Ratios Matter

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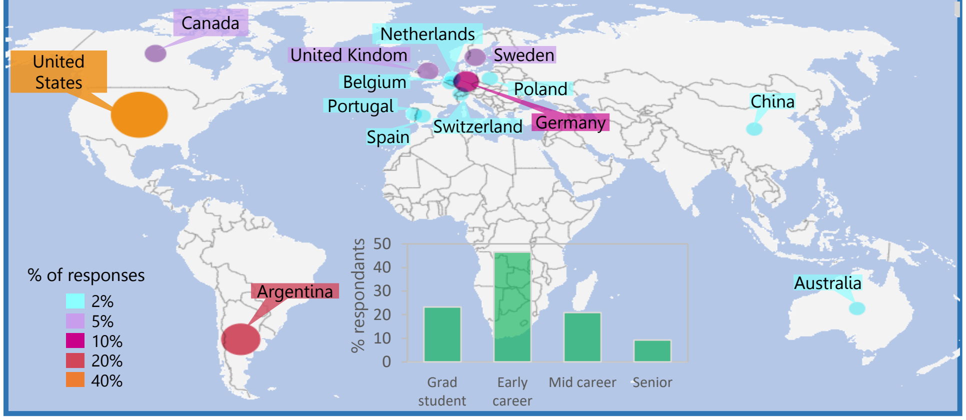
Stoichiometric Survey: The results are in...

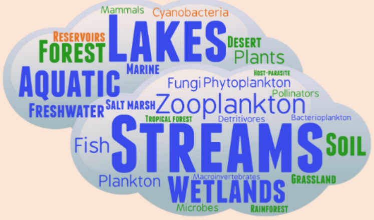
We asked the readers of Ratios Matter for their thoughts on ecological stoichiometry (ES) and what areas would benefit more from the use of ratios. We received 43 responses from 13 different countries. Thanks to everyone who participated in the first global survey on ecological stoichiometry!

Who completed the survey?

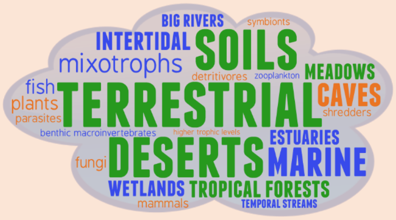
Scientists from 13 countries. Mostly early career researchers (<10 years post PhD).



Survey respondents study...



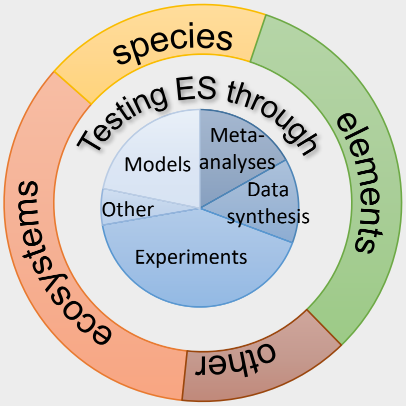
Which environments/organisms are understudied in ES?



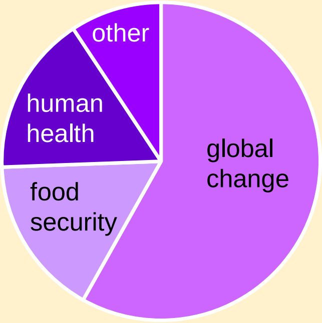
Most of our respondents work on aquatic environments/organisms (blue words). However, 63% thought that there are organisms or ecosystems underrepresented in studies of ES...which ones? Mostly terrestrial (green words).

What is needed to advance ES?

- Most felt that to advance the field of ES, we need additional data on ecosystems (35%) and other elements (33%). The "other" category included opinions that asked for more eco-evolutionary studies or at different scales (individuals/cells).
- Most said we should test ES mainly through experiments (42%) with broad support for models and aggregating data from multiple sources. "Other" approaches included calls for work at the molecular level and on elements beyond C:N:P.



