Ratios Matter

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Woodstoich 4: Five days of Peace & Stoichiometry

After Norway, Japan, and Australia, Woodstoich 4 (Woodstoich.org) was held for the first time in the United States. As in the past, Woodstoich brought together early-career scientists and stoichiometry enthusiasts for five days of peace and elemental balance. This version had 25 attendees congregating at Flathead Lake Biological Station (https://flbs.umt.edu/newflbs) in Montana. Also attending and advising were three special stoichiometry guests, Zoe Cardon (MBL), Jenn Schweitzer (University of Tennessee), and Jotaro Urabe (Tohoku University, Japan). During the workshop, five groups prepared and finalized stoichiometric manuscripts, which were speed-reviewed during the workshop (thanks to all editors and reviewers!). These groups focused on a range of exotic topics including stoichiometry of socio-ecological systems, soil organic matter dynamics, cryosphere ecology, C:N:P coupling to silica, and eco-evolutionary dynamics. Keep an eye out for these papers, which will soon appear in Frontiers in Ecology and Evolution (2 already accepted; https://www.frontiersin.org/research-topics/10239/emerging-frontiers-in-ecological-stoichiometry)! The workshop organizers, Michelle Evans -White (University of Arkansas, also a Woodstoich 1 attendee) and Jim Elser (University of Montana), made sure the participants stayed balanced by dissipating excess carbon through traditional tie-dye shirt making, rafting in the Glacier National Park, and a groovy dance party.

Contributed by Nico Martyniuk

Stoichiometry in Summer 2020!

- **Are you looking for exciting stoich-centric discussions?**
- **Looking for new collaborators in ecological stoichiometry?**
- **Have emerging stoichiometry research you want to share?**

Then mark your calendar for the 2020 Gordon Research Conference "Unifying Ecology across Scales"

Dates: July 26 - 31, 2020
Location: Southern New Hampshire University, Manchester, New Hampshire, USA
Conference Chair: Angelica L. Gonzalez (Rutgers)
Click here for more information: **https://www.grc.org/unifying-ecology-across-scales-conference/2020/**

N-limitation decouples C and N uptake in stream ecosystems

Light is essential to photosynthesis, so organisms that rely on this pathway must fix all the carbon necessary for their maintenance and growth during daytime. In many aquatic systems, C and N uptake seem to be stoichiometrically linked in time down to the hour, with the highest biological uptake of nitrogen occurring during the day. What happens to these stoichiometric relationships though, when N becomes limiting and uptake rates fall? Modeling suggests it is possible for the uptake of C and N to become decoupled in time so that producers can access N during the nighttime as well as the daytime to increase their total N uptake and meet their stoichiometric demands (Appling & Heffernan 2014. Am. Nat.). For our study, we wanted to see if this prediction plays out in the real world.

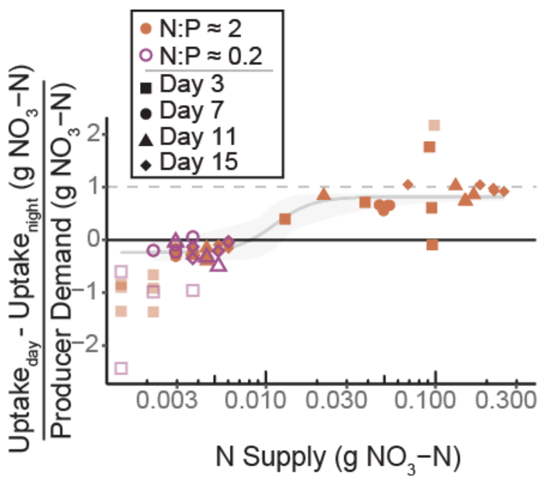


Figure 2b (with modifications). The proportion of biological N demand that was satisfied by the extra daytime N-uptake switched between ~0% at low N supply and ~100% at high N supply.

To test the idea that N limitation affects the timing of N uptake, we conducted a mesocosm experiment. We added N and P to 20 recirculating artificial streams at different N:P ratios and total concentrations to create a range of N and P supplies. On 4 days during the experiment we measured the concentrations of N as nitrate in each stream, every hour for 24 hr, so that we could calculate differences in N uptake between the day and night.

