Ratios Matter

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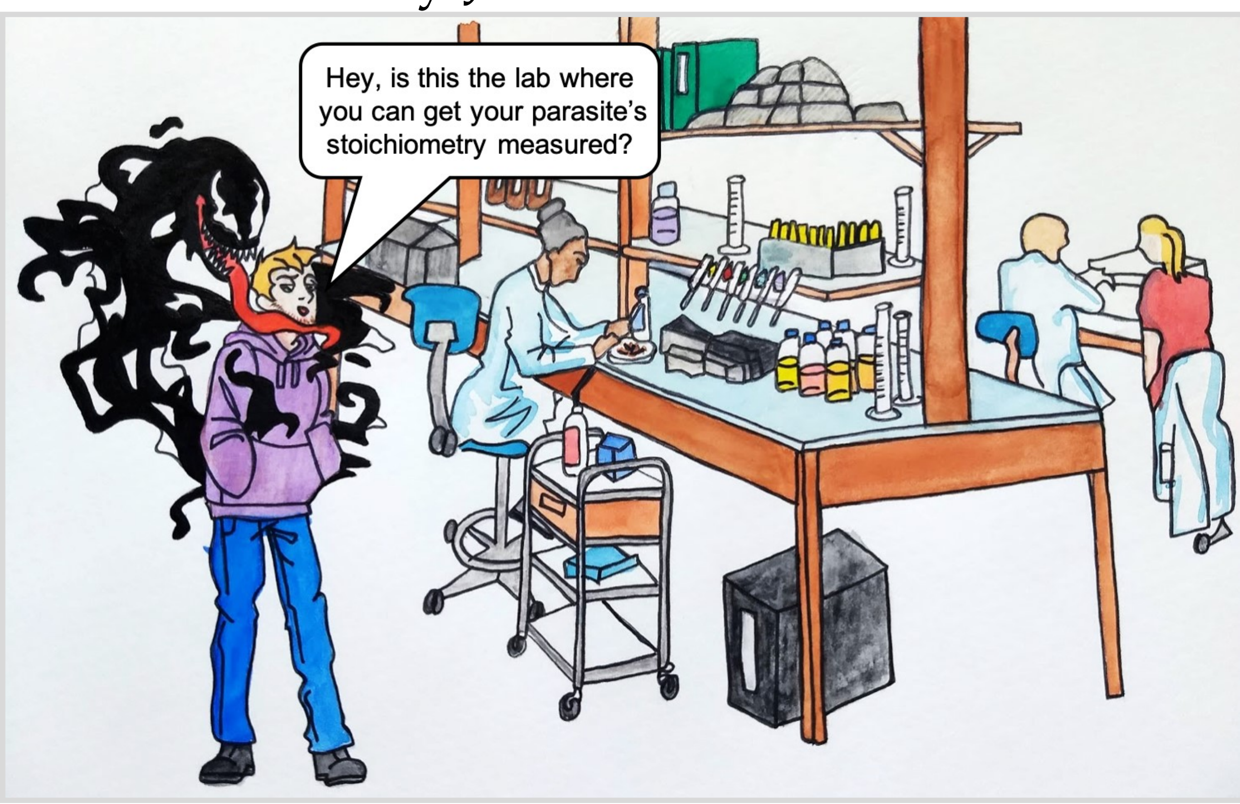
Noted Ecological Stoichiometrist Elected to US National Academy of Science

Congratulations to Jim Elser (University of Montana) for being elected to the US National Academy of Sciences. Election to the National Academy of Sciences is one of the highest scientific honors in the United States. Jim helped formalize the conceptual framework underlying ecological stoichiometry and has been a tireless promoter of its application on a variety of biological topics. Jim has tested its predictions across multiple disciplines (e.g., ecosystem ecology, evolution, cancer biology, ecophysiology) and facilitated the involvement of early career scientists in the field (e.g., Woodstoich). This is a well deserved honor for Jim and we expect he will make important contributions to the National Academy of Sciences in the coming years. For more on this announcement, click here.

Here, Jim prepares to test predictions of ecological stoichiometry at Cuatro Ciénegas, Mexico (see pg. 8 for more information on this site). Photo by Jessica Corman.

