Ratios Matter

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Spotlight on Landscape Stoichiometry

This issue of *Ratios Matter* features an invited editorial from Dr. Shawn Leroux of Memorial University (Canada). This editorial was motivated by Shawn's recent *Ecology Letters* paper, which describes a framework, based on stoichiometric distribution models, that can be used to understand spatial patterns in organismal stoichiometry. With growing interest in using the ES framework to understand patterns across regions or continents, Leroux et al. (2017) is an important contribution because it provides an explicit modeling framework for integrating stoichiometry concepts into the fields of landscape ecology and global change biology.

The stoichoimetric distribution models described by Leroux et al. (2017) use the mathematical framework of species distribution models and enable ecologists to relate elements and environmental covariates in a spatially-explicit framework. They use moose and white birch in Newfoundland, Canada as an example of how this modeling framework could be applied and summarize ideas about how it might be applied to meta-ecosystem theory, macro-stoichiometry, and remotely sensed biogeochemistry.

***Ratios Matter* thanks Shawn** for providing his perspective about spatially-explicit ecological stoichiometry in this issue of *Ratios Matter* and recommends Leroux et al. (2017) for readers who are interested in learning more about this research area.

Leroux, S.J., E. Vander Wal, Y.F. Wiersma, L. Charron, J.D. Ebel, N.M. Ellis, C. Hart, E. Kissler, P.W. Sanders, L. Moudrá, A.L. Tanner and S. Yalcin. 2017. Stoichiometric distribution models: ecological stoichiometry at the landscape extent. Ecology Letters **20**: 1495-1506.

Memorial
University of Newfoundland

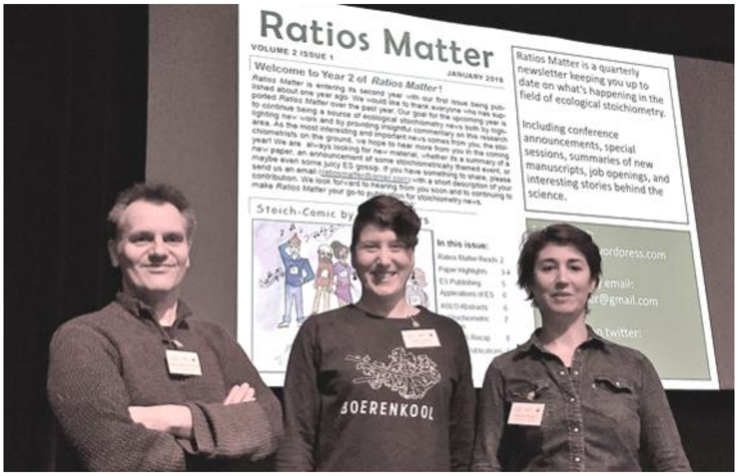
Guest commentary by **Shawn Leroux** of Memorial University (Canada). For information on Shawn and his research, visit his website.

Spatially explicit ecological stoichiometry at the landscape extent

The field of ecological stoichiometry is based on a long history of theory and small-scale experiments (Sterner & Elser 2002). However, there has been less application of stoichiometric concepts and theories to spatially explicit problems, particularly at the landscape or seascape extent (hereafter landscape). Notable examples of spatial ecological stoichiometry exist at macroecological extents in terrestrial (e.g., Borer et al. 2013), freshwater (e.g., Yan et al. 2016), and marine ecosystems (e.g., Galbraith & Martiny 2015). Some of this research has investigated spatial patterns and drivers of variation in lake stoichiometry at landscape extents (Collins et al. 2017; Prater et al. 2017). Here I argue that further development of spatially explicit models of organismal stoichiometry at landscape extents also promises to inform natural resource management and conservation of biodiversity. *Continued on pg. 8*.

Editorial Board

Conference Stoichiometry



Harry Olde Venterink, **Judith Sitters**, and **Vanessa Minden** organized the special session, ‘Ecological stoichiometry: Alterations through environmental change and impacts on organisms and ecosystems’ at the recently held Netherlands Annual Ecology Meeting 2018…and promoted Ratios Matter!

