Volume 4 Issue 2 May 2020

Ratios Matter

Ecological Stoichiometry during the COVID-19 Pandemic

This issue of *Ratios Matter* was produced against a backdrop of the global COVID-19 pandemic. Like everyone else, we have been stuck at home, wondering about our field seasons and pending experiments, and trying to otherwise work under a variety of stressful and non-optimal conditions. Through it all, we are here to tell you that ratios are still worth thinking about, elements are important to ecology, and mass balance constraints still constrain. We haven't jumped on COVID-19 research yet (although it would be interesting to know the N:P ratio of the virus) and, after this first page, this issue includes our normal mix of summaries, short articles, and stoichiometric news. As always, we hope you enjoy the newsletter and find it a short respite from the news of the day.

Stoich-Comic by Judith Sitters

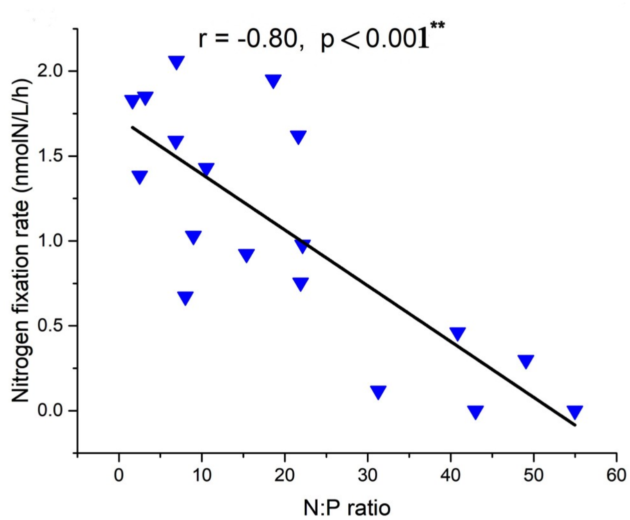
We have a new website!

You can now visit Ratios Matter on the web at: ratiosmatter.org. Meet the editorial team, find old issues, and learn how to submit your own contribution to *Ratios Matter*.

***Ratios Matter* is pleased** to announce that Robert Buchkowski has joined our Editorial Board. Rob is currently an NSERC Postdoctoral Fellow at Western University in London, Ontario after completing degrees at Lakehead and Yale. He studies the role animals, plants, and microorganisms play in cycling of elements through terrestrial ecosystems using field experiments and theoretical models.

Stoichiometry controls nitrogen fixation in a tropical estuary (Cochin estuary, Kerala, India)

The bioavailability of N and P are critical in regulating N_2 fixation, and shifts in one of these elements can lead to changes in the nutrient ratio, promoting either P-limitation or N-limitation. Because estuaries receive an excessive amount of anthropogenic inputs, including nutrients from various sources, they are an ideal experimental system for assessing the role of alterations in nutrient stoichiometry on N_2 fixation. In the tropical Cochin estuary, in southwest India, a proportionally greater input of P will imbalance nutrient stoichiometry and, in turn, may influence N_2 fixation. Jabir et al. (2020) used this system to address important questions such as: 1) is nutrient stoichiometry influencing N_2 fixation and the distribution of diazotrophs? and 2) do monsoon-induced changes in nutrient stoichiometry cause seasonal variations in N_2 fixation and the distribution of diazotrophs? They found that N_2 fixation rates displayed a seasonal pattern with high N_2 fixation rates during pre-monsoon and post-monsoon seasons and decreased rates during the monsoon. This seasonal pattern of N_2 fixation was correlated with the dissolved N:P ratio of the system, with low N:P observed in the pre- and post-monsoon season and high N:P observed during the monsoon season. Interestingly, the abundance of diazotrophs was influenced more by P while the N_2 fixation rates were more influenced by N. Different diazotrophs were responsible for the high N_2 fixation rates seasonally, with cyanobacteria dominating in the pre-monsoon season and heterotrophic bacteria dominating in the post-monsoon season. This study highlights the utility of this estuarine model system for examining the relationships between biodiversity and ecosystem functioning and determining how this relationship is mediated by ecological stoichiometry.



Reduced N_2 fixation was found associated with higher molar N:P ratio in the estuary. Figure from Jabir et al. (2020).