Stoich-Comic by Judith Sitters



Comictary on Paseka and Grunberg (2019) Oikos.

See *Ratios Matter* 2019, Volume 3, Issue 1 for more details.

Share Your Stoichiometric Thoughts and Content with *Ratios Matter*

Do you have stoichiometric news to share? We are always looking for new content *from our readers*. This could be a summary of your new **stoichiometry** article, a photo of **stoichiometry** research, or possibly some commentary on an emerging **stoichiometric** topic. Or maybe you have inside information on upcoming conference sessions, workshops or new collaborative projects that would be of interest to **ratio**-oriented researchers. Submissions are screened for relevance and may be lightly edited. All feedback on ***Ratios Matters*** is also greatly appreciated. Tell us if you like what you are seeing or if there are features that you would like to see. We look forward to hearing from you soon.

Ratios Matter Editor Visits Baylor University!

Dedmer Van de Waal recently made a trans-Atlantic journey from the Netherlands to Texas to visit Thad Scott's lab (@ScottBiogeochem) at Baylor University to talk about ecological stoichiometry and harmful cyanobacterial blooms. Stoichiometry was discussed throughout the week, which ended with Dedmer giving a seminar to the Department of Biology that mentioned *Ratios Matter*!

Left- Dedmer promotes *Ratios Matter* at the end of his seminar. Right- Dedmer and Thad Scott on Eagle Mountain Lake monitoring water quality. Left photo by Nicole Wagner.

Ecological Stoichiometry and the Biogeochemical Niche

Stoichiometric research has largely, and understandably, focused on the key elements C, N, and P, but, of course, there are more than a dozen other elements that are key for a multitude of physiological processes across the Tree of Life. The development of high-throughput elemental measurement techniques has allowed us to determine additional elements in our samples with nearly no preparation and at the click of a mouse revealing hitherto little explored elemental interactions within and between organisms.

The 'biogeochemical niche' is an emerging concept based on the Hutchinsonian niche concept but explores how different species use elements and how this is expressed phenotypically. While Peñuelas et al. (2019) do not claim to have invented this concept, they provide a lucid and compelling outline of its importance in their paper. Their major contribution here is the outline of three basic rules of the biogeochemical niche. The first is that distinct taxonomic groups exhibit differential patterns of elemental composition (the 'elementome' or 'ionome'), the second is that co-existing species have differing elemental make-up to minimize competition between them, and the third is that species have different degrees of plasticity in their elemental make-up. The way that species apply these rules then leads to a broad range of biogeochemical strategies among co-existing species.

Analysis of the whole organism 'elementome' can be straightforward. Then, using statistical methods of varying complexity, the hypervolume of a species' niche can be determined and potential overlaps in niche space among species and their shifts under altered environmental conditions can be quantified. This concept has a number of applications: we can use it to predict alterations to the biogeochemical niche with environmental perturbations and how these alterations might change competitive interactions with implications for co-existence or local extirpation. It can also be used to assess large-scale patterns of community assembly. For example, do species with greater plasticity in their biogeochemical niche exhibit broader ranges and could this lead to a greater chance of future speciation? While the biogeochemical niche concept is based on a static measure of elemental usage, future studies could expand upon this by considering, for example, nutrient use efficiency or, as the closely related field of 'ionomics' has done, links between elemental profiling and specific gene functions. Overall, this paper makes an excellent review for anyone new to the topic and provides a clear synthesis for those working in this field already.

From the Paper: *"...a biogeochemical niche is characterized by a particular elementome defined as the content of all (or at least most) bioelements."*

Contributed by Francis Q. Brearley

Peñuelas, J., M. Fernández-Martínez, P. Ciais, D. Jou, S. Piao, M. Obersteiner, S. Vicca, I.A. Janssens and J. Sardans. 2019. The bioelements, the elementome, and the biogeochemical niche. *Ecology* 100 p.e02652. doi: 10.1002/ecy.2652.

