Ratios Matter

Volume 5 Issue 3 December 2021

Ratios Matters – 5 years and counting

Our final issue of 2021 marks the end of five years for the world's only stoichiometric newsletter, *Ratios Matter*. We originally started the newsletter as a way to share news about ecological stoichiometry. Over the years, we have highlighted recent advances, profiled researchers, told stories of stoichiometric field sites, and included interesting stoichiometric tidbits. Much of the credit for *Ratios Matter* goes to our amazing Associate Editors, who have curated, written, and helped produce all of these issues. We also couldn't have done this without you. Each issue usually includes one or two summaries and stories contributed by stoichiometrists working on diverse topics in diverse areas. It has been great working with each set of authors in producing these articles and helping raise the profile of their work. If you have missed an issue or two, you will find all of our back issues free to download at http://ratiosmatter.org .

Our goal for doing all of this has been to create a place where we could highlight, amplify, and broadcast the work of any and all stoichiometrists. There are really no limits to this promotion– it is open and free to all. So consider adding your recent paper, new project, on-going collaborations, classroom activity, or stoichiometric whatever in an upcoming issue. Or perhaps you have some ratios-related news to share or something to advertise. Send your ideas to us at ratiosmatter@gmail.com and we will work with you to develop and produce your stoichiometric story. If you are really excited about *Ratios Matter*, consider applying to join our editorial board by sending us an email inquiry along with a recently updated *curriculum vitae*. We will send more details about these positions and arrange for further discussions. We look forward to hearing your ideas and learning about your new stoichiometric content soon.

Stoichiometry is now available for streaming on your favorite music app*

*It could be worth a listen, but we don't really know. We just needed to use up this space and thought the album cover was pretty cool.

Calling All Aquatic Stoichiometricists

Research Topic

Nutrient Dynamics in the Modern Hydrosphere

Stoichiometric manuscripts wanted! Consider submitting your next paper to the special research topic in Frontiers exploring nutrient dynamics in the modern hydrosphere with a focus on how human-derived global changes influence the transport and transformation of nutrients.

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Manuscript Deadline
March 11, 2022

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Better growth rules than Liebig's law of the minimum

The growth of biological organisms has long been interpreted using Liebig's law of the minimum (LLM), which states that the stoichiometrically most limiting nutrient controls the growth. Most studies on stoichiometric regulation of biological growth have regarded LLM as the golden standard. However, some observations have suggested otherwise. For example, when applied to bacterial growth, LLM implies a fixed elemental stoichiometry, in contrast to the observed stoichiometric fluctuation in bacterial biomass. Moreover, LLM is an empirical rule and has yet to be put into a framework that is based on first principles. By starting from the presumption that biological growth emerges from biochemical reactions, which can be described by law of mass action, we showed that biological growth can be represented by one of three models: the synthesizing unit model, the additive model, or LLM. These three models represent approximations to the law of mass action with decreasing numerical accuracy while employing the same model parameters (Fig. 1). We evaluated the three models against measured algal growth and plant growth under two co-limiting nutrients. The results indicated that for algal growth, the three models obtained similar model-data agreement, but LLM obtained model parameters that differed significantly from the other two models, whose parameters were very similar. For plant growth, the synthesizing model and additive model performed much better than LLM, and the synthesizing model and additive model performed equally well with the same model parameter values. We therefore **recommend researchers to use the additive model when interpreting multiple-substrate co-limited growth**, because the additive model is simpler than the synthesizing unit model, and is numerically more accurate than LLM.

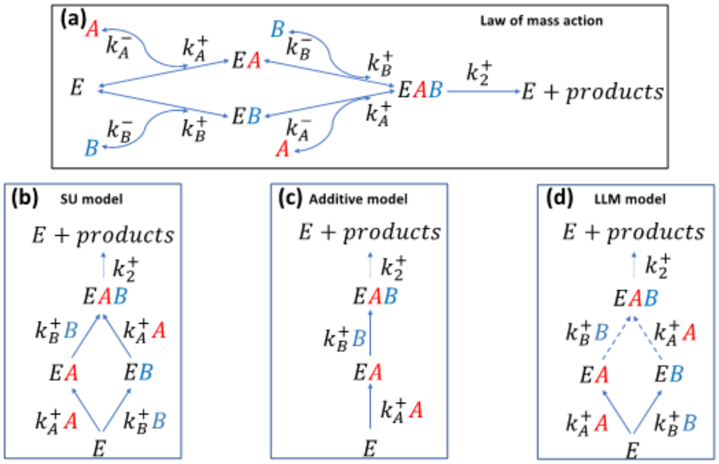


Figure 1. Two-substrate co-limited growth represented by law of mass action (a) and its approximation by the synthesizing unit model (b), additive model (b), and Liebig's law of the minimum (LLM) model (d) with decreasing numerical accuracy (as indicated by the decreased number of solid lines starting from E to E+products). Modified from Tang and Riley (2021).