Stoich-Comic by Judith Sitters

Comictary on Sha et al. (2017) Scientific Reports 7: 15706.
See *Ratios Matter* (2018) Vol. 2, Issue 1 for more details (link)

Resource Competition and Natural Phytoplankton Populations: A Story of Stoichiometry and Light

One critique of stoichiometric control of phytoplankton community structure is the inconsistency of patterns at high, non-limiting nutrient loads. This has led to debate about the importance of ecological stoichiometry in predicting community dynamics and for managing eutrophication.

To help untangle the interplay of nutrient ratios and absolute loads in shaping phytoplankton communities, a recent paper by **Burson et al. (2018)** examined responses of natural marine phytoplankton populations to several N:P ratios and under varying nutrient loads. By extending the classic resource-ratio theory to include light as a third limiting resource, five major predictions of the nutrient-load hypothesis model* were examined. Experiments were conducted using seven controlled chemostat culture vessels, each supplied with a unique combination of N:P ratio and concentration. N-, P- and light (co-)limitations were successfully induced in target chemostats, resulting in significant changes to the phytoplankton community structure. Although the same species coexisted in nearly all the cultures at steady state, the relative dominance of individual species was clearly driven by nutrient limitation under low nutrient loads and co-limitation with light at moderate nutrient loads. Light limitation, a result of self-shading from increased biomass developed under high nutrient loads, also induced changes in relative species dominance, even when N:P ratios remained consistent.

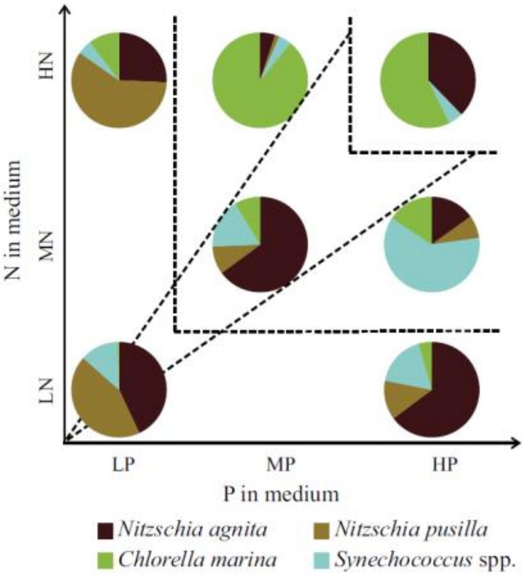


Figure from Burson et al. (2018) showing the phytoplankton community composition at steady state in the competition experiments. Community composition is displayed as the relative contributions of the different taxa to the total biovolume. Dashed lines delineate the targeted resource limitation boundaries.

Studies such as this are becoming ever more pertinent in areas like the North Sea, where anthropogenic eutrophication followed by de-eutrophication efforts have resulted in large shifts in nutrient stoichiometry and altered limitation patterns from N to P in nearshore regions. This work provides experimental confirmation of the importance of considering both stoichiometry and total loading when attempting to predict the impact of nutrient management strategies on phytoplankton community structure.

From the paper: *“These results illustrate that a further integration of nutrient-based and light -based approaches contributes to improved understanding and prediction of how changes in nutrient loads will affect the species composition of natural communities.”*

Contributed by Amanda Burson & communicated by Clay Prater

Burson, A., Stomp, M., Greenwell, E., Grosse, J. and Huisman, J., 2018. Competition for nutrients and light: testing advances in resource competition with a natural phytoplankton community. *Ecology.* doi.org/10.1002/ecy.2187