Rebalancing River Stoichiometry

Eutrophication is a major threat to the world's aquatic ecosystems. For many years, efforts to prevent it have focused on reducing N and/or P loads, but this has proven difficult in agricultural landscapes where fertilizers support economic activity and food production. As a result, researchers and management agencies began looking for ways to minimize the *impact* of nutrient loads, even if the load itself cannot be reduced. Stutter et al. (2018) explores the stoichiometry of this problem. Their premise is that in-stream microbial communities might be managed to reduce availability of N and P to downstream waters. In particular, they argue that reconnecting agricultural and urban water sources to organic carbon (OC) sources is needed to create nutrient limitation in heterotrophic microbes, which may reduce downstream N and P availability.

In temperate lakes, "eutrophication" is often manifested as cyanobacterial blooms, which can have greater negative impacts when they produce toxins. Like others, Stutter et al. (2018) identified river ecosystems as places where the availability of N and P loads could be altered by in-stream processing. Stutter et al. (2018) hypothesize that fueling heterotrophic stream metabolic processes with new OC sources may 're-unbalance' the stoichiometry of nutrients and increase stream retention of N and P.

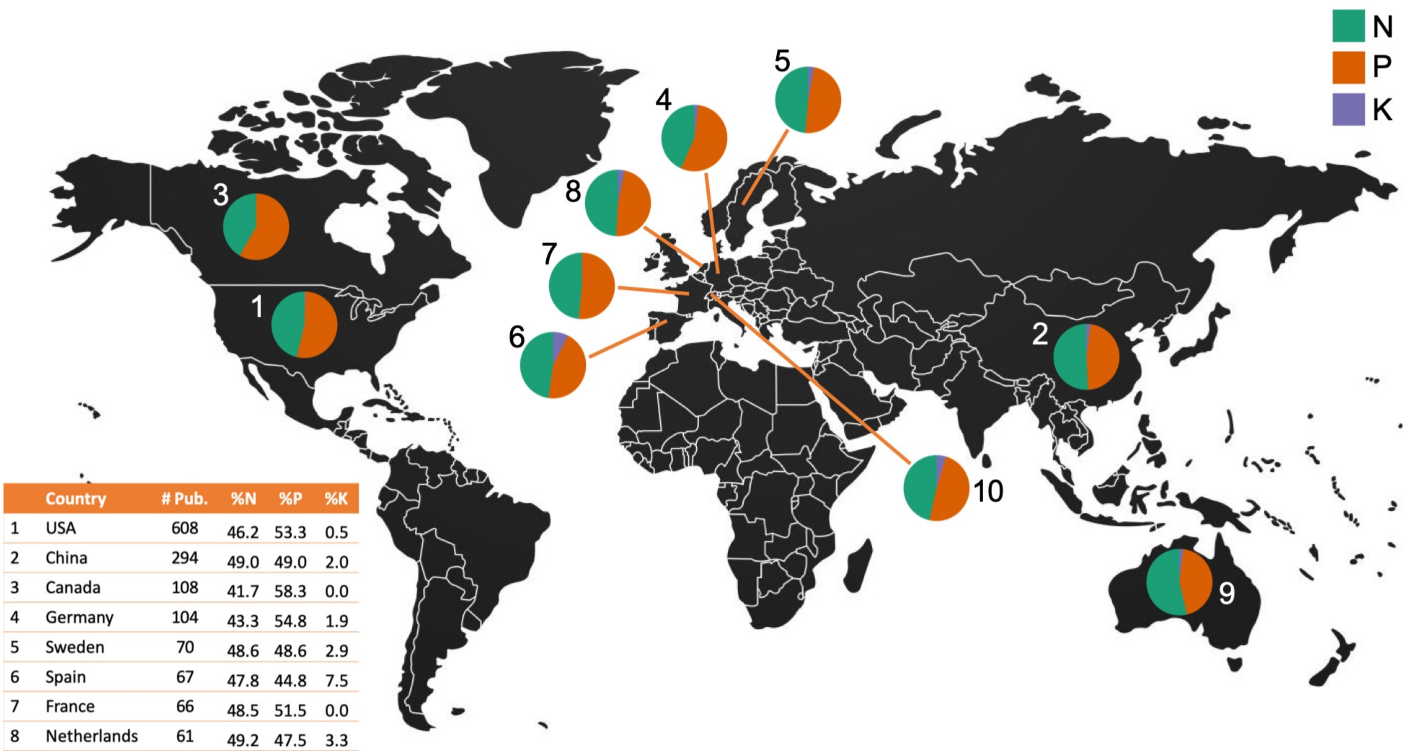
Stutter et al. (2018) performed a literature review to establish boundaries on the potential for microbial mitigation of nutrient inputs in streams and the relative contribution of different potential source waters. They found that urban and agricultural runoff often had stoichiometric imbalances (e.g., too much N and P), and that water derived from wetlands had organic carbon excesses, which indicates that these waters could support more heterotrophic microbial activity. This article also highlights existing gaps in our understanding of how naturally-occurring dissolved organic matter interacts with nutrient processes and competitive interactions between microbes. Their management recommendations are similar to current best management practices to reduce P and sediment inputs (e.g., reconnect streams to wetlands), but the implication is that the benefits would occur far beyond the immediate area. Overall, the article provides ample data to support the ideas and should inform efforts to think outside the box about how to mitigate the negative impacts of nutrient loading in freshwater ecosystems.

