Ratios Matter

Volume 9 Issue 1 August 2026

Ratios Matter for Ecosystem Ecology since 1986

Daniel Graeber
Helmholtz-Centre for Environmental Research

Reiners' seminal 1986 paper on complementary models for ecosystems turns 40 this year. This paper laid the framework for ecological stoichiometry at the ecosystem scale, is cited in the foreword of "Ecological Stoichiometry" by Sterner & Elser (2002), and has shaped my own thinking on ecosystems ever since. It is an overlooked gem, as relevant now as it was then, and worth reading by anybody working at the ecosystem scale, with stoichiometry or with any other kind of ecosystem model.

Matter Flows

Reiners (1986) argues that ecosystem ecology needs a matter model alongside energy-based models. Energetics cannot explain how matter limits life or why the biosphere has the chemical composition it has. So Reiners built on laws explicitly derived from stoichiometry, and laid it out as a chain of deductions, nine axioms and six theorems in his original flowchart, shown here in reduced form (Fig. 1).

The flowchart shows what one takes for granted if one writes, for example, "the world's biota drives and regulates the global biogeochemical cycles" in a paper introduction: Organisms have a regular composition and matter is conserved, which connects the supply of an element to growth and turns any net change in biomass into a change in the surrounding medium. Reaching the planet takes one further assumption, that biological uptake and release are unique in kind and large enough to set the levels in major abiotic pools. Only then does the biota drive the global cycles.

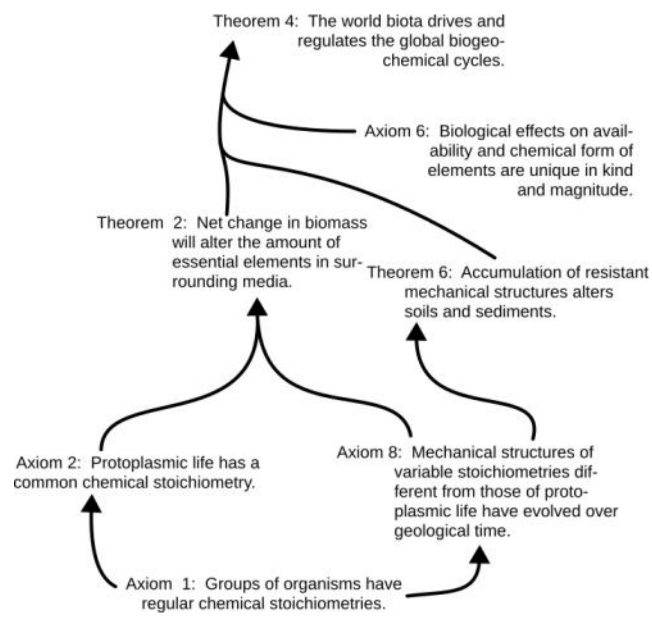


Figure 1. Reiners' (1986) flowchart linking organismal stoichiometry to biospheric biogeochemistry, highly reduced from his Figure 1. I dropped several axioms and theorems for space but kept the original numbering, so each can be traced back to the paper.

Continued on page 3.

Recent Changes at Ratios Matter

Ratios Matter is happy to announce the addition of three new Associate Editors. **Isabelle Andersen** (left) is currently a postdoctoral research associate at Miami University, where she studies nutrient effects on phytoplankton community composition. **Daniel Graeber** (center) works at the Helmholtz Centre for Environmental Research – UFZ in Germany. He studies how C, N, and P move through inland water ecosystems, and how their ratios end up steering ecosystem functioning. **Carly Olson** (right) is a postdoctoral research associate at the University of Wyoming and works on the ecosystem stoichiometry of lakes.

Ratios Matter for Ecosystem Ecology since 1986 continued from page 1.

Forty years on, the chart in Reiners (1986) and the thinking behind it deserve revisiting, since many of its parts are still not fully assessed even in the most recent literature. It could also be extended with boxes and flows that Reiners could not have drawn, as the methods for resolving how organisms interact with their environmental resources keep developing.

Reiners (1986) also provides a word of caution. Energy and matter models together still cannot tell us how many species an ecosystem holds, how energy flow is apportioned among populations, what the biological basis of regulation and homeostasis is, or how ecosystems respond to disturbance. The matter model is one of the complementary approaches, but not the whole answer.