From the paper: *"… if LLM is used to model biological growth, it should only be applied to the cellular quota of the complementary nutrients, i.e., the modeled organism must be explicitly represented with nutrient storage pools and flexible stoichiometry."*

Contributed by Jinyun Tang

Tang, J.Y. and W.J. Riley. 2021. Finding Liebig's law of the minimum. Ecological Applications. doi: 10.1002/eap.2458

Where does your food's stoichiometry take you?

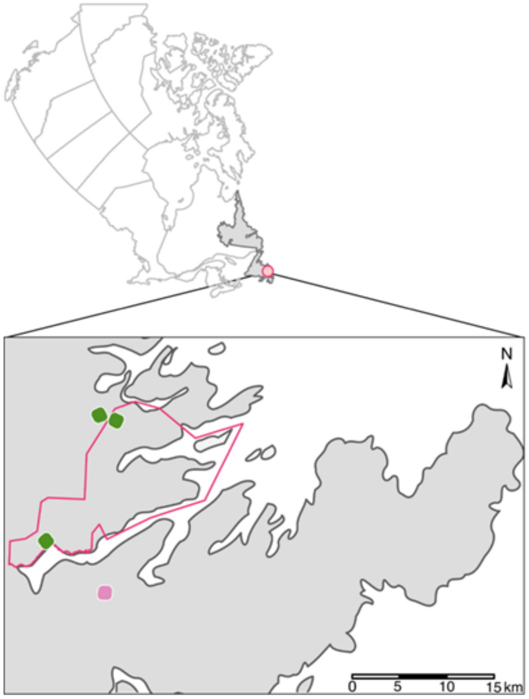


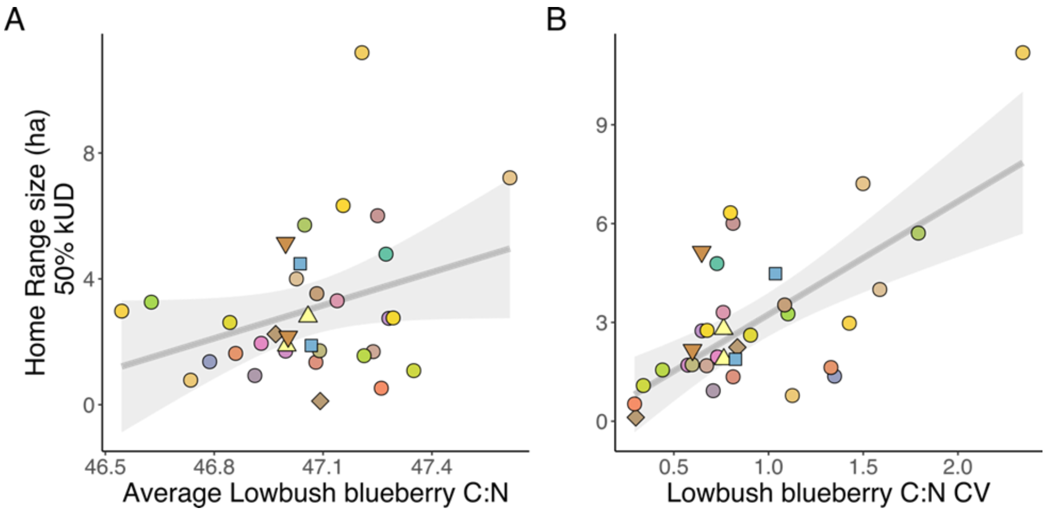
Figure 1. Map of the study area. Top, the position of the island of Newfoundland within Canada, with the pink dot showing the location of our study area. Bottom, study area detail. The magenta line encloses Terra Nova National Park, located on the east coast of Newfoundland (grey polygon). Green squares show the study sites where we sampled plant material only, the pink square is the site where we collected both plant material and snowshoe hare space use data. The scale bar refers to the detail of study area map only.