From the paper, "*Considering dissolved OC, N and P, we found many river waters and catchment sources that have a strong stoichiometric imbalance against aquatic microbes*."

Contributed by James Larson

Stutter, M. I., D. Graeber, C. D. Evans, A. J. Wade, and P. J. A. Withers. 2018. Balancing macronutrient stoichiometry to alleviate eutrophication. Science of the Total Environment 634:439–447.

Global Origins of Ecological Stoichiometry Publications



	Country	# Pub.	%N	%P	%K
1	USA	608	46.2	53.3	0.5
2	China	294	49.0	49.0	2.0
3	Canada	108	41.7	58.3	0.0
4	Germany	104	43.3	54.8	1.9
5	Sweden	70	48.6	48.6	2.9
6	Spain	67	47.8	44.8	7.5
7	France	66	48.5	51.5	0.0
8	Netherlands	61	49.2	47.5	3.3
9	Australia	54	53.7	44.4	1.9
10	Switzerland	43	46.5	48.8	4.7

Ever wonder about the global origins of publications on ecological stoichiometry? We determined the top 10 countries publishing on ecological stoichiometry as indicated by information in author addresses using a Web of Science search. Using the search terms, “ecological stoichiometry” and either “nitrogen”, “phosphor*” or “potassium”, we tallied the number of papers published since 1990. Publications examining more than one element were counted in each category. The highest volume of ecological stoichiometry publications originates from the USA, China, Canada, and a handful of European countries with nearly equal treatment of N and P. We also searched for “ecological stoichiometry” and either “iron”, “calcium”, “magnesium”, or “potassium”. We didn’t display these in the map because the number of publications was too low to see clearly in the pie charts. The USA and China were the top publishers on ecological stoichiometry and Fe, Ca, and Mg. Another interesting result was for Spain which published stoichiometry on a particularly diverse array of nutrients including over 7% on K. Spain was the third highest publisher of ecological stoichiometry on non-N and P elements. Overall it is clear that ecological stoichiometry is being examined in many parts of the world but with a particularly strong focus in North America and Europe.

Contributed by Charlotte Narr and Judith Sitters

Stoichiometry on Location:
Cuatro Ciénegas, Coahuila, Mexico

The Cuatro Ciénegas basin (outlined in blue) in northern Mexico (indicated by star in inset map).


Poza Escobedo is a typical mineral-rich spring-fed pool in the basin

About the Location. The Cuatro Ciénegas basin is an area of about 1200 km^2 in the Chihuahuan desert of northern Mexico. Despite its small area, it is often considered the region with the highest degree of endemism in North America. This includes endemic species of fishes, plants, snails, microbes, and the world's only known aquatic box turtle. Some surface waters in the basin host living stromatolites. Springs in the basin, particularly in the southwestern portion, are threatened by groundwater withdrawals for irrigated agriculture.


Native fishes of Cuatro Ciénegas including the cichlid *Herichthys minckleyi*, the Mexican tetra *Astyanax mexicanus*, the pupfish *Cyprinodon bifasciatus*, and the livebearer *Gambusia marshi*.