Why ratios matter for ecosystem ecology

I would like to finish with a summary of why I use ratios and why ratios matter for ecosystem ecology. They do three things at once, all following Reiners' logic:

Ratios are why matter can limit life. If organisms could take up elements in arbitrary proportions, nothing would ever be limiting. Fixed proportions, in organisms and in the processes they drive, plus conservation of matter make a supply rate binding. Energetics cannot close that gap, since a joule is a joule and a model with no compositional term cannot generate a limiting nutrient.

Ratios are conservative and evolutionarily variable at the same time. The composition of living cell material is nearly the same across the tree of life, while the departures from it (e.g., shells, wood, bone, chitin, etc.) are systematic and evolutionarily produced. A single type of variable therefore encodes both a universal constraint and an evolutionary record.

Ratios can bridge scales. A single axiom can carry Reiners' argument from Redfield's plankton up to the composition of the atmosphere and down into population ecology on the way. A ratio is a cell property, an organismal trait, a competitive currency, a soil-forming agent and a planetary state variable at once.

To end with Reiners' (1986) own conclusion: "*The most profound result of the stoichiometry of life has been the wholesale reorganization of the biosphere to a chemical state we now regard as normal. The maintenance of a stable climate and chemical environment in the biosphere by the world's biota is perhaps the most unifying and significant phenomenon of ecology*."

Reiners, W. 1986. Complementary Models for Ecosystems. The American Naturalist 127: 59-73.

From Stoichiometry to Metabolism to Nutrient Recycling: The sEXCRETE Working Group

Angélica L. González
Rutgers University

Ecological stoichiometry has transformed our understanding of how the elemental composition of organisms shapes ecological phenomena. Yet one of its most important predictions, that consumers regulate ecosystem nutrient availability through the release of carbon (C), nitrogen (N), phosphorus (P), and other elements, has remained surprisingly fragmented across taxa and ecosystems.

The sDiv working group sEXCRETE (Examining Consumer Resource Exchange in Aquatic and Terrestrial Ecosystems) is supported by the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig. iDiv brings together researchers from different disciplines to advance integrative biodiversity science, and its synthesis working groups foster international collaborations that integrate diverse knowledge, theories, data, and methods to identify general ecological principles across taxa and ecosystems.

Researchers have long used stoichiometric and metabolic approaches to understand how factors such as diet, body elemental composition, body size, and metabolism influence nutrient release by consumers. However, many of these approaches have been developed for particular animal groups, ecosystems, or forms of nutrient cycling. Some focus primarily on excretion, others on egestion, while mechanistic models may require detailed physiological information that is difficult to obtain across diverse species. As a result, predicting nutrient recycling across the enormous diversity of animal life remains challenging.

sEXCRETE aims to bridge these approaches by integrating Ecological Stoichiometry with the Metabolic Theory of Ecology to develop a general mechanistic framework for consumer-driven nutrient recycling. The goal is to identify a common set of physiological processes from which predictions can be generated across animals that differ widely in body size, diet, body stoichiometry, and life history. The framework is designed to be simple and modular, allowing additional biological complexity to be added as data become available while retaining a common foundation for comparison across taxa and ecosystems.

This approach also broadens the way nutrient recycling is considered. Rather than treating excretion and egestion as separate physiological processes, sEXCRETE asks a more general question: How do the elemental demands, composition, and metabolism of animals determine the quantity and ratios of elements they return to ecosystems? Answering this question requires integrating information on body size, elemental composition, metabolism, diet, physiology, and biodiversity across both vertebrate and invertebrate life in aquatic and terrestrial ecosystems.

During its first meeting, participants began assembling complementary data and developing the mathematical framework needed to advance these ideas. A major goal is to determine which controls on nutrient recycling are general across animals and which depend on particular biological or environmental contexts. The group will then explore how these individual-level processes scale through animal abundance, demography, and biodiversity to influence nutrient cycling at population, community, and ecosystem levels.

For the ecological stoichiometry community, sEXCRETE represents an exciting next step: moving from models developed largely within particular taxa or ecosystems toward a common predictive framework for animal-mediated nutrient recycling. Ultimately, the group aims to improve our ability to predict how changes in animal abundance and biodiversity alter nutrient cycling and to strengthen the representation of animals in ecosystem and Earth-system models.