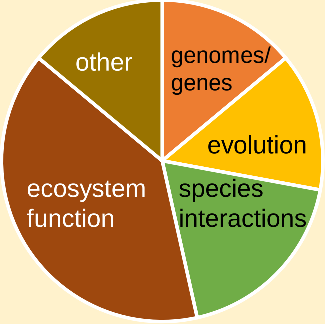
Possible uses of ES?



Almost 60% thought ES should be used to help address global change. For the "other" category, most said we should address all the three aspects together as they are all interconnected and highly important.

More links of ES to?

Close to 40% felt more ES work needed to address ecosystem function. However, many used the "other" to combine answers, to include evolution or genes. Besides these, "other" hoped to see links between ES and applied research questions and nutrient transport processes.



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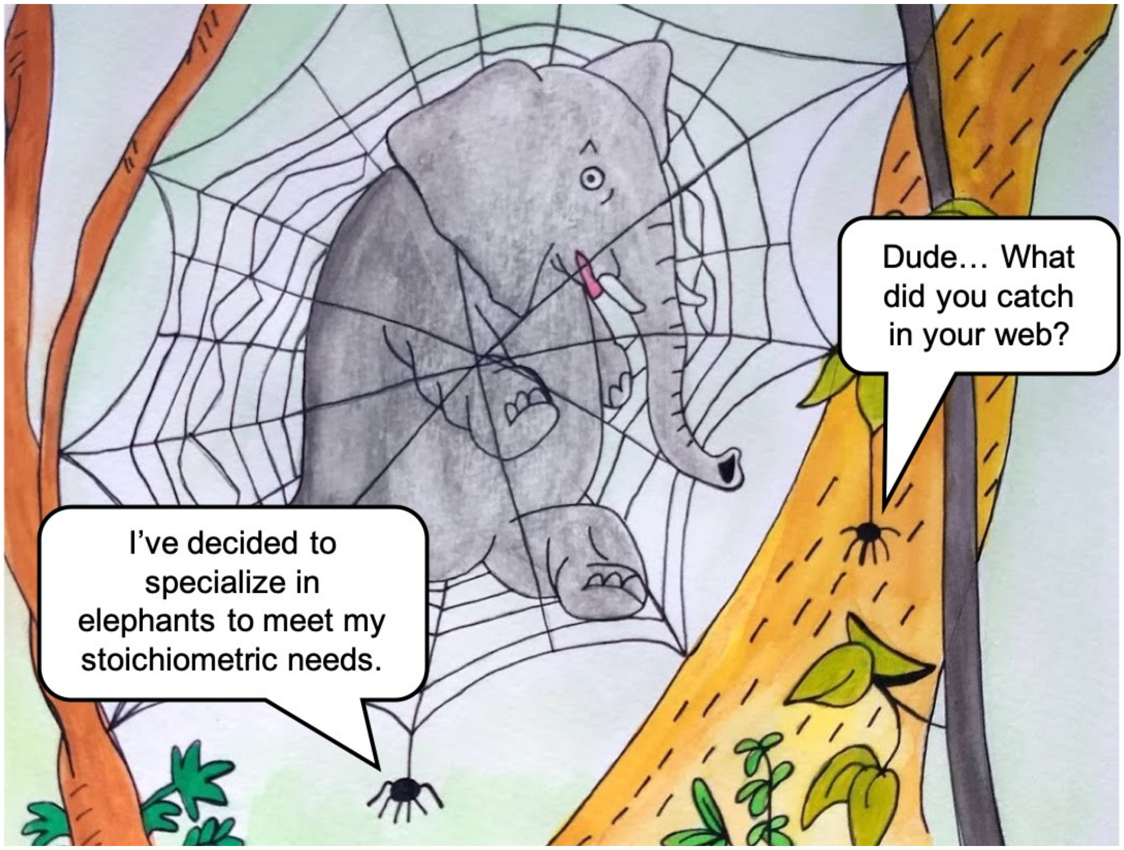
***Ratios Matter* is happy** to announce the addition of three new Associate Editors to our Editorial Board: **Francis Brearley, Jessica Corman**, and **James Larson**. We look forward to their contributions to *Ratios Matter* and their assistance in continuing to collect and publicize stoichiometric news of all forms. At the same time, *Ratios Matter* would like to thank our departing Associate Editors, **Casey Godwin** and **David Ott**, for their contributions to the newsletter over the past two years. They were both instrumental in establishing and innovating *Ratios Matter* during our early issues. Thanks again to both!