Stoichiometric History. Early scientific work in Cuatro Ciénegas was led by W.L. Minckley, an ichthyologist from Arizona State University. His work, and that of his students and collaborators such as Salvador Contreras-Balderas and Dean Hendrickson, focused on the basin's fishes and surface waters. Minckley later convinced a young limnologist named Jim Elser to visit the area after he was hired at ASU. "What drew me there was the epic beauty of the area and the chance to do experiments with living stromatolites," said Jim. "We soon discovered that most of the systems had extremely imbalanced N and P stoichiometry and that severe P limitation was likely a prevailing condition. This was supported by subsequent experiments and even led us to propose a sort-of far-fetched idea that the Cambrian explosion was triggered by big changes in the global P cycle. It's an idea that is easier to write about than to test!" Jim began working with Valeria Souza, a microbiologist from La Universidad Autónoma de Mexico, to test these ideas.

Key Contributions. As Jim noted, much of the stoichiometric work in Cuatro Ciénegas has focused on how aquatic and soil microbes manage life in an incredibly P-poor environment. Work by Jim, Valeria, and their students and colleagues has tested the growth rate hypothesis in microbes such as in the experiment pictured in the image at the right. Early evidence for the “stoichiometric knife-edge” hypothesis also came from experiments with snails grazing on stromatolites in the basin. This in turn led to the hypothesis that the Cambrian explosion may have been driven by changes in P availability over geological time. The unique geochemistry of the basin has also provided a basis for examining how geological processes alter nutrient limitation in soils and aquatic ecosystems.

A phosphorus fertilization experiment in a shallow pond, with an unfertilized pond for contrast in the background.

Contributed by Eric Moody

Selected Stoichiometric Publications from Cuatro Ciénegas

Corman J.R., Poret-Peterson A.T., Uchitel A., & Elser J.J. 2016. Interaction between lithification and resource availability in the microbialites of Rio Mesquites, Cuatro Ciénegas, Mexico. Geobiology 14: 176-189.

Elser J.J., Watts J., Schampel J.H., & Farmer J. 2006. Early Cambrian food webs on a trophic knife-edge? A hypothesis and preliminary data from a modern stromatolite-based ecosystem. Ecology Letters 9: 295-303.

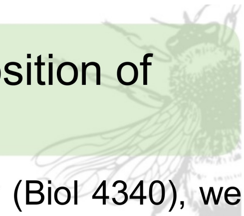
Moody E.K., Carson E.W., Corman J.R., Espinosa-Pérez H., Ramos J., Sabo J.L., & Elser J.J. 2018. Consumption explains intraspecific variation in nutrient recycling stoichiometry in a desert fish. Ecology 99: 1552-1561.

Peimbert M., Alcaraz L.D., Bonilla-Rosso G., Olmedo-Álvarez G., García-Oliva F., Segovia L., Eguiarte L.E., & Souza V. 2012. Comparative metagenomics of two microbial mats at Cuatro Ciénegas Basin I: Ancient lessons on how to cope with an environment under severe nutrient stress. Astrobiology 12: 648-658.

Souza V., Moreno-Letelier A., Travisano M., Alcaraz L.D., Olmedo G., & Eguiarte L.E. 2018. The lost world of Cuatro Ciénegas, a relictual bacterial niche in a desert oasis. eLife 7: e38278.

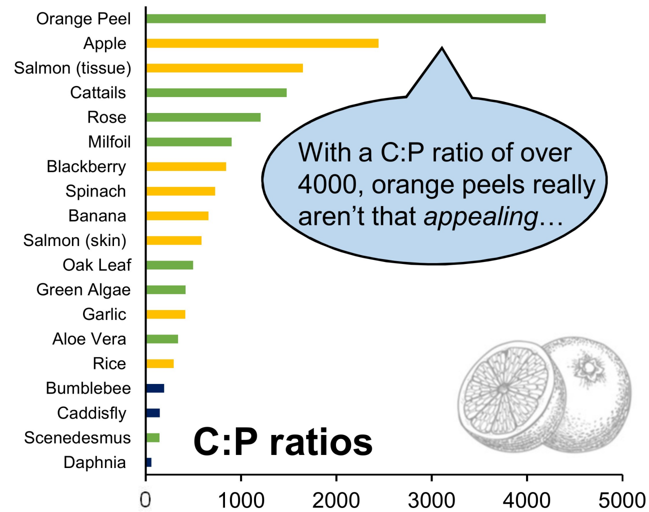
Tapia-Torres Y., Elser J.J., Souza V., & García-Oliva F. 2015. Ecoenzymatic stoichiometry at the extremes: How microbes cope in an ultra-oligotrophic desert soil. Soil Biology and Biochemistry 87: 34-42.