Learn more about sEXCRETE here:

https://www.idiv.de/research/sdiv/working-groups/sexcrete/

sEXCRETE Working Group. Leipzig, Germany. December 2025

Front row (left to right): Amanda Subalusky (University of Florida; Co-PI), Letícia Gonçalves Ribeiro (Universidade Estadual Paulista), Michael Vanni (Miami University), Rana El-Sabaawi (University of Victoria), Angélica González (Rutgers University; Co-PI), Sikander Khare (University of Florida), and Elizabeth Le Roux (Hluhluwe-iMfolozi Park, South Africa; Co-PI).

Back row (left to right): Shawn Leroux (Memorial University of Newfoundland), Nina Schiettekatte (MARE, Facultade de Ciências, Universidade de Lisboa), Roel van Klink (iDiv), Stanley Harpole (iDiv), Jamie Gillooly (University of Florida), and Diego Barneche (Australian Institute of Marine Science)

Jess Hines (iDiv), Ulrich Brose (iDiv), Jim Elser (University of Montana), and Marcus Clauss (University of Zurich) are not in the photo but are part of the working group.

Interview with a Stoichiometrist Michał Filipiak, Jagiellonian University

Nicole Wagner
Oakland University

Francis Brearley
Manchester Metropolitan University

RM: Has your view of ecological stoichiometry changed since you first entered the field? If so, how? MF: Yes. I entered the field thinking of ecological stoichiometry as a powerful theory, but I now see it as a remarkably versatile language for connecting biochemistry, evolution, organismal biology, food webs, and biogeochemical cycling. Once we step beyond its familiar boundaries, we discover how little of this intellectual landscape has been explored and how vast the horizon remains.

RM: What assumptions in your field do you think deserve to be challenged? MF: The assumption that C:N:P captures everything important. It does not: life is built from approximately 25 elements, and their interactions, limitations, and imbalances open questions that three-element stoichiometry alone cannot answer.

RM: What is the coolest fact about insect nutrition or elemental biology that almost nobody knows? MF: In a solitary bee, approximately 55–75% of the phosphorus accumulated during larval development is ultimately packaged into the cocoon rather than being retained by the emerging adult. Therefore, measuring only the adult provides an inaccurate representation of both the bee's developmental demand for phosphorus and its total elemental investment over its lifetime.

RM: What result has surprised you the most during your career? MF: We recently found that mowing can radically reorganise the multi-elemental stoichiometry of an urban lawn. While I expected some effect, I did not anticipate such a significant transformation from an activity that at first glance appeared so innocent.

RM: If you could add one new element to the ecological stoichiometry "core curriculum," what would it be and why? MF: Why stop at one? Life depends on approximately 25 elements, and the greatest explanatory power may lie not in adding another isolated element to C:N:P, but in understanding how the full elemental recipe is assembled, balanced, and constrained.

RM: Is there a stoichiometric pattern in insects that you think deserves much more attention than it currently receives? MF: In the context of herbivore and detritivore needs, the elemental poverty of plant structural matter remains widely underestimated: breaking cellulose, hemicellulose, and lignin into smaller molecules does not create the missing elements required to build an animal. While gut microbes can transform compounds and obtain some nitrogen from the air, they cannot conjure up phosphorus, sodium, copper, zinc, and the other elements necessary for life from matter that does not contain them.

Larva of the wood-eating, longhorn beetle, *Stictoleptura rubra*

RM: Outside of research, what hobby or interest unexpectedly influences how you think about science? MF: Making music taught me that ambitious work is rarely a solo performance. Science, like a good ensemble, depends on different instruments entering at the right moment, listening to one another, and creating something larger than any individual contribution.

RM: What's a paper you've written that you're particularly proud of, even if it isn't your most cited? MF: I am especially fond of the 2023 Ecology paper written with Zuzanna Filipiak and Jeff Ollerton on the role of K:Na balance in bee ecology and evolution. The collaboration was wonderfully creative, and I think the final paper combines a serious elemental problem with unusual clarity and intellectual energy.

RM: What is one result from your research that completely changed the way you think about how insects interact with their environment? MF: While following the multielemental stoichiometry of wood-eating beetles through larval development, we found that their nutritional environment also changes over time, almost as if the dead wood matures alongside the insect. The larva does not experience one fixed stoichiometric mismatch, but a succession of changing constraints created by the joint development of consumer and resource.

