticity in algal stoichiometry: Experimental evidence of a temperature-induced shift in optimal supply N:P ratio. Limnol. Oceanogr. 62:1346-1354. doi:10.1002/lno.10500

Weyhenmeyer, G.A. and D.J. Conley. In press. Large differences between carbon and nutrient loss rates along the land to ocean aquatic continuum-implications for energy:nutrient ratios at downstream sites. Limnol. Oceanogr. doi:10.1002/lno.10589

Zhang, J. and J.J. Elser. 2017. Carbon:Nitrogen:Phosphorus stoichiometry in fungi: A meta-analysis. Front. Microbiol. 8: 1–9. doi:10.3389/fmicb.2017.01281