We found that the mesocosms receiving adequate amounts of N had higher N uptake during the day than at night. This extra daytime uptake was approximately what we would expect it to be based on levels of gross primary production and the biomass stoichiometry of producers. The mesocosms that were N-limited, however, showed nearly constant uptake rates over the 24 hr period. Our experiment found that the transition between the two states happened at water column supply/biological demand ratios of about 1.5-2. Limitation can be expected when individual supply/demand ratios become smaller than 1, and the closeness of our results to this ratio tells us that the transition between coupled and decoupled uptake happens fairly suddenly when N starts to become limiting, even though some inefficiencies in uptake from the water column still persist.

Our results indicate that the daily variations in N-uptake that produce nitrate concentration swings in rivers should only occur when N is not limiting. Based on this, we propose that the presence of biologically produced daily nitrate concentration swings in natural systems might be an indication that these systems are not N limited.

From the paper, "*This phenomenon, if extended to the field at hydrologically and biologically stable points in time and in systems where nutrient loading and GPP are well characterized, may prove a useful in-situ measure of nutrient limitation in a range of water bodies.*"

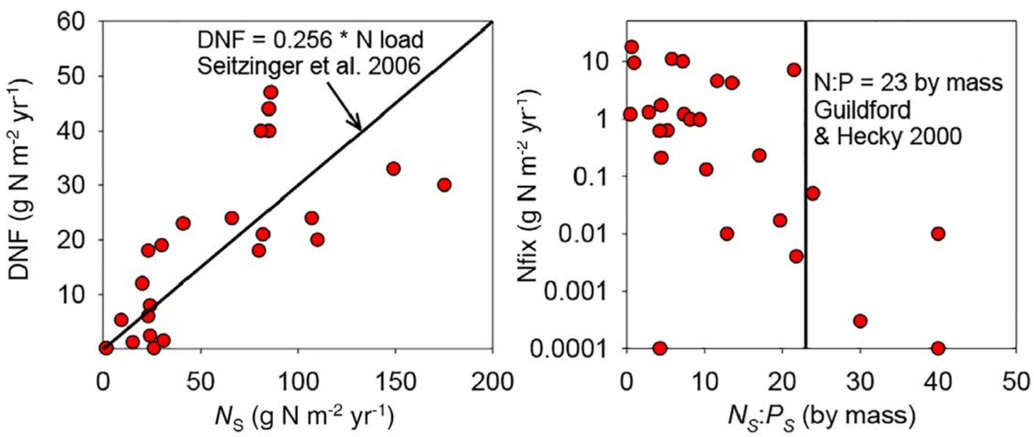
Contributed by Catherine Chamberlin

Chamberlin, C.A., E.S. Bernhardt, E.J. Rosi and J.B. Heffernan. 2019. Stoichiometry and daily rhythms: experimental evidence shows nutrient limitation decouples N uptake from photosynthesis. Ecology. DOI: 10.1002/ecy.2822

Losing N like there is no tomorrow: Implications for lake nutrient stoichiometry

The balance of nutrients in lakes has long been an important research topic in limnology. Yet, this topic has remained quite topical and continues to produce a lively debate. One widely held understanding rooted in stoichiometry that emerged from whole-ecosystem experiments was that lake-wide stoichiometric N:P imbalances could be rebalanced by external N-fixation. In other words, N limitation wasn't expected to persist because N-fixing cyanobacteria make new bioavailable N available to the ecosystem. More recently, researchers have found that cyanobacteria N-fixation rates are often slow and denitrification rates are high, particularly in eutrophic systems. This indicates that N-limitation may persist despite the presence of the N-fixing cyanobacteria and that the net N available in lake ecosystems reflects the balance of N fixation and loss. Despite this, the applicability of this perspective across lakes remains constrained in the absence of broader geographical patterns in N and P cycling among lakes and lake regions.