RM: If ecological stoichiometry had a mascot, what organism would you nominate and why? (We could all say *Daphnia*, but could be other mascots)
MF: Undoubtedly, Osmia bees are unique: their nests provide easy access to their entire larval food supply, 100% of feces, successive developmental stages, cocoons, and adult bodies. This offers a unique insight into their life histories. It's as if the Osmia genus has been designed specifically to enable us to reconstruct complete elemental budgets. The Osmia genus is also common worldwide, easy to breed, and ideal for diet manipulation experiments. I still cannot understand why it is not the standard stoichiometric model organism.

In Case You Missed It

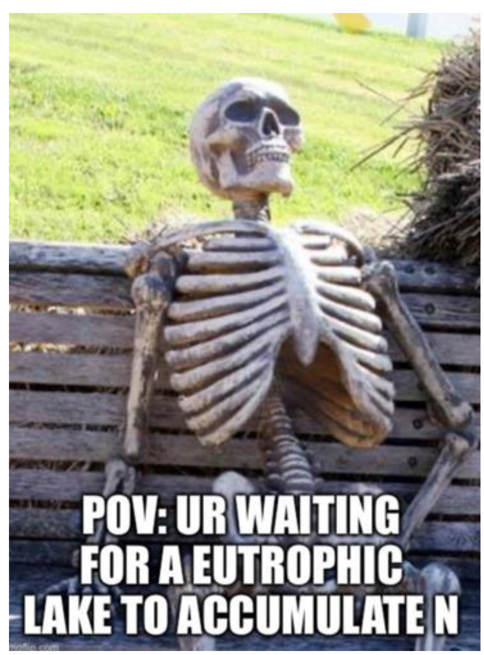
Nitrogen accumulation in eutrophic lakes: Slower than your advisor responding to emails

Isabelle Andersen
Miami University

Foundational studies on ecosystem-scale stoichiometric dynamics suggested that primary production may be proximately limited by nitrogen (N) but ultimately limited by phosphorus (P) because N_2 fixation contributes new N that accumulates relative to P. However, in eutrophic lakes, the time required for a transition from proximate N limitation to ultimate P limitation is not well understood. In Andersen et al. (2025), we fertilized open-top and open-bottom mesocosms with the same amount of P and different amounts of N to achieve 4 target N:P ratio treatments (molar): 2.2, 16, 55, 110 (low N, medium-low N, medium-high N, high N). This fully replicated, multi-year, mesocosm experiment tested three hypotheses regarding how fast N accumulates in the water column to shift the nutrient limitation status by examining phytoplankton biomass (as chlorophyll-a), N_2 fixation (F_{fix}), and N imbalance relative to P (N_I) through time and between treatments.

H1) The shift from N limitation to P limitation occurs quickly (weeks to months) due to seasonal accumulation of N relative to P.
H2) The shift from N limitation to P limitation occurs at a moderate pace (year[s]) due to interannual accumulation of N relative to P.
H3) The shift from N limitation to P limitation occurs slowly (decades) or not at all due to no interannual accumulation of N relative to P.

In the two lowest N treatments, N_2 fixation was unable to fully alleviate N imbalance relative to P to enable equal phytoplankton biomass with medium-high and high N treatments, leading us to reject hypothesis 1 (Fig. 1). And while we saw that fixed N inputs raised N imbalance relative to P in the 2.2 treatment seasonally, that fixed N did not accumulate over multiple years, leading us to reject hypothesis 2. These experimental findings best support hypothesis 3, that eutrophic lakes transition from proximate N limitation to ultimate P limitation slowly (greater than 3 years), if at all, because fixed N did not measurably accumulate relative to P annually, nor was there evidence that N_2 fixation was slowing in response to accumulating N.



These findings suggest that ecological constraints on N_2 fixation, combined with the removal of available N through denitrification, have the potential to keep eutrophic lakes N limited for years- especially eutrophic lakes that have a low N nutrient supply. In contrast to oligotrophic lakes, where fixed N can build up over time, eutrophic lakes see the opposite pattern, as N inputs generally don't exceed N losses from burial or denitrification. This highlights why managing both P and N is crucial for controlling eutrophication and adds to broader discussions about long-term N:P stoichiometry dynamics in freshwater, marine, and terrestrial ecosystems.