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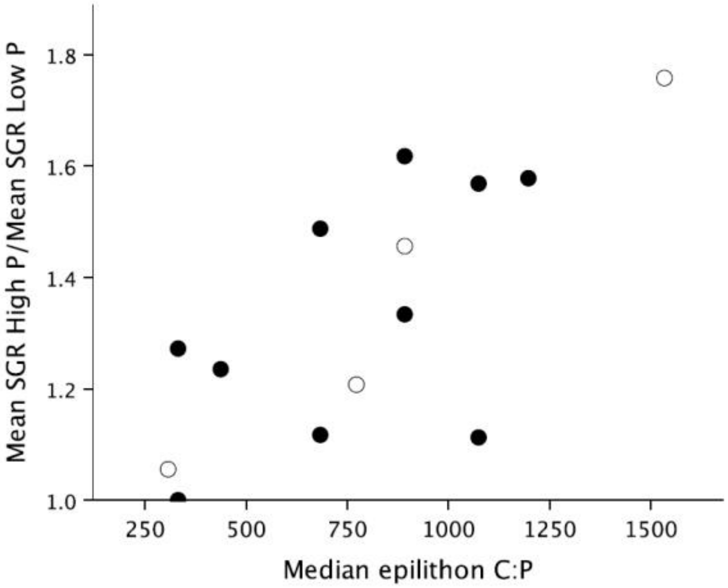
*Brauer, V.S., Stomp, M. and Huisman, J., 2012. The nutrient-load hypothesis: patterns of resource limitation and community structure driven by competition for nutrients and light. *The American Naturalist, 179(6), pp.721-740.*

Lingering Effects of Diet P on Snail Growth in New Environments

For a juvenile snail, growing is the number one priority, so why do snails from some populations grow faster on P-limited diets than others? Krist and colleagues (2017) suspected that on P-limited diets, snails from P-limited lakes would show lower reductions in growth than snails from P-rich lakes. The reason is that they would be better at upregulating their alkaline phosphatase enzymes than snails adapted to high P diets. To find out, they took juvenile snails from a number of lakes that differed in snail diet C:P ratios, fed them high and low P diets, and measured their growth rates and alkaline phosphatase activities.



Growth responses of snails to higher food P availability increased with the median C:P ratio in periphyton sampled in their source lakes.

In contrast to their expectations, snails from low P lakes were more affected by dietary P than those from high P lakes. The authors suggest that the low P-lake snails may respond more to high P-availability because they have evolved an ability to take advantage of brief periods of increased food quality. Snails from P-poor lakes also displayed lower alkaline phosphatase activities than those from P-rich lakes. Why? The authors point out that it is costly to upregulate enzymes. Under severe P-limitation, reduced RNA production or increased investment in the proteins required for growth may have prevented the upregulation of alkaline phosphatase. Their results add to a growing body of research indicating that responses to nutrient limitation vary dramatically both among and within species.

From the paper: *“Taken together, our results demonstrate genetic and spatial variation and multifaceted responses to a critical and often variable component of the natural environment, nutrient availability, in a prominent model system.”*

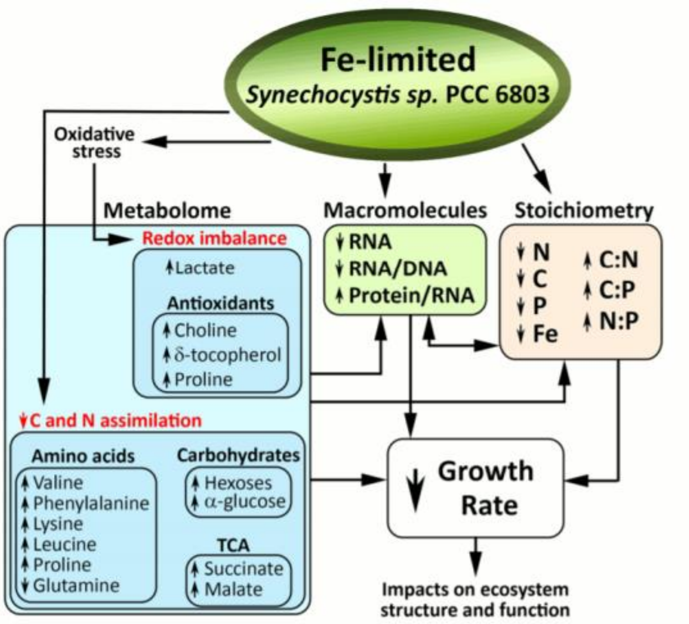
Contributed by Charlotte Narr

Krist, A.C., L. Bankers, K. Larkin, M. Larson, D.J. Greenwood, M.A. Dyck and M. Neiman. 2017. Phosphorus availability in the source population influences response to dietary phosphorus quantity in a New Zealand freshwater snail. *Oecologia. 185:595-605.* doi: 10.1007/s00442-017-3983-4