Stoich-Comic by Judith Sitters



Comictary on Ludwig et al. 2018. Ecology and Evolution. See Ratios Matter 2018, Volume 2, Issue 4 for more details

Mite Variance Might Mean More than the Mighty Mean

Here at Ratios Matter, we are always looking for new and interesting ideas or study systems (please feel free to email us with yours). As part of this effort, just before the end of 2018 while approaching peak academic burnout mode, I came across an interesting paper sporting a snappy title that immediately spoke to me: "Nutrient quality modulates trait variability" by Brückner *et al.* (2018). This study examined differences in the mean and variance of nine traits among clonal Oribatid mite populations grown across dietary C:N ratio gradients composed of multiple resource items such as blood, fungi, and pollen. Although I have some questions about the role of population-level and auxiliary dietary factors in this work, I found the study to have important insights for trait-based stoichiometric research.

First off, the authors found evidence of knife-edge like changes in normalized chemical defense, life-history, and morphological traits across the dietary C:N gradient with trait optima differing from C:N ratios of 8-12. Secondly, they observed an inverse pattern for trait variance (measured as coefficients of variation) and linear decreases in these values above the threshold with higher trait means. Assuming these patterns aren't being driven by statistical artifacts or experimental error, this result would mean that food quality may have a more extensive role in shaping consumer life-history than previously imagined. These non-linear patterns in trait variance also suggest that consumer traits may vary more extensively in organisms consuming non-optimal diets. Since similar patterns in stoichiometric trait variance have not been reported in other organisms, including the extensively studied clonal system, *Daphnia*, it is unclear whether these results are a general feature of trait-food quality relationships, which is an idea that certainly seems worth studying in the future.

In a broader context, as life-history and physiological traits can have their own elemental signatures, variability in stoichiometrically-linked traits could be an important source of organismal elemental variation. While we obviously still have a lot to learn about drivers of stoichiometric trait variability, the results of this study are in line with a considerable body of recent work linking ecological/dietary factors to consumer stochiometric trait variation (Ratios Matter, Volume 1 Issue 3) and highlights the potential to discover future stoichiometric insights if we continue to explore this variation.

From the Paper: *"Generally, there are no multicellular organisms without a certain plasticity, because intra-individual trade-offs as reactions towards environmental conditions like temperature, salinity or resource availability, but also biotic factors like predation will lead to variation of traits."*

Contributed by Clay Prater

Brückner, A., R. Schuster, K. Wehner and M. Heethoff. 2018. Nutritional quality modulates trait variability. Frontiers in Zoology 15:50. doi.org/10.1186/s12983-018-0297-2

Can N_2 fixation “fix” imbalanced N:P stoichiometry in P-rich lakes?

While looking at recent stoichiometric papers on cyanobacteria, I came across Hayes et al. (2019) and thought it would be of interest to the *Ratios Matter* community. Although the paper isn’t exclusively about stoichiometry, we can infer some interesting stoichiometric mechanisms from the results. Lake nutrient management strategies largely focus on controlling P alone because N removal may be compensated through N_2 fixation by diazotrophic cyanobacteria. It has been argued that this atmospheric N source pushes ecosystems towards P-limitation over longer time periods. Whether cyanobacterial N_2-fixation produces or promotes algal P-limitation in lakes remains contentious and there appears to be evidence that this may not be the case for all lakes. Hayes et al (2019) tested if ecosystem N demands is met by cyanobacterial N_2-fixation in P-rich lakes in Canada’s central prairies, which would be evidence that N-limitation could be alleviated by atmospheric N sources. The authors used data collected in productive lakes (mesotrophic to hypereutrophic) over two decades to estimate N_2-fixation and phytoplankton N demands. In these lakes, N_2-fixation accounted for 0-13% of the N standing stocks and met only about 12%, on average, of the N requirements of phytoplankton. When examining each lake independently, N_2-fixation met phytoplankton N demands in only 20% of the surveyed years and, in hypereutrophic lakes, it rarely exceeded 5% of demand. From a stoichiometric standpoint, these results indicate that P-rich lakes will not necessarily become P-limited or, even simply in balance with N, only through N_2-fixation.