From the Paper: "*High N_2 fixation rates occurred in the Cochin estuary when the N:P ratio in the estuary was close or lower than the canonical Redfield ratio. Increased N:P ratio suppressed the N_2 fixation rates and abundance of heterotrophic diazotrophs…..*"

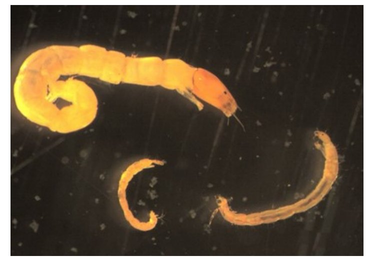
Contributed by Thajudeen Jabir, Francis Q. Brearley, and Nicole Wagner

Jabir, T., Vipindas, P.V., Jesmi, Y., Valliyodan, S., Parambath, P.M., Singh, A. and A. A. Mohamed Hatha., 2020. Nutrient stoichiometry (N: P) controls nitrogen fixation and distribution of diazotrophs in a tropical eutrophic estuary. Marine Pollution Bulletin 151: 110799. https://doi.org/10.1016/j.marpolbul.2019.110799

We Asked, They Answered

If you could study the stoichiometry of any organism, community, or ecosystem (assuming you have no financial or logistical constraints), what would it be?

***Wyatt Cross**, Montana State University*. I would go after those pesky midges – i.e., Chironomidae. They are such an important component of most freshwater food webs, particularly within benthic environments. Understanding variation in their stoichiometric requirements could go a long way towards linking structure and function for these '*Daphnia* of the benthos'!



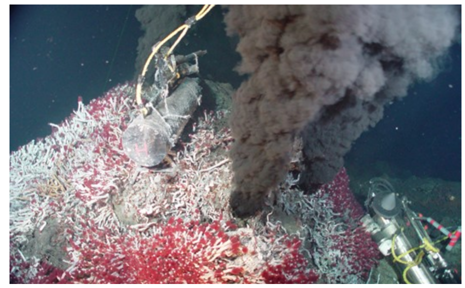
***Rachel Paseka**, University of Minnesota*. All microbes associated with the human body, including pathogens and the non-pathogenic microbiome. Understanding the stoichiometric demands of microbes within the body and how resources shape microbial community composition and function would give us novel insights into human health.

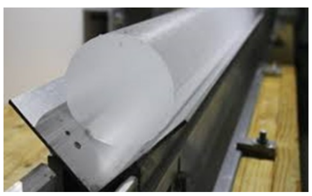
***Cody Starke**, Trent University.* Komodo Dragons have long held my fascination. I recall how excited I was when the Toronto Zoo announced the introduction of these magnificent beasts into their zoo. You better believe I was there that summer, snapping endless photos of Komodo Dragons with my disposable camera (remember those)? One common misconception about Komodo Dragons is that they have multiple strains of bacteria in their saliva which helps to poison the blood of their prey. Turns out that is FAKE NEWS!

Instead, Komodo Dragons have multiple venom ducts between their teeth to carry out the deed. But what about the stoichiometry of Komodo Dragons? It turns out that they are osteoderms, which means they have a "chain mail" of bones embedded within the skin for an extra layer of protection. Imagine determining the Ca and P content of this 150-pound killing machine. It would be fascinating!

Bob Sterner, *University of Minnesota, Duluth*. Mixotrophs have always fascinated me. There have been some very good recent studies on mixotrophic C:N:P ratios, but given their diversity, I think the jury is still out on whether mixotrophs look like autotrophs, heterotrophs, or some combination depending on how they switch their metabolism.

Angelica Gonzalez, *Rutgers University.* I would study the stoichiometry of extremophile organisms, such as those living on glaciers, the bottom of the sea, hydrothermal vents, and hot springs. As they thrive under extreme conditions of temperature, (lack of) light, pressure, pH, energy, and nutrient limitation, they can provide insights into the stoichiometric boundaries of life.