As a group of ecosystem, landscape, and terrestrial mammal ecologists, we wanted to know: Do terrestrial mammals respond to the stoichiometric quality of forage in their environment by changing their habitat use? We asked this question in a snowshoe hare-plant system on the island of Newfoundland, Canada (Fig. 1). To answer it, we ran an observational study to investigate whether the stoichiometric quality of snowshoe hares' preferred forage species varied in our study system, and whether that changed how they used their space. We used four sampling sites: each site housed live traps to capture hares and saw multiple rounds of plant sampling to assess the leaf stoichiometry of the plants eaten by snowshoe hare (Fig. 2).

As we experienced mixed fortunes with our snowshoe hare live-trapping, radio-collaring, and telemetry efforts, it took years to collect our results. Over these years, we collected, analysed, and then used plant stoichiometric data to model the distribution of leaf stoichiometry across our study area. We focused on two facets of food elemental quality in space: a site's average leaf C:N ratio (among-areas variation) and its spatial variability (within-area variation). We paired these measures of plant C:N ratio across space with estimates of snowshoe hare home range size estimated from hours of telemetry. Since animals do not use their home ranges uniformly, we considered different subsets of their habitat use derived from each hare's utilization distribution. Armed with these data, we used linear models to test our predictions on how naturally variable food elemental quality influences the size of snowshoe hares' home range, hence their space use.

Figure 2. (A) Lowbush blueberry, one of the preferred forage species of snowshoe hare in summer and one of our plant study species. (B) MR setting up a live trap to capture snowshoe hares at dusk in Fall 2017. (C) A radio-collared snowshoe hare about to be released after collar-fitting. (D) MR performing VHF telemetry on radio-collared snowshoe hares.

Figure 3. Home range size of snowshoe hares varies with two facets of forage elemental quality. (A) Size of high-use, "core" areas of snowshoe hare home ranges increases as the average quality of an area decreases—i.e., as the average C:N ratio of lowbush blueberry increases. (B) Home range "core" area size strongly increases when food elemental quality is more heterogeneous—i.e., the coefficient of variation (C.V.) for lowbush blueberry increases. Each symbol represents the home range size estimate for an individual hare. Circles denote individual hares sampled during a single year between 2017–2019, different shapes (i.e., squares, diamonds, triangles, upsidedown triangles) represent individual hares that survived through two consecutive sampling seasons (n = 4, one in 2017–2018, three in 2018–2019).



We found that the home range size of snowshoe hares varied with the elemental quality of their food—particularly lowbush blueberry (Fig. 3). Snowshoe hare home range size was larger in areas of lower average blueberry elemental quality (i.e., higher C:N; Fig. 3a) or in areas of highly heterogeneous blueberry quality (Fig. 3b). These results show that food stoichiometry can influence the spatial ecology of mammalian herbivores. So, an area's average food elemental quality may influence spatial selection processes at the landscape level, whereas variation within an area may change how herbivores use different portions of it.

Our results show that snowshoe hare space use varies with the spatial ecological stoichiometry of their preferred forage species. Perhaps because of the stronger constraints that regulate their homeostasis, terrestrial mammals appear to respond to the elemental make-up of their environment by varying their space use to access better or more abundant foraging resources. In the future, we hope to study whether this food quality-informed, differential space use has consequences for ecosystem dynamics and functions.

From the paper: "*Overall, our results provide evidence that ecological stoichiometry may help researchers understand fundamental components of consumers' spatial ecology.*"

Contributed by Matteo Rizzuto, Shawn J. Leroux, Eric Vander Wal, Yolanda F. Wiersma, and Travis R. Heckford.
Associate editor: Robert Buchkowski.

Rizzuto M, Leroux SJ, Vander Wal E, et al (2021) Forage stoichiometry predicts the home range size of a small terrestrial herbivore. Oecologia 197:327–338. https://doi.org/10.1007/s00442-021-04965-0

Bringing the Plankton Net Approach to a Tropical Rain Forest

Photo credit: M.A. Cavaleri

Stoichiometry tells us a lot about the relationship between organisms and their environment. But which organisms, and which environments? Ocean-going research vessels can drag a net and sample entire communities. Without a plankton net in our arsenal, land-based stoichiometrists have had to hand-select leaves, and even remote sensing can't see the chemistry below the uppermost canopy. Tropical rain forests, in particular, have tall canopies (regularly exceeding 40 meters) with leaves all along the way. Since all tropical rain forest leaves contribute to the impressive carbon uptake of this biome, we set out to determine the stoichiometry of the *entire* photosynthetic surface in one tropical rain forest.