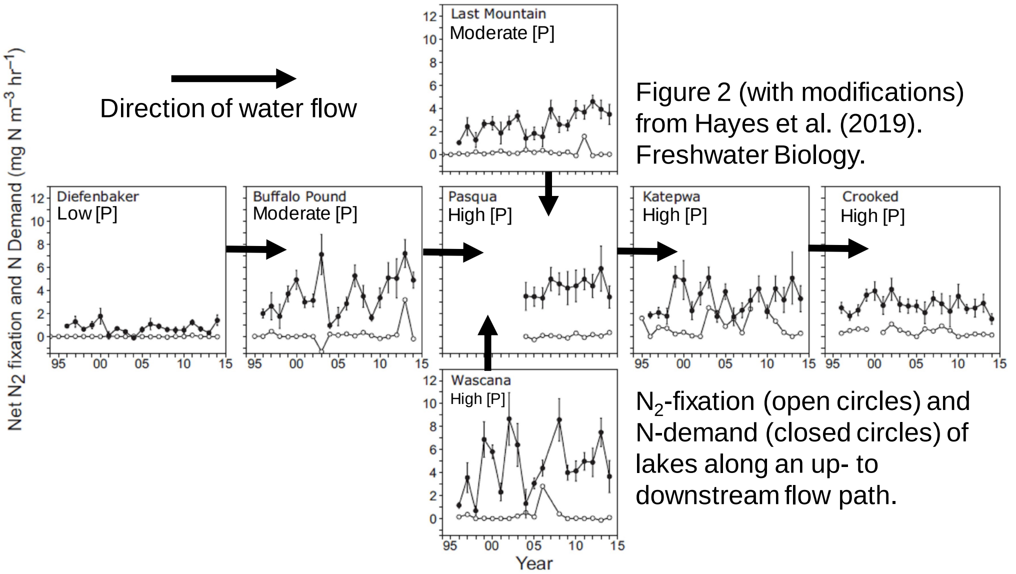


Figure 2 (with modifications) from Hayes et al. (2019). Freshwater Biology.

N_2-fixation (open circles) and N-demand (closed circles) of lakes along an up- to downstream flow path.

From the paper, “*While fixed N was an occasionally important source of N to phytoplankton, there was limited evidence that N_2 fixation alleviated N deficits or initiated P limitation of phytoplankton growth in these highly P-rich ecosystems at catchment or decadal scales.*”

Contributed by Nicole Wagner

Hayes N.M., A. Patoine, H.A. Haig, G.L. Simpson, V.J. Swarbrick, E. Wiik and P.R. Leavitt. 2019. Spatial and temporal variation in nitrogen fixation and its importance to phytoplankton in phosphorus-rich lakes. Freshwater Biology 64:269–283. http://doi.org/10.111/fwb.13214

Stoichiometric Diversity in Macroparasites

Parasites are incredibly diverse in form and function. Does this diversity correspond to variation in elemental content? Motivated by this question, Rita Grunberg and I surveyed the stoichiometric diversity of macroparasites in freshwater ecosystems of New Jersey, USA. We aimed to analyze as many macroparasite species as we could; collecting enough biomass of these microorganisms was our major constraint. Luckily, Rita and I were both PhD candidates studying aquatic parasite ecology at the time, and we knew where to find fantastically infected populations of fish and macroinvertebrate hosts.