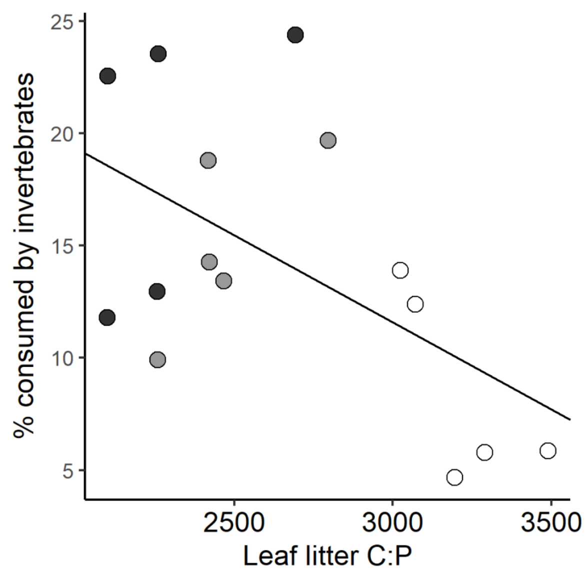
Ryan Sherman, *MacMurray College.* Microbial communities in Antarctic ice cores. This could provide some insight into the structure and functioning of aquatic food webs of the ancient past from a stoichiometric perspective.

Shawn Leroux, *Memorial University*. Moose. I am fascinated by how challenging it is to process large animals for stoichiometric analysis. From a technical standpoint, I think moose would be interesting and with sufficient funding could help refine terrestrial mammal lab protocols. We have ~ 700 moose vehicle collisions on the island of Newfoundland every year so getting carcasses would not be a problem. I will, however, need a bigger lab! As moose are broadly distributed across one of the world's largest biomes. They co-occur with some common plant/herbivore/predator species across their circumboreal range but there is also significant variation in their ecological networks across their range. Having samples across the broad distribution of the species would allow for testing hypotheses pertaining to large scale biotic and abiotic drivers of moose stoichiometry.

Jeff Back, *Baylor University*. I would investigate insects that have detritivore/herbivore larvae and predaceous adults (and vise versa). Why? Because larval contributions of nutrients to adults could be quite different and have implications for adult body size and fecundity.

In the flow: Tracing the effects of altered resource stoichiometry through detrital food webs

A central goal of stoichiometric research is to characterize how elemental supply ratios influence biological processes across organismal and ecosystem-level scales. A recent study by Demi et al. investigated how N and P enrichment modified material flows through macroinvertebrate food webs via microbially modulated shifts in basal resource stoichiometry. Five forested headwater streams were continuously enriched with N and P at unique dissolved N:P ratios (2:1-128:1) for two years, following a year of pre-enrichment monitoring. The goal was to characterize the effects of experimental nutrient enrichment on the trophic basis of macroinvertebrate production and biomass flows of dominant food resources to consumers and predators. Following N and P enrichment, total organic matter flows of all resources to consumers increased, on average, due to reduced stoichiometric constraints on community secondary production. Flows from leaf detritus, wood, and diatoms to macroinvertebrates were negatively related to resource C:P across all five streams during the three-year study, increasing with stream water P supply. Nutrient enrichment also increased the efficiency with which leaf litter, the dominant material flow pathway, was channeled to macroinvertebrates, with the proportion of leaf litter being consumed by invertebrates (as opposed to other sources of loss) increasing with P-enrichment of leaf litter (see Figure). Despite increased flows of basal resources to primary consumers, there was not a subsequent increase of flows of animal prey to predators during the three-year study, suggesting that reduced stoichiometric constraints at the base of food webs will not always propagate to higher trophic levels. This study provides strong support for ecological stoichiometry as a tool for predicting the consequences of altered N and P availability for food web dynamics.



Proportion of leaf mass loss consumed by macroinvertebrates under leaf litter enrichment. Open circles indicate pre-enrichment years, while grey and black circles represent enrichment years 1 and 2 respective-

From the Paper: "*Annual fluxes of multiple organic matter pools to macroinvertebrate food webs were negatively related to resource C:P, a sign of wide-spread P-limitation of these detritus-based stream food webs*".