Stoichiometry in the Classroom

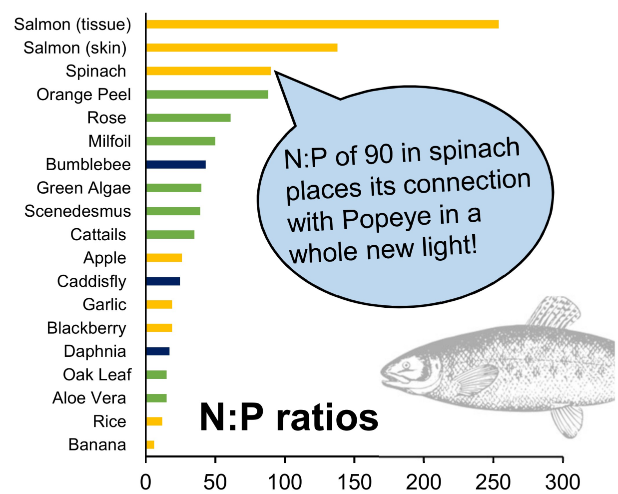


Organic Matter that Matters: The C:N:P composition of various plants, animals and foods

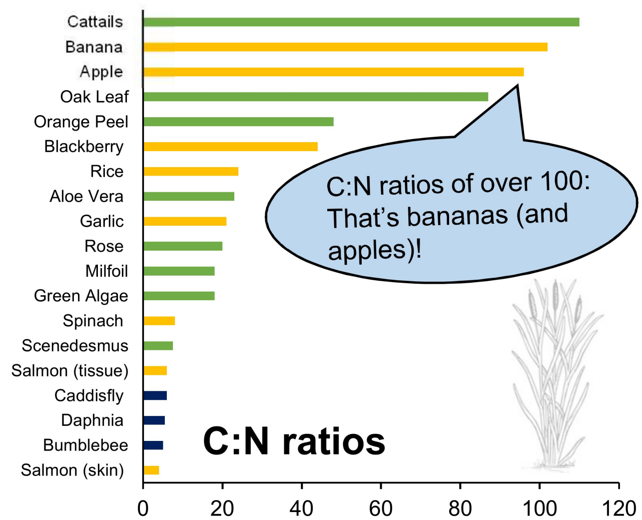
As part of our course on biological stoichiometry at Trent University (Biol 4340), we measured the C:N:P content from various samples of organic matter of interest (plants, animals, food). The purpose of this activity was for us to learn more about how C, N, and P are measured and reported by stoichiometrists. We found some interesting results that we hope the readers of *Ratio Matters* will enjoy!



Figures. Stoichiometric ratios (C:P, C:N, N:P; all molar) for samples of food, plants, and animals. Data is based on samples measured by classes of 2015, 2016, and 2019 at Trent University. For all, materials are categorized as food (orange), plants (green), or animals (blue).



Methods. Samples were dried, homogenized, and weighed. C:N:P composition was measured using a C:N analyzer and with colorometric chemical assays.



Notable Findings. Big differences in C:P and C:N ratios among plants, foods, and animals. Some food for thought, humans have a C:N:P ratio of 84:6.3:1 but have high energy requirements. What food mixture would be 'optimal' for us to eat?

Contributed by Trent's Biol 4340 course: Christopher Chavez-Flores, Robert Chin, Alicia Halhed, Adam Herman, Mendel Hinton, Ardent Horlings, Fook Lim, Tyler Scriver, Chelsea Seusahai, Marina Taskovic, Samantha Wark and Paul Frost.