The TOWERS experiment brought the plankton net approach to La Selva Biological Station in Costa Rica. We could not drop plankton nets down, so we built them from the ground up. We started by constructing a scaffolding module of 2 x 2 x 2 meters on the forest floor and collecting every leaf that intersected the module. This was a sample of the bottom of the photosynthetic zone. We added another 2 x 2 x 2 m module on top for our next sample (see photo), and kept going up one module at a time until there were no more leaves above us. We repeated this at 45 stratified random sites across the old-growth forest, capturing a representative range of soil phosphorus and topographic conditions.

Unlike most foliar stoichiometric studies which compare leaves or individual plants, we used the cumulative foliar stoichiometry of an entire collection tower in our analysis of horizontal stoichiometric trends. Using a regression tree statistical approach, we asked what, if anything, explained the variance in foliar stoichiometry from location to location.

We also explored vertical trends by treating each 2 m height increment as a canopy level. We pooled all samples from across the forest by canopy level and then used linear regression to test for vertical stoichiometric trends.

So what did we find? For every phosphorus atom in this tropical forest foliage, there are 48 nitrogen atoms. This ratio did not vary vertically, but did vary (significantly albeit subtly) with soil phosphorus. In foliage from those parts of the forest with above 670 ppm total soil phosphorus, N:P was 46 molar. In the rest of the forest falling below that threshold, N:P was 53 molar.

In contrast to N:P, many other ratios change vertically. Relative to nitrogen and phosphorus, every other element we measured became less abundant with height: K, Ca, Mg, S, Na, Zn, Mn, and Al. One of the steepest vertical trends was that, for every phosphorus atom in leaves growing near the forest floor, there are about 2.2 sodium atoms. At the canopy top, there were 106 phosphorus atoms for every sodium.

La Selva is just one tropical rain forest. Bringing the plankton net approach to some others would greatly deepen our understanding of the biome.

From the paper: "*Rather than denoting limitation to productivity, as has long been theorized, foliar stoichiometric differences could be another mechanism by which lowland tropical rainforests maintain relatively constant productivity across a wide range of soil conditions.*"

Contributed by Audrey Massmann and Stephen Porder

Massmann, A., M.A. Cavaleri, S.F. Oberbauer, P.C. Olivas and S. Porder. 2021. Foliar stoichiometry is marginally sensitive to soil phosphorus across a lowland tropical rainforest. Ecosystems. 24(5).

Main text open access: http://rdcu.be/ckdS7
Supplemental files: http://doi.org/10.1007/s10021-021-00640-w

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JASM 2022 Special Session

Stoichiometry in a Changing World: Assessing Elemental Ratios from Organisms to Ecosystems

We can all probably agree that it's been waaaay too long since we've gotten to nerd out about elements at a conference together! If you're an aquatic researcher or will be anywhere near Grand Rapids, Michigan during the week of May 14th-20th, 2022, please consider joining the special Biogeochemistry session that will be focused on cross-scale and organism-to-biosphere level stoichiometric dynamics related to global change. This is going to be a dynamic session with a mixture of short and long talk formats with lots of discussion. Rumor has it that a special guest may even show up. Hint- an author of a book very near and dear to all of us (No, not J.R.R Tolkien, although this guest is resembling Gandolf the Grey more and more each year).

If you're interested in joining our Fellowship, please take a look at the session description here (https://jasm2022.aquaticsocieties.org/session-list/) and submit your abstract by January 10th, 2022. See you soon!

2022
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Teach Your Children (Stoichiometry) Well

Raise your hand if you can recall your frustration the first time you were asked to balance a set of reactions in chemistry class. Now, imagine how you might have felt if you were asked to tackle this problem in another language with terminology and symbols that have no link to your everyday life. A new study by Bhukuvhani et al. (2020) has quantified the effects of culture on the understanding of stoichiometric concepts by Zimbabwean secondary school children. Using diagnostic tests, questionnaires, and reflective discussions, they focused on the effects of three aspects of culture (language and symbols, values and attitudes, and scientific culture) on student understanding of stoichiometric concepts. Students had trouble understanding stoichiometry problems when discussed solely in English but fared much better when discussing problems using a mixture of their native dialect and English. Despite limited scientific training and an inability to explain underlying mechanisms behind stoichiometric reactions, students performed better when balancing reactions linked to everyday chemistry such as iron rusting in the presence of moisture.