Contributed by Mick Demi

Demi, L.M., J.P. Benstead, A.D. Rosemond and J.C. Maerz. In Press. Experimental N and P additions relieve stoichiometric constraints on organic-matter flows through five stream food webs. Journal of Animal Ecology. DOI: https://doi.org/10.1111/1365-2656.13197

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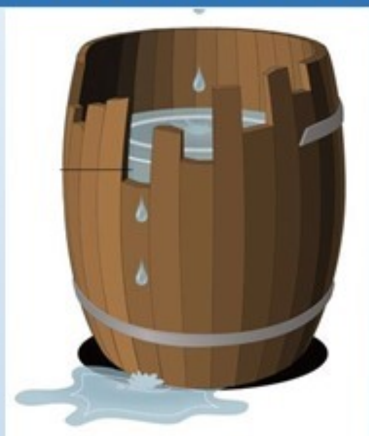

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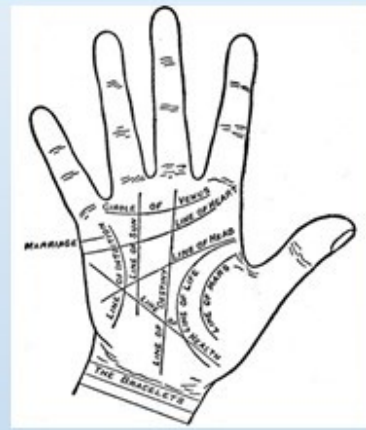

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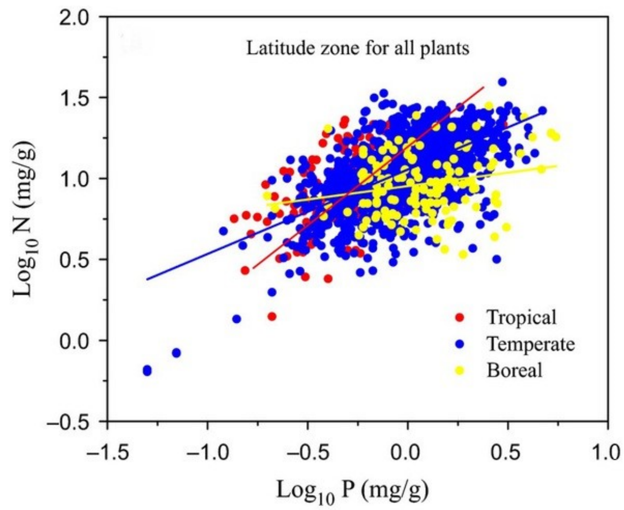
Global root nutrient stoichiometry

Ecology now routinely draws together large amounts of data from previously published studies to make important conclusions about ecological processes at broader scales. This approach has been particularly important for ecological stoichiometry where we have elemental datasets with high potential for compilation and synthesis. For example, there are reams of data available on N and P concentrations in many plant taxa from geographically disparate ecosystems. The organs that are routinely sampled for this are leaves given their key role in photosynthesis. These data are useful to estimate mean foliar N:P ratios but can also reveal the scaling relationship between N and P concentrations in leaves. Roots are arguably as important as leaves for plant responses to nutrient supply because they access nutrients and water for plant growth, but their nutrient ratios are rarely studied. A recent study by Wang et al. (2019) has now provided the most extensive synthesis on root N:P relationships to date, and draws some interesting conclusions on these less studied organs.



Relationships between fine root nitrogen and phosphorus in three latitudinal zones (from Wang et al. 2019).

Across 433 sites globally, the authors found the fine root N:P log-log scaling exponent (0.82) to be greater than that for leaves (0.67, as reported by Reich et al. 2010; Proc. R. Soc. B 277:877), although they showed a latitudinal gradient ranging from 0.98 in the tropics to 0.71 in boreal regions. This gradient was particularly apparent for woody species. Consistent with prior work, this indicates a clear latitudinal variation in nutrient allocation patterns. The mean N:P (on a mass basis) was 13:1 compared to 11:1 for leaves, suggesting greater N limitation in leaves. This makes sense given that N is required in large amounts for photosynthesis. The concept of 'limitation' for different plant organs is perhaps not the most appropriate term but indicates that there is a difference in how plants partition resources between different organs. Similarly, scaling relationships differed between plant organs. These differences may be caused by phylogeny and/or sampling issues. Of course, these environmental and physiological differences could be specific to the communities and species sampled, but they could also point to the lack of a 'global' relationship.

More broadly, this study acts as a call to make our data publicly available for syntheses such as these. We may not be rewarded directly, but we know that we are making a contribution by moving our science forward.