The parasites we sampled varied widely in mean elemental content, with nearly 5-fold variation in both %N and %P and nearly 12-fold variation in N:P across species. These species spanned 4 phyla and varied in body size, life cycle stage, feeding strategy, and trophic level. Parasite %P scaled negatively and C:P scaled positively with body size across species. Variation in N was related to life cycle stage, with species sampled during reproductively active life cycle stages higher in %N and lower in C:N than encysted larvae. Surprisingly, parasite elemental content did not vary among phyla. For the species that we sampled, functional traits related to growth and reproduction outperformed taxonomic identity as predictors of parasite stoichiometry.

Host-parasite interactions are linked with elemental cycles through a variety of mechanisms, but we don't yet know how variation in parasite organismal stoichiometry shapes the nature of these relationships. If you would enjoy spending countless hours pulling microscopic worms out of fish intestines (or your own favorite parasite and host taxa) to pool them on fiberglass filters, you're in luck—we still have many important stoichiometric questions about parasite ecology and evolution to answer!

Contributed by Rachel Paseka

Photos by R. Paseka and R. Grunberg

Macroparasites sampled from 4 phyla (Acanthocephala, Annelida, Nematoda, and Platyhelminthes) varied substantially in %N, %P, and N:P across species.

Paseka, R. and R. Grunberg. 2019. Allometric and trait-based patterns in parasite stoichiometry. Oikos 128: 102-112.

Profiles in Stoichiometry

Nine Questions for Nicolas Martyniuk

Please tell us about yourself and how you became interested in ecological stoichiometry. I'm a postdoc researcher in the Laboratorio de Limnología in Bariloche, Patagonia, Argentina. The first time that I heard the words ecological stoichiometry was in the Community Ecology course that I took during my graduate studies in Biology from my professor, Esteban Balseiro. I am so thankful for that, as I had always been interested in ecology and chemistry; this was the ideal combination for me. From that moment on, I've always related everything from science to beer to my thinking on stoichiometry.

What is your current research in ecological stoichiometry? I'm interested in the effects of climate change and how changes in glacier melting rates affect organisms that live in downstream lakes and streams. I am assessing the physiological and ecological alterations on primary producers in glacier-fed streams, primarily through changes in photosynthetic parameters, stoichiometry, and community composition. Also, I have studied the effects of nutrients on interactions between periphyton and benthic macroinvertebrates. Over the last 2 years, I have included proglacial lakes and phytoplankton in my scientific world.

What's been your biggest challenge in completing stoichiometric research? One of the most challenging things working in stoichiometry is the field work. Field work and experimental studies are hard labor that must be done in an organized way and where everything, or almost everything, must be taken into account. As a PhD student, I had to carry out an experiment three times because, in the first opportunity, the stream flow took my experiment downstream. During the second time, the experiment was buried by 60 cm of rocks! It's challenging to carry out experiments, especially as one must be very creative in designing them in such a way that the results speak for themselves. In my opinion, researchers must often design simple experiments from which interesting and complex results can be obtained.

What stoichiometric paper influenced you the most? In the early stage of my doctoral studies, I read Woodward and Hildrew's (2002)* paper on riverine food webs. This is not a strict stoichiometric work, but I really like this review and it was quite influential to me. This paper showed a point of view that summarizes the way that we should conduct ecological research by linking different scales. Thus, I was taken by how a macroecological approach and a holistic view may enhance stoichiometric analyses.

*Woodward, G. and A.G. Hildrew. 2002. Food web structure in riverine landscapes. Freshwater Biology 47: 777-798.

Tell us about working in Bariloche. Bariloche is a city located in a region that has a lot of contrasting scenery. Partly due to this, Bariloche is one of the best places in the world to work. Within a 100 km, we have diverse environments, like glaciers, several types of forests, ecotones, and steppe. There is similar diversity in the surrounding freshwater environments, including many types of lakes and streams. As Bariloche offers a great number of ecosystems, we have a large living laboratory and many options for choosing field sites. However, the biggest problem for us is accessibility to field sites, as in some cases, we need to drive ~150 km to reach our field locations.