Poster by Alex Bell (Washington DFW)

Metabolic Responses to Iron-Limitation in a Cyanobacterium

Typically in ecological stoichiometry, we assume that an organism will contain less of the limiting element in their cellular and body materials. However, less is known about how non-limiting elements, macromolecules, and metabolites change when an organism is nutrient-limited. Rivas-Ubach et al. (2018) addressed this issue by asking the question: How does the cyanobacterium, *Synechocystis*, alter its elemental, macromolecule, and metabolomic profile when grown under iron (Fe)-limitation? They grew two cultures of *Synechocystis* under Fe-rich and Fe-limited conditions. The Fe-poor media contained 1/10 the amount of Fe in the Fe-rich media. Cells were then harvested for analysis of growth, elemental and macromolecule content, and of non-targeted metabolomics.



Summary of main responses in *Synechocystis* to iron-limitation. Reproduced with permission of Springer Nature.

Fe-limited cultures displayed decreased growth and RNA content, which is consistent with the growth rate hypothesis. While the Fe-limited cultures had less C, N, and P, cellular C:N and C:P ratios increased in these cells. Many of the other elements, including Fe, also decreased under Fe-limitation. A drastic increase of copper was also noticed, which was thought to be caused by increased use of Cu-rich proteins in place of the normal Fe-containing proteins (such as ferredoxin). Even though total protein content was not different between Fe-limited and replete cultures, the authors suggest that the cyanobacterium may have experienced N- limitation, due to increased C:N ratios, greater content of sugar metabolites and decreased abundance of some amino acids. Additionally, *Synechocystis* appeared to experience more oxidative stress under Fe-limitation, as indicated by the increased presence of antioxidative metabolites such as proline, choline and tocopherols.

From the paper: *"The understanding of metabolic changes of cyanobacteria under Fe limitation thus provides crucial insights into how those shifts in cells potentially scale to changes in ecosystem function by cascade effects through trophic webs."*

Contributed by Nicole Wagner

Rivas-Ubach, A., A.T. Poret-Peterson, J. Peñuelas, and others. 2018. Coping with iron limitation: a metabolomic study of Synechocystis sp. PCC 6803. Acta Physiol. Plant. 40: 28. doi:10.1007/s11738-018-2603-1

Stoichiometry in the Classroom

This is summary of the Ecological Stoichiometry seminar at Large Lakes Observatory and University of Minnesota-Duluth was written jointly by Donn Branstrator, Nicki DeWeese, Paul Frost, Moji Fakhraee, John Pastor, Kaitlin Reinl, Kirsten Rhude, Bob Sterner and Maggie Xenopoulos

Taking advantage of Paul's (*Ratios Matter* Editor-in-Chief) and Maggie Xenopoulos's sabbatical visit to the Large Lakes Observatory (Duluth, Minnesota), a group of faculty and graduate students met weekly during Spring Semester, 2018 to discuss the foundations and current trends in Ecological Stoichiometry. Students enrolled in this seminar to gain a broader understanding of ES primarily by discussing papers with other students and with experts in the field. Faculty joined the effort as a good excuse for missing committee meetings, to participate in some quality discussions, and to gain from the insights of others.

We began by reading foundational papers and defining ES. The group decided that the defining feature of ES was the co-occurring mass balances of two or more elements, which provide a strong constraint on organisms and their interactions in nature. Many "stoichiometric" studies don't consider a full mass balance even if they may provide essential foundational information. These coupled mass balances result in characteristic nutrient ratios in organisms and consequently nutrient ratios and contents are phenotypic traits that may be subject to natural selection. During later discussions, we explored topics ranging from cells to ecosystems and covered concepts such as the meaning of threshold elemental ratios and the optimum N:P ratio, homeostasis, evolution, landscape ecology and global change. Several open questions were identified and returned to several times were: 1) How are homeostasis and threshold elemental ratios related? 2) Does the increase of nitrogen in an ecosystem have the same effect as decreasing phosphorus, even though they converge on a similar N:P ratio? 3) What is the mapping between elemental content and related biological traits, and how do these two things factor into evolutionary processes? 4) How do we best phrase questions regarding the connections between ES and evolution? and 5) How does model behavior change with the introduction of stoichiometric constraints such as homeostasis? We also spent one meeting in groups creating a set of stoichiometric models on the chalkboard and discussing those.