Scott et al. (2019) address this gap by examining whether lakes (n=1964) in the National Lakes Assessment (NLA) are net sinks or sources of atmospheric N_2. To do this, they modeled N fixation, denitrification and the stoichiometric N:P imbalance in this wide array of lakes. They used parameter values estimated from lakes with more complete datasets or estimated via model fit comparisons. Scott et al. (2019) found that most lakes from the NLA are likely experiencing a net loss of N_2 to the atmosphere, which would create and/or sustain low N availability in the ecosystem. While this was especially true for more eutrophic lakes, oligotrophic lakes also appeared to experience a net N loss and thus remain susceptible to low N:P ratios. They concluded that external N loads likely are important in driving eutrophication in lakes, because denitrification is able to remove more N than diazotrophic cyanobacteria supply. In other words, many eutrophic lakes probably can't balance atmospheric N fixation to match high P loads.



Relationship between denitrification (DNF) and external N loads (left) and rates of N-fixation and external N:P ratios in lakes (right). Note difference in the scale of the Y-axes. Modified Figure 4D from Scott et al. (2019).

From the paper, "*The results of this analysis indicate that biological N-transformations, particularly in more productive lakes, may perpetuate N-deficient conditions for primary production. This result suggests the potential need for a paradigm shift in limnology.*"

Contributed by James Larson

Scott J.T., M.J. McCarthy and H.W. Paerl. 2019. Nitrogen transformations differentially affect nutrient limited primary production in lakes of varying trophic state. *Limnology and Oceanography Letters:lol2.10109. DOI: 10.1002/lol2.10109*

Stoichiometry and vector-borne virus transmission

Have you ever wondered how larval nutrition affects vector-borne virus transmission? Well, look no further than the recent study by Paige et al. (2019) that examined Zika infection rates in *Aedes aegypti* mosquitoes. Larval nutrition was varied by altering the ratio of detritus (low N diet) to animal material (high N diets). Development time, survival, and adult stoichiometry were then related to Zika infection rates after a Zika infected blood meal.

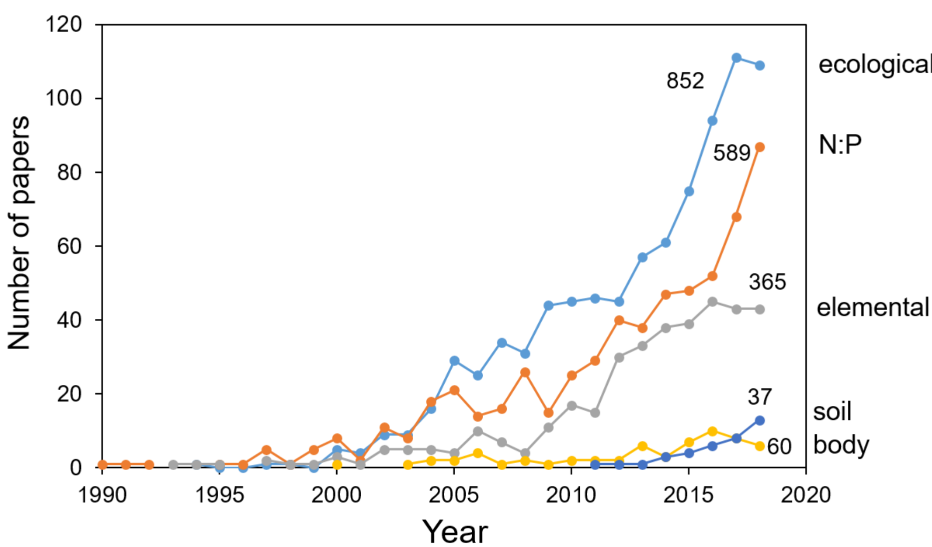
The authors report that larval mosquitoes fed high leaf detritus:animal (low animal content) diets had lower survival rates, longer development time, and weighed less compared to low leaf detritus:animal (high animal content) diets. Mosquito N content was positively correlated with the amount of animal material in the larval diet and negatively correlated with Zika infection and transmission rates. Taking everything together, Paige et al. (2019) conclude that N-limitation in the larval stage reduces survival, but adults that do survive are more likely to transmit Zika and potentially other viruses if they are exposed.