Do you have a favorite stoichiometric concept? My favorite stoichiometric concept is the Light-Nutrient Hypothesis (LNH). I choose this concept because LNH connects a great number of stoichiometric mechanisms. For example, it links the relative supplies of key resources with the nutrient content of tissues of producers. Thus, there are a lot of concepts related to LNH like imbalances and homeostasis in producers. In part, the Growth Rate Hypothesis can be viewed as partly based on the LNH. Additionally, some food quality effects directly connect to the LNH by way of the producer's physiology. However, I have had little fights with LNH. This was because my first results did not fit with the LNH pattern- I found a negative correlation of light:phosphorus supply with algal C:P content. I also found that periphyton primary producers under higher irradiances (beyond photosaturation levels of 400 µmol photons m^{-2} s^{-1}) reduced C fixation and therefore had a lower C:N:P. This was a consequence of changes by the photosynthetic machinery to excessive light levels.

Periphyton stoichiometry- How does it differ from phytoplankton? One of the most important issues for primary producers (periphytic and phytoplanktonic organisms) is the balance between C fixation and photoinhibition. In this sense, migration to deeper levels can be a suitable strategy for motile phytoplanktonic cells; however, periphytic primary producers cannot migrate deeper into the water column. In addition, the complexity of the periphytic matrix itself means that light exposure differs at different levels in the substrata. I like to compare the periphyton matrix to a forest with an understory because this analogy is useful to explain what is periphyton and how it works. Given this, these communities should be dominated by periphytic growth forms that balance the utilization of light. Consequently, the final stoichiometric composition of periphyton can be expected to result from light and nutrient availability and is related to periphyton biomass diversity and species composition. In summary, periphyton stoichiometry can have higher ratios and wider ranges of C:N and C:P than phytoplankton.

Any thoughts on studying the stoichiometry of Nahuelito? Well, honestly the main problem will be to locate Nahuelito. The problem isn't that it's a very busy animal, but that it has a large (557 km^2) and deep (464 m) lake to hide in. Undoubtedly, working with N = 1 would be difficult, and so perhaps it would be good to collaborate with Scottish colleagues since, with Nessy, we could reach N = 2. Even then, my main problem will be how to put Nahuelito in the CN analyzer.

EARLY CAREER APPLICANTS SOUGHT FOR WOODSTOICH 4

One week of peace and stoichiometry at Flathead Lake

Woodstoich 4 will be held August 13-17, 2019 at Flathead Lake Biological Station, Montana. The workshop is being organized by Dr. Michelle Evans-White (University of Arkansas) and Dr. Jim Elser (University of Montana). Woodstoich aims to create a diverse community of early career scientists to invigorate ecology and evolution by improving and expanding the use of stoichiometric theory in novel research areas.

This year's working groups will apply stoichiometric theory to: (1) link environmental change with public health, (2) improve emerging models of terrestrial organic matter dynamics, (3) explore the role of silicon in elemental ratios across ecosystems, (4) describe the ecological stoichiometry of the cryosphere, and (5) understand eco-evolutionary dynamics in altered environments.

Why participate?
Publish: Woodstoich is a product-driven workshop. Manuscripts will be submitted and rapidly reviewed for potential publication in *Frontiers in Ecology and Evolution* during the workshop.
Enjoy beautiful Montana: The workshop is free to accepted participants (including food and lodging at FLBS) and travel expenses in the USA will be compensated.
Find groovy collaborators: Participants will make up a diverse and dynamic community of early career scientists. Qualified ratio enthusiasts from across the biological sciences are encouraged to apply; prior stoichiometric research is not required.

Who can apply?
We encourage applications from all qualified candidates, especially individuals who contribute to the diversity of the workshop. Applications from current PhD students and postdocs will receive priority consideration, but applications from other early career scientists (e.g., assistant professors) will also be accepted.