Acknowledgements. Special thanks to the Frost lab for help completing these measurements over the years.

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Selected Recent Stoichiometry Publications

Abail, Z. and J.K. Whalen. 2019. Nitrous oxide *in vivo* emission may regulate nitrogen stoichiometry in earthworm body tissues. Eur. J. Soil Biol. 91: 25–31. doi:10.1016/j.ejsobi.2019.01.002

Bell, A.T.C., D.L. Murray, C. Prater and P.C. Frost. 2019. Fear and food: Effects of predator-derived chemical cues and stoichiometric food quality on *Daphnia*. Limnol. Oceanogr. In Press: doi:10.1002/lno.11145

Butler, O.M., T. Lewis, M.R. Rashti, S.C. Maunsell, J.J. Elser and C. Chen. 2019. The stoichiometric legacy of fire regime regulates the roles of micro-organisms and invertebrates in decomposition. Ecology In Press: doi:10.1002/ecy.2732

Dolezal, A.G., J. Carrillo-Tripp, T.M. Judd, W. Allen Miller, B.C. Bonning and A.L. Toth. 2019. Interacting stressors matter: Diet quality and virus infection in honeybee health. R. Soc. Open Sci. 6: 181803. doi:10.1098/rsos.181803

Dynarski, K.A., S.L. Morford, S.A. Mitchell and B.Z. Houlton. 2019. Bedrock nitrogen weathering stimulates biological nitrogen fixation. Ecology In Press: doi:10.1002/ecy.2741

Filipiak, M. 2019. Key pollen host plants provide balanced diets for wild bee larvae: A lesson for planting flower strips and hedgerows. J. Appl. Ecol. In Press: doi:10.1111/1365-2664.13383

Hou, S.L., X.T. Lü, J.X. Yin and others. 2019. The relative contributions of intra- and inter-specific variation in driving community stoichiometric responses to nitrogen deposition and mowing in a grassland. Sci. Total Environ. 666: doi:10.1016/j.scitotenv.2019.02.322

Ji, H., V. Ossipov, B. Du, J. Wen and C. Liu. 2019. Differences in the relationship between metabolomic and ionomic traits of *Quercus variabilis* growing at contrasting geologic-phosphorus sites in subtropics. Plant Soil In Press: doi:10.1007/s11104-019-04020-1

Lewington-Pearce, L., A. Narwani, M.K. Thomas, C.T. Kremer, H. Vogler and P. Kratina. 2019. Temperature-dependence of minimum resource requirements alters competitive hierarchies in phytoplankton. Oikos In Press: doi:10.1111/oik.06060

Liefer, J.D., A. Garg, M.H. Fyfe and others. 2019. The macromolecular basis of phytoplankton C:N:P under nitrogen starvation. Front. Microbiol. 10: 763. doi:10.3389/fmicb.2019.00763

Loladze, I. 2019. Iterative chemostat: A modelling framework linking biosynthesis to nutrient cycling on ecological and evolutionary time scales. Math. Biosci. Eng. 16: 990–1004. doi:10.3934/mbe.2019046

Moody, E.K., N.K. Lujan, K.A. Roach and K.O. Winemiller. 2019. Threshold elemental ratios and the temperature dependence of herbivory in fishes. Funct. Ecol. In Press: doi:10.1111/1365-2435.13301

Rudman, S.M., J.M. Goos, J.B. Burant, K.V. Brix, T.C. Gibbons, C.J. Brauner and P. D. Jeyasingh. 2019. Ionome and elemental transport kinetics shaped by parallel evolution in threespine stickleback. Ecol. Lett. 22: 645–653. doi:10.1111/ele.13225

Trakimas, G., R. Krams, T. Krama and others. 2019. Ecological Stoichiometry: A link between developmental speed and physiological stress in an omnivorous insect. Front. Behav. Neurosci. 13: 42. doi:10.3389/fnbeh.2019.00042

White, A.E., S.J. Giovannoni, Y. Zhao, K. Vergin and C.A. Carlson. 2019. Elemental content and stoichiometry of SAR11 chemoheterotrophic marine bacteria. Limnol. Oceanogr. Lett. 4: doi:10.1002/lol2.10103