These results highlight the importance of socio-culturally reinforced instructional methods in scientific education, which is a lesson that is important in any classroom. For instance, one can't help but wonder about all the diverse insights we might be missing out on in our own education systems where chemical reactions are often separated from their biological context and ecological phenomena are explained by complex concepts often abstracted from their more intuitive physiochemical drivers. The beauty of general stoichiometric equations such as: X Consumer Biomass + Y Resources = X Consumer Biomass + aY New Consumer Biomass + (1-a) Y Waste Products (from Sterner and Elser 2002) is that they can be explored using "boots and buckets" in the field, test tubes in the lab, or computer hard drives, yielding a more balanced and exciting view of chemical reactions that appeal to a wider range of students. This dynamic interplay between biology and chemistry is what Lotka may have had in mind when describing biology in theatrical terms. It also sparked some of the first ecological stoichiometry research (See Ratios Matter Vol. 1 Issue 1: **Out of Africa**) that continues to inspire our own work. Just something to keep in mind at the end of a long semester… and the next time a student falls asleep in your class!

From the paper: *"School teachers should allow students to conceptualize issues and develop their arguments in an environment that respects students' local knowledges."*

Contributed by Clay Prater

Bhukuvhani, C., A. Chiromo, and C. Chikunda. 2020. Influence of culture on secondary school students' learning of stoichiometry: A case of a Guruve district school, Zimbabwe. Journal of New Vision in Educational Research 1:245-262.

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🌶️ Off to a Hot Start!

Here are the results of a Web of Science search for the most cited papers published in 2021 using "ecological stoichiometry" in the title, abstract, or keywords. Listed below are the top ~10% of the 146 papers that were returned by this search in order of decreasing citations. This is a remarkable list that captures the current state of our field with papers from around the globe on topics ranging from bees and mudflats to cyanobacteria and chicken farming.

Xie, X.F., et al. 2021. Differential effects of various reclamation treatments on soil characteristics: an experimental study of newly reclaimed tidal mudflats on the east China coast. Science of the Total Environment **768**.

Bai, X.J., M.A. et al. 2021. Extracellular enzyme activity and stoichiometry: The effect of soil microbial element limitation during leaf litter decomposition. Ecological Indicators **121**.

Capek, P., M. Choma, K. Tahovska, J. Kana, J. Kopacek and H. Santruckova. 2021. Coupling the resource stoichiometry and microbial biomass turnover to predict nutrient mineralization and immobilization in soil. Geoderma **385**.

Filipiak, M., M. Woyciechowski and M. Czarnoleski. 2021. Stoichiometric niche, nutrient partitioning and resource allocation in a solitary bee are sex-specific and phosphorous is allocated mainly to the cocoon. Scientific Reports **11**.

Sardans, J., I.A. Janssens, P. Ciais, M. Obersteiner and J. Penuelas. 2021. Recent advances and future research in ecological stoichiometry. Perspectives in Plant Ecology Evolution and Systematics **50**.

Wang, C.T., Y. Sun, H.Y.H. Chen and H. H. Ruan. 2021. Effects of elevated CO2 on the C:N stoichiometry of plants, soils, and microorganisms in terrestrial ecosystems. Catena **201**.

Fernandez-Martinez, M., et al. 2021. Bryophyte C:N:P stoichiometry, biogeochemical niches and elementome plasticity driven by environment and coexistence. Ecology Letters **24**:1375-1386.

Gong, H.Y., Y.F. Li and S.J. Li. 2021. Effects of the interaction between biochar and nutrients on soil organic carbon sequestration in soda saline-alkali grassland: A review. Global Ecology and Conservation **26**.

Osburn, F.S., N.D. Wagner and J. T. Scott. 2021. Biological stoichiometry and growth dynamics of a diazotrophic cyanobacteria in nitrogen sufficient and deficient conditions. Harmful Algae **103**.

Krams, I.A., et al. 2021. Developmental speed affects ecological stoichiometry and adult fat reserves in Drosophila melanogaster. Animal Biology **71**:1-20.

Andrieux, B., J. Signor, V. Guillou, M. Danger and F. Jabot. 2021. Body stoichiometry of heterotrophs: Assessing drivers of interspecific variations in elemental composition. Global Ecology and Biogeography **30**:883-895.

Zhang, X.P., et al. 2021. Effects of chicken farming on soil properties and root-associated bacterial communities in a bamboo (Phyllostachys praecox) ecosystem. Applied Soil Ecology **157**.