From the paper, "*Given that adults are often limited by nitrogen, this area of research could prove fruitful for linking fine-scale patterns of resource environments to human outbreaks of arbovirus induced disease.*"

Contributed by Nicole Wagner

Paige, A.S., S.K. Bellamy, B.W. Alto, C.L. Dean and D.A. Yee. (2019) Linking nutrient stoichiometry to Zika virus transmission in a mosquito. Oecologia https://doi.org/10.1007/s00442-019-04429-6

What's your favorite type of stoichiometry?



Using each of these terms plus stoichiometry (e.g., "ecological stoichiometry"), we searched the Web of Science for the number of papers published yearly between 1990 and 2018. The earliest paper was on "N:P stoichiometry" in 1990 and all terms showed considerable increases since the publication of Sterner and Elser (2002) Ecological stoichiometry. While "soil stoichiometry" didn't make an appearance until 2011, these papers are beginning to accumulate rapidly in the literature.

Dispatches from the Stoichiometry Session at SFS 2019

As a new school year looms, we here at RM want to take a moment to remember the invigorating spirit of Spring, especially those inspiring moments from this year's ES session, moderated by **Scott Tiegs (Oakland Univ.)**, at the Society for Freshwater Science in Salt Lake City, Utah. Decomposition and harmful algal blooms were hot topics, but we also learned about intraspecific variation in snail stoichiometry and interspecific variation in the effects of parasites on consumer-driven nutrient recycling.

David Costello (Kent State Univ.) used a massive field study to show that decomposition decreased the C:N of cotton strips in streams (but not riparian zones), and decomposition rates were inversely correlated with C:N ratios. **Kevin Kuehn (Southern Mississippi Univ.)** presented a meta-analysis lead by **Hal Halvorson (Univ. Central Arkansas)** that also demonstrated the importance of N in decomposition. They showed that algal priming intensity was strongly positively correlated with dissolved N:P, surmising that increased N lead to the production of more N degrading enzymes.

If that makes you wonder how N:P stoichiometry affects algae, you're in luck. Experiments presented by **Felicia Osburn (Baylor Univ.)** showed how diazotrophic cyanobacteria blooms yielded lower biomass under N limiting (low N:P) conditions and fixed N more efficiently after acclimation to low N conditions. **Lienne Sethna (Indiana Univ.)** took a longer term look at agricultural effects on algal blooms and used 17 years of data to show how high discharge rates earlier in the year increased N:Si ratios, potentially increasing the risk of blooms.

Moving up a trophic level, Amy Krist (Univ. Wyoming) showed how ploidy, genetics, and local adaptation affect intraspecific variation in the P content and growth rates of snails and suggested that selection may drive snails from low P lakes to grow faster than those from high P lakes when P availability is increased. Finally, **Andrew Sanders (North Carolina State Univ.)** brought us to the top of the session's trophic level by showing us, through multiple experiments, that the effects of parasites on host N and P release rates varied dramatically across parasite-host systems likely due to variation in the effects of parasites on host metabolism.

Contributed by Charlotte Narr

Ratios in Retrospect

The research by Professor Ulrich Sommer (GEOMAR, Kiel) on phytoplankton community dynamics is renown among ecologists worldwide and his work has long inspired researchers in stoichiometry. This legacy is well captured by one of his earlier studies (Sommer 1984) that examined how nutrient supply ratios, in combination with delivery method (continuous vs. pulse), affects phytoplankton diversity. This paper has and continues to have a great impact on the fields of trait-based ecology and biodiversity. Since its publication, it has been cited 174 times, with numerous publications related to nutrient limitation and stoichiometry. Surprisingly, there seems a recurring interest in this paper with an apparent periodicity in citations of about 7 years. There also appears to be new interest with increasing citations in recent years, peaking in 2018 (15 citations; Fig.1).