From the paper: "*In contrast to the 2/3 foliar scaling relationship, fine roots appear to conform to a general 0.82-power law.*"

Contributed by Francis Q. Brearley

Wang, Z., Yu, K., Shiqi, L., Niklas, K.J., Donko Mipam, T., Umaña, M.N., Zhao, Q., Huang, H., Reich, P.B. (2019) The scaling of fine root nitrogen versus phosphorus in terrestrial plants: a global synthesis. Functional Ecology 33: 2081-2094

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Selected Recent Stoichiometry Publications

Bergström, A.K., A. Jonsson, P.D.F. Isles and others. 2020. Changes in nutritional quality and nutrient limitation regimes of phytoplankton in response to declining N deposition in mountain lakes. Aquat. Sci. 82: 31. doi:10.1007/s00027-020-0697-1

Bomfim, B., L.C.R. Silva, B.H. Marimon-Júnior and others. 2020. Fire affects asymbiotic nitrogen fixation in southern Amazon Forests. J. Geophys. Res. Biogeosciences 125: e2019JG005383. doi:10.1029/2019JG005383

Brookshire, E.N.J., P.C. Stoy, B. Currey and B. Finney. 2020. The greening of the Northern Great Plains and its biogeochemical precursors. Glob. Chang. Biol. In Press: 1–10. doi:10.1111/gcb.15115

Du, E., C. Terrer, A.F.A. Pellegrini and others. 2020. Global patterns of terrestrial nitrogen and phosphorus limitation. Nat. Geosci. 13: 221–226. doi:10.1038/s41561-019-0530-4

Francois, C.M., L. Simon, F. Malard and others. 2020. Trophic selectivity in aquatic isopods increases with the availability of resources. Funct. Ecol. 34: 1078–1090. doi:10.1111/1365-2435.13530

Garcia, C.A., G.I. Hagstrom, A.A. Larkin and others. 2020. Linking regional shifts in microbial genome adaptation with surface ocean biogeochemistry. Philos. Trans. R. Soc. B Biol. Sci. 375: 20190254. doi:10.1098/rstb.2019.0254

He, X. and W.-X. Wang. 2020. Allocation and stoichiometric regulation of phosphorus in a freshwater zooplankton under limited conditions: Implication for nutrient cycling. Sci. Total Environ. 728: 138795. doi:10.1016/j.scitotenv.2020.138795

Jeyasingh, P. D., J. M. Goos, P. R. Lind and others. 2020. Phosphorus supply shifts the quotas of multiple elements in algae and *Daphnia*: ionomic basis of stoichiometric constraints. Ecol. Lett. In Press: 1–9. doi:10.1111/ele.13505

Modenutti, B. and E. Balseiro. 2020. Mixotrophic ciliates in north-patagonian andean lakes: Stoichiometric balances in nutrient limited environments. Limnetica 39: 263–274. doi:10.23818/limn.39.17

Mori, T. 2020. Does ecoenzymatic stoichiometry really determine microbial nutrient limitations? Soil Biol. Biochem. 146: 107816. doi:10.1016/j.soilbio.2020.107816

Orłowski, G., L. Mróz, M. Kadej and others. 2020. Breaking down insect stoichiometry into chitin-based and internal elemental traits: Patterns and correlates of continent-wide intraspecific variation in the largest European saproxylic beetle. Environ. Pollut. 262: 114064. doi:10.1016/j.envpol.2020.114064

Penuelas, J., I.A. Janssens, P. Ciais and others. 2020. Anthropogenic global shifts in biospheric N and P concentrations and ratios and their impacts on biodiversity, ecosystem productivity, food security, and human health. Glob. Chang. Biol. 26: 1962–1985. doi:10.1111/gcb.14981

Rinehart, S. and D. Hawlena. 2020. The effects of predation risk on prey stoichiometry: a meta-analysis. Ecology In Press: 1–12. doi:10.1002/ecy.3037

Sach, F., L. Yon, M.D. Henley and others. 2020. Spatial geochemistry influences the home range of elephants. Sci. Total Environ. 729: 139066. doi:10.1016/j.scitotenv.2020.139066

Smith, N.J., G.W. McDonald and M.G. Patterson. 2020. Biogeochemical cycling in the anthropocene: Quantifying global environment-economy exchanges. Ecol. Modell. 418: 108816. doi:10.1016/j.ecolmodel.2019.108816