From the paper: "…*we found no evidence that N accumulation from N_2 fixation was sufficient to trigger a transition to ultimate P limitation seasonally or across our three-year experiment. Rather, our results indicate that proximate N limitation perpetuates in eutrophic lakes*…"

Andersen, I.M., J.M. Taylor, P.T. Kelly, A.K. Hoke, C.J. Robbins and J.T. Scott. 2025. Nitrogen fixation may not alleviate stoichiometric imbalances that limit primary production in eutrophic lake ecosystems. Ecology 106: e4516

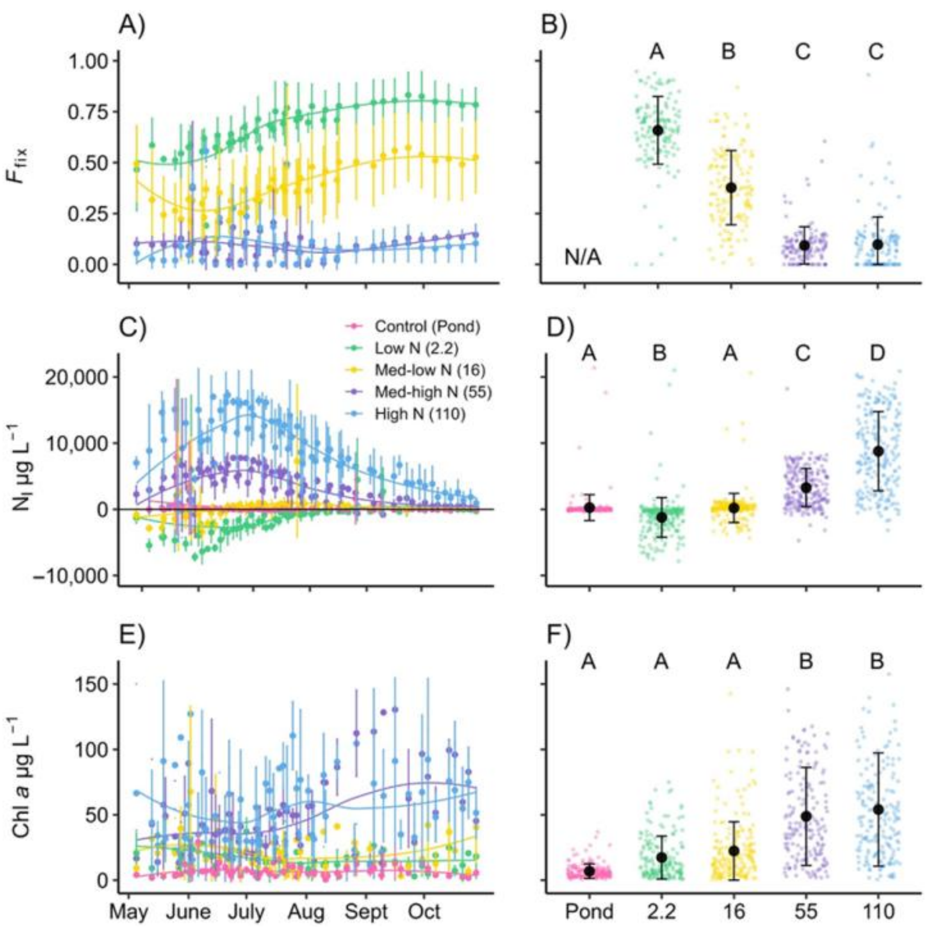


Figure 1. Treatment mean±SD per sample event with corresponding LOESS lines for fractional contribution of fixed N_2 in seston (F_{fix}, A), N imbalance relative to P (N_I, C), and chlorophyll -a (chl-a, E) demonstrate temporal changes throughout the sampling season. The black y=0 line (C) indicates an N_I of 0. Values above the line indicate the N surplus relative to P and values below the line indicate the N deficit relative to P. Data from all three years are plotted using Julian date. The mean±SD for each treatment across all years for F_{fix} (B), N_I (D), and chl-a (F) are represented by the black dot and error bars and are plotted on top of raw data points. Recreated Figure 4 from Andersen et al. (2025).

Treetop Nutrient Pumps

Trophic position, phenology and body size shape nutrient release in migratory songbirds

Catriona Jones
Queen's University Belfast

Studies on the biogeochemical effects of birds have historically skewed toward seabirds and waterfowl, whose colonial nesting and aquatic-terrestrial movements make nutrient subsidies straightforward to measure. Songbirds remain comparatively unstudied despite contributing substantially to avian diversity and undergoing large seasonal shifts in diet and body composition. Ecological stoichiometry predicts that an animal's waste composition should track two things: the elemental content of its diet and its physiological demands for growth and maintenance. Migratory songbirds shift both diet and physiology across the annual cycle, as insect-rich spring diets give way to fruit-heavy fall foraging ahead of fat storage for migration.