At the end of the course, students were asked how this seminar changed the way they think about their own research. They felt the class gave them new ways of perceiving relationships among organisms and their environment. The ideas from this course provided more insight into diversity and why some species have competitive advantages over others. Further, the class challenged students to think about the connections among nutrients and ecosystems and how differing nutrient ratios and availability can impact organism growth and survival. On a broader time-scale, we were intrigued that ES might provide a framework for thinking about the evolution of early life in the ocean and the transition from unicellular to multicellular life!


Ecological stoichiometry being discussed. Left to right: Nicki DeWeese, Kaitlin Reinl, Moji Fakhraee, Bob Sterner and Kirsten Rhude

Spatially explicit stoichiometry. Continued from pg. 1.

Consumers respond to direct (e.g., McNaughton 1988) and indirect (reviewed in Boersma et al. 2008) elemental limitation. Consequently, spatially explicit models of resource stoichiometry could help describe consumer patterns and dynamics across landscapes. Such models could also assess the role of resource quality (e.g., C:N ratio) versus quantity (e.g., g N/m^2) in driving the spatial distribution of consumers. A greater understanding of the spatial patterns and dynamics of consumers may be particularly relevant for developing conservation and restoration plans for species at risk. Ecosystem-based management has emerged in response to the failures of single species or community-based approaches in conservation biology (Slocombe 1993). Spatially explicit models of organismal stoichiometry can be used to identify biogeochemical hot and cold spots within and across ecosystems (sensu McClain et al. 2003). These spatially explicit maps could inform the establishment of protected area networks seeking to conserve biogeochemical gradients and the biodiversity along these gradients. The integration of studies at multiple spatial extents (i.e., local, landscape, macro) may reveal emergent patterns and dynamics not discernable at any one scale (Kaspari & Powers 2016).

A major challenge in studying spatially explicit patterns in organismal stoichiometry is the need for spatially explicit data on resource and/or consumer stoichiometry and environmental covariates. For organismal data, the field of ecological stoichiometry has already accumulated a large body of data, which could be synthesized to address spatially explicit questions at landscape extents. Several models in other fields exist for such a data repository (e.g., movebank.org). For environmental data, the current push towards open science and data will benefit the development and applications of spatial ecological stoichiometry. Novel high-resolution remote sensing products such as the Global Ecosystem Dynamics Investigation (Qi & Dubayah 2016) set to be installed on the International Space Station in early 2019 have the potential to greatly improve the predictive power of spatial stoichiometry models. Small aerial vehicles (i.e., drones; Anderson & Gaston 2013) or wave gliders, which are now commonly used in ecology, also may be useful tools in the spatial ecological stoichiometry toolbox.

Overall, the logistics of working in this emerging field also may be challenging. Two key logistical challenges are: i) a shift of the field of ecological stoichiometry from experiments to observational studies and ii) empirical design that controls for the many drivers of temporal variation in organismal stoichiometry (e.g., plant senescence, aspect, elevation). In the end, the need for spatially explicit data and robust spatial study design also represents an opportunity to develop new collaborations with colleagues (e.g., landscape ecology, wildlife biology) already collecting spatially explicit data on organisms at landscape extents. It is an exciting time to study spatial ecological stoichiometry as researchers are beginning to overcome the challenges and develop tools which will enable ecological stoichiometry to contribute to the conservation and management of natural resources.

Acknowledgements

Eric Vander Wal and Yolanda Wiersma have greatly shaped my vision for spatial ecological stoichiometry. I thank Paul Frost and Sarah Collins for constructive feedback on earlier drafts.

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Selected Recent Stoichiometry Publications

Ball, B.A., B.J. Adams, J.E. Barrett, D.H. Wall and R.A. Virginia. 2018. Soil biological responses to C, N and P fertilization in a polar desert of Antarctica. Soil Biol. Biochem. 122: 7–18. doi:10.1016/j.soilbio.2018.03.025

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