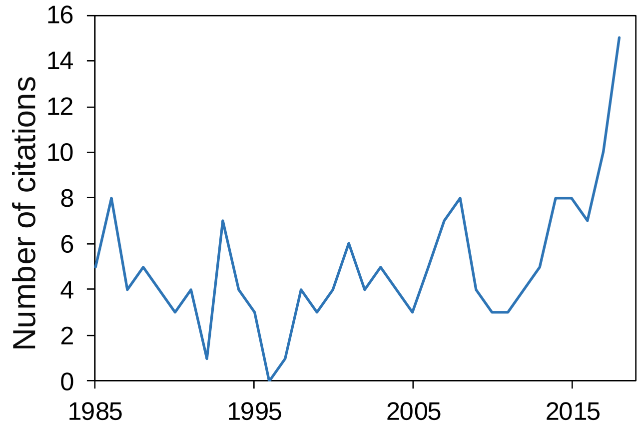


Figure 1. Number of citations by year.
Source: Web of Science

In Sommer (1984), we find an elegant study describing a chemostat experiment where a natural phytoplankton community from Lake Constance was exposed to a gradient in silicate (Si) concentrations combined with weekly phosphorus (P) pulses. This led to a gradient in average Si:P ratios from 0:1 to 200:1. After several weeks, a stable oscillating equilibrium in species biomass developed, with some species revealing oscillations in biomass synchronized with the pulsed P additions, while other species maintained stable biomass. Interestingly, steady state conditions led to loss of species at the extreme Si:P ratios with only a single species able to persist. In contrast, more diversity was maintained across a wide range of Si:P ratios when nutrients were provided under a stable oscillating equilibrium.

This paper is a cornerstone in trait-based ecology, as it describes how traits such as “velocity adapted”, “storage specialists” and “affinity-adapted” determine the response of species to environmental changes, such as fluctuations in nutrient supply. With climate change, extreme events are expected to become more frequent, work like that of Sommer (1984) is still highly relevant even when published over 30 years ago. Particularly as it shows us how to gain a mechanistic understanding of community dynamics due to the role of nutrients, their ratios and the way they are supplied.

Contributed by Dedmer van de Waal

Sommer, U. 1984. The paradox of the plankton: Fluctuations of phosphorus availability maintain diversity of phytoplankton in flow-through cultures 1. *Limnol. Oceanogr. 29*: 633-636.

Did you know?

Vultures have stoichiometry…

Photo by Beks on Unsplash

Griffon vultures are scavengers that feed on ungulate carcasses, which is a diet that can be extremely low in calcium (Ca) and too rich in phosphorus (P). The Ca:P imbalance results if the vultures eat too much tissue (low Ca content) and inadequate quantities of bone (high Ca content), which affects the whole calcium metabolism of these birds. This can be exacerbated when consumed Ca ions are tied up into insoluble calcium phosphate. Low Ca intake can result in metabolic bone disease (MBD), which results in twisted or broken bones and elevated mortality in vulture chicks. MBD can be treated by increasing the dietary content of Ca rich foods (i.e., bones), especially during nesting periods.

Vultures are strongly dependent on the activities of large carnivores, especially on spotted hyaenas, to obtain bones and their fragments. Bone fragments are produced when hyenas crush skeletons and provide a Ca-rich resource to vultures. However, in most ranching areas of southern Africa, spotted hyaenas are not tolerated by ranchers and have been largely excluded. This leaves jackals as the only common carnivore, but they are unable to crush bones. Ranching areas thus largely lack smaller bones that can be used by vultures. The lack of extra Ca supply is evident in ranching areas, where the vultures experience a high incidence of MBD.

One solution to MBD in vultures is to establish "bone restaurants" where carcass skeletons are crushed to provide small bone fragments for vultures (Richardson et al. 1986). Bone restaurants were found to greatly reduce the incidence of MBD in vultures, from 17% to 2.5% after a six-year period. Restaurants have been used as a management tool in combating calcium deficiencies in birds, perhaps with some varying success (Reynolds et al. 2004). They nonetheless provide an interesting example of the importance of dietary stoichiometry and its effects on an animal population.