In this paper, Chen et al. (2026) sampled waste from 151 individual songbirds across 31 species at a stopover site on Lake Ontario. Sampled material was from birds captured over two days during both fall 2021 and spring 2022. Because bird waste combines excreted and egested material into one product, the authors could measure C, N, and P content and stoichiometric ratios without the excretion-versus-egestion split that complicates comparisons across other vertebrate groups. They used δ15N in waste as a short-term proxy for trophic position and tested it alongside body mass and season in linear mixed-effects models with species as a random intercept.

Trophic position correlated positively with %N and negatively with C:P ratios in waste material, matching expectations that insect-heavy diets result in the release of more N and P than fruit-based ones. Season produced the same pattern from a different angle: birds released material with higher %N and lower C:N ratios in spring, when they fed at higher trophic levels, than in fall, when diets shifted toward carbon-rich fruit ahead of migration (Fig. 1). Body mass complicated the picture. Fall birds carried higher fat scores, and body mass had its strongest effect on C, N and C:N ratios in released material in that season, suggesting that fat accumulation for migration reshapes nutrient excretion independent of diet.

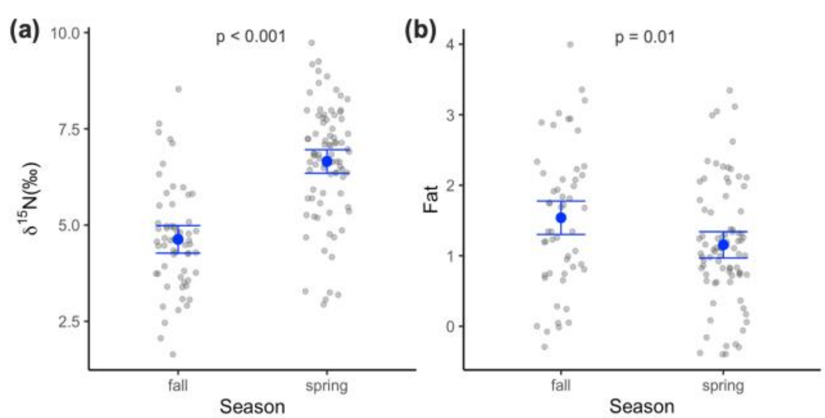


Figure 1. Seasonal differences (spring vs. fall) in (a) $\delta^{15}N$ of songbird waste (reflecting variation in trophic feeding position) and (b) fat score of birds (reflecting variation in fat storage). Recreated from Figure 4 in Chen et al. (2026).

Trophic position and body mass were also negatively correlated in the dataset: heavier species such as Grey Catbird and Swainson's Thrush fed at lower trophic levels than smaller, more insectivorous species like Blackpoll Warbler, leaving the two variables difficult to fully separate even where both remained significant predictors.

The authors position their results as a foundation for scaling songbird nutrient contributions to stopover and breeding habitats, an area of biogeochemistry still dominated by seabird and waterfowl studies. With well over half of North American migratory bird species in decline, tying diet, phenology, and body size to nutrient release gives conservation arguments for stopover habitat a strong mass balance perspective.

From the paper: "*With approximately 58% of 419 North American migratory bird species experiencing declines due to human impacts, understanding their zoogeochemical roles is essential for appreciating the broader consequences of biodiversity loss and emphasizing the influence of conserving and restoring migratory birds as natural nutrient pumps."*

Chen, L., A.S. Flecker and E.S. Duvall. 2026. Diet, phenology and body size shape nutrient release by songbirds. Functional Ecology, 00, 1–13. https://doi.org/10.1111/1365-2435.70275

Stoichiometry at ASLO-SIL 2026 Joint Meeting

There was no shortage of stoichiometry at the recent ASLO-SIL meeting in Montreal, Quebec, held in May 2026. There were special sessions honoring the careers of two top-notch stoichiometrists: Jim Elser and Jim Cotner. For both sessions, there was a fantastic line-up of former students, esteemed colleagues, and past collaborators, who spoke about the influence of both Jims on limnological research, their role in the development and application of ecological stoichiometry, and their love of great science (mostly on ratios). Our new AE, Isabelle Andersen, was the lead organizer of an entire special session dedicated to ecological stoichiometry: *C, N, P, and Stoichiometry Tea: The hottest insights on ratios from organisms to ecosystems.* This session included excellent talks and posters that covered a wide variety of emerging stoichiometric topics ranging from nutrient limitation in a shallow Chinese sub-tropical lake to the stoichiometry of snow algae. Overall, it was great to see so much exciting new stoichiometry at the meeting. Great job to all of the organizers and presenters.