Find out more and apply online at https://woodstoich.org/
Applications are due March 1, 2019.

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Selected Recent Stoichiometry Publications

Barnes, C.L., D. Hawlena, M.D. McCue and S.M. Wilder. 2018. Consequences of prey exoskeleton content for predator feeding and digestion: black widow predation on larval versus adult mealworm beetles. Oecologia In Press. https://doi.org/10.1007/s00442-018-4308-y

Chen, J., J. Seven, T. Zilla, M.A. Dippold, E. Blagodatskaya and Y. Kuzyakov. 2019. Microbial C:N:P stoichiometry and turnover depend on nutrients availability in soil: A ^{14}C, ^{15}N and ^{33}P triple labelling study. Soil Biol. Biochem. 131: 206–216. https://doi.org/10.1016/J.SOILBIO.2019.01.017

Demi, L.M., J.P. Benstead, A.D. Rosemond and J.C. Maerz. 2019. Experimental N and P additions alter stream macroinvertebrate community composition via taxon level responses to shifts in detrital resource stoichiometry. Funct. Ecol. In Press. https://doi.org/10.1111/1365-2435.13289

Dissanayake, C., L. Juan, K.R. Long, A. Peace and M.M. Rana. 2019. Genotypic selection in spatially heterogeneous producer-grazer systems subject to stoichiometric constraints. Bull. Math. Biol. In Press. https://doi.org/10.1007/s11538-018-00559-9

Gülzow, N., Y. Wahlen and H. Hillebrand. 2019. Metaecosystem dynamics of marine phytoplankton alters resource use efficiency along stoichiometric gradients. Am. Nat. 193: 35–50. https://doi.org/10.1086/700835

Hodapp, D., H. Hillebrand and M. Striebel. 2019. “Unifying” the concept of resource use efficiency in ecology. Front. Ecol. Evol. 6: 233. https://doi.org/10.3389/fevo.2018.00233

Landeira-Dabarca, A., J. Pérez, M.A.S. Graça and L. Boyero. 2019. Joint effects of temperature and litter quality on detritivore-mediated breakdown in streams. Aq. Sci. 81: 1–10. https://doi.org/10.1007/s00027-018-0598-8

McDowell, W.H., W.G. McDowell, J.D. Potter and A. Ramirez. 2019. Nutrient export and elemental stoichiometry in an urban tropical river. Ecol. Appl. In Press. e01839. https://doi.org/10.1002/eap.1839

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Prater, C., D.E. Scott, S.L. Lance, S.O. Nunziata, R. Sherman, N. Tomczyk, K.A. Capps and P.R. Jeyasingh. 2019. Understanding variation in salamander ionomes: A nutrient balance approach. Freshwater Biol. 64: 294–305. https://doi.org/10.1111/fwb.13216

Rivas-Ubach, A., J. Peñuelas, J. Hódar, M. Oravec, L. Paša-Tolić, O. Urban and J. Sardans. 2018. We are what we eat: A stoichiometric and ecometabolomic study of caterpillars feeding on two pine subspecies of *Pinus sylvestris*. Int. J. Mol. Sci. 20: 59. https://doi.org/10.3390/ijms20010059

Su, H., Y. Wu, W. Xia, L. Yang, J. Chen, W. Han, J. Fang and P. Xie. 2019. Stoichiometric mechanisms of regime shifts in freshwater ecosystem. Water Res. 149: 302–310. https://doi.org/10.1016/j.watres.2018.11.024

Tamminen, M., A. Betz, A.L. Pereira, M. Thali, B. Matthews, M.J.F. Suter and A. Narwani. 2018. Proteome evolution under non-substitutable resource limitation. Nature Comm. 9: 4650. https://doi.org/10.1038/s41467-018-07106-z

Wenger, S.J., A.L. Subalusky and M.C. Freeman. 2019. The missing dead: The lost role of animal remains in nutrient cycling in North American rivers. Food Webs 18: e00106. https://doi.org/10.1016/j.foodweb.2018.e00106