Contributed by Cecilia Laspoumaderes

Richardson et al. (1986) J. Zool., Lond. 210: 23–43
Reynolds et al. (2004) Ibis 146: 601–614

Contact us by email:
ratiosmatter@gmail.com

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Selected Recent Stoichiometry Publications

Atkinson, C.L., A.V. Alexiades, K.L. MacNeill, A.C. Encalada, S.A. Thomas and A.S. Flecker. 2019. Nutrient recycling by insect and fish communities in high-elevation tropical streams. Hydrobiologia 838: 13–28. doi:10.1007/s10750-019-03973-9

Chen, M., R. Bi, X. Chen, Y. Ding, H. Zhang, L. Li and M. Zhao. 2019. Stoichiometric and sterol responses of dinoflagellates to changes in temperature, nutrient supply and growth phase. Algal Res. 42. doi:10.1016/j.algal.2019.101609

Faithfull, C. and E. Goetze. 2019. Copepod nauplii use phosphorus from bacteria, creating a short circuit in the microbial loop. Ecol. Lett. 22: 1462–1471. doi:10.1111/ele.13332

Gerhard, M., A.M. Koussoroplis, H. Hillebrand and M. Striebel. 2019. Phytoplankton community responses to temperature fluctuations under different nutrient concentrations and stoichiometry. Ecology 00: e02834. doi:10.1002/ecy.2834

Glibert, P.M. 2019. Harmful algae at the complex nexus of eutrophication and climate change. Harmful Algae In Press: 1–15. doi:10.1016/j.hal.2019.03.001

Halvorson, H.M., C.L. Fuller, S.A. Entrekin, J.T. Scott and M.A. Evans-White. 2019. Interspecific homeostatic regulation and growth across aquatic invertebrate detritivores: a test of ecological stoichiometry theory. Oecologia 190: 229–242. doi:10.1007/s00442-019-04409-w

Herstoff, E.M., S.B. Baines, M. Boersma and C.L. Meunier. 2019. Does prey elemental stoichiometry influence copepod movement over ontogeny? Limnol. Oceanogr. In press: 1–11. doi:10.1002/lno.11198

Heyburn, J., P. McKenzie, M.J. Crawley and D.A. Fornara. 2017. Effects of grassland management on plant C:N:P stoichiometry: Implications for soil element cycling and storage. Ecosphere 8: e01963. doi:10.1002/ecs2.1963

Jiang, J., Y.P. Wang, Y. Yang, M. Yu, C. Wang and J. Yan. 2019. Interactive effects of nitrogen and phosphorus additions on plant growth vary with ecosystem type. Plant Soil 440: 523–537. doi:10.1007/s11104-019-04119-5

Kayler, Z.E., K. Premke, A. Gessler and others. 2019. Integrating aquatic and terrestrial perspectives to improve insights into organic matter cycling at the landscape scale. Front. Earth Sci. 7: 127. doi:10.3389/feart.2019.00127

Lapointe, B.E., R.A. Brewton, L.W. Herren, J.W. Porter and C. Hu. 2019. Nitrogen enrichment, altered stoichiometry, and coral reef decline at Looe Key, Florida Keys, USA: a 3-decade study. Marine Biology 166:108. doi:10.1007/s00227-019-3538-9

Martin, R.E. and T. Servais. 2019. Did the evolution of the phytoplankton fuel the diversification of the marine biosphere? Lethaia In press: 1–27. doi:10.1111/let.12343

Ren, Z., D. Niu, P. Ma, Y. Wang, H. Fu and J.J. Elser. 2019. Cascading influences of grassland degradation on nutrient limitation in a high mountain lake and its inflow streams. Ecology 100: e02755. doi:10.1002/ecy.2755

Six, D.L. and J.J. Elser. 2019. Extreme ecological stoichiometry of a bark beetle–fungus mutualism. Ecol. Entomol. 44: 543–551. doi:10.1111/een.12731

Smith, G.R. and J. Wan. 2019. Resource-ratio theory predicts mycorrhizal control of litter decomposition. New Phytol. 223: 1595–1606. doi:10.1111/nph.15884