The Green Consumers: What Plant Parasites Reveal about Terrestrial Stoichiometry

Luis Y. Santiago-Rosario
University of Minnesota

Although decades of research have evaluated how terrestrial consumers acquire and regulate carbon, nitrogen, and phosphorus, we still know very little about the role of the broader ionome in trophic interactions, especially under natural conditions. Plant parasites provide an exceptional system for addressing this knowledge gap because they function as both consumers and producers. Hemiparasitic mistletoes obtain water, nutrients, and even some carbon directly from their plant hosts while maintaining their own photosynthesis, providing a natural experiment for understanding how terrestrial consumers assimilate, concentrate, and regulate their **ionomes**.

In a recent manuscript (Santiago-Rosario et al. 2026), we quantified the concentrations of 14 elements in 168 Australian mistletoe-host pairs spanning 90 species combinations. Rather than simply comparing elemental concentrations, we combined **ratios of bioconcentration factors** with measures of **stoichiometric regulation** (log-log scaling relationships). We used bioconcentration ratios to identify which elements the mistletoes preferentially accumulated or excluded from their hosts, and we used the measures of regulation to reveal whether those elements are maintained through physiological control or simply reflect resource availability. This dual approach revealed striking differences across the ionome. Mistletoes consistently bioconcentrated potassium, sodium, boron, copper, and phosphorus while under accumulating iron and nitrogen (Fig. 1).

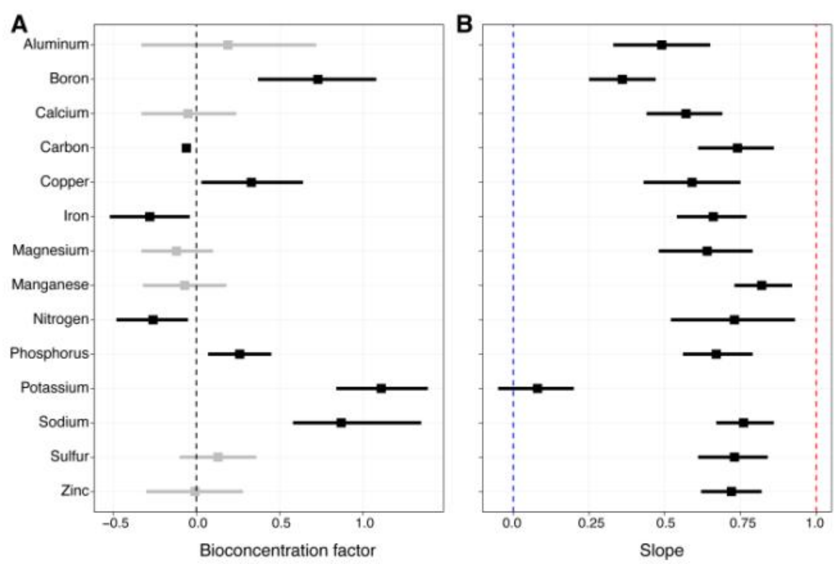


Figure 1. Bioconcentration ratios (A) and stoichiometric regulation (B) of 14 elements in Australian mistletoes relative to their hosts. Together, these metrics distinguish elements that are selectively accumulated from those that are tightly regulated across host species. From Santiago-Rosario et al. (2026).

Contact us by email:
ratiosmatter@gmail.com

Find us on the web:
ratiosmatter.org

Ratios Matter is a non-profit, informational newsletter that is independently published primarily for news and educational purposes. We will automatically send you each new issue; send us an email requesting your free subscription. Comments, suggestions, and submissions including photos, graphics, and paper summaries are always welcome. Contact us at **ratiosmatter@gmail.com** with your submission ideas.

However, accumulation alone only told part of the story. Potassium was not only highly enriched but also tightly regulated in mistletoe across host species, suggesting that maintaining elevated potassium concentrations is a fundamental physiological requirement of the mistletoe lifestyle. In contrast, sodium also accumulated strongly, but it closely tracked host concentrations, indicating much weaker physiological regulation (Fig.1). Importantly, these patterns remained robust after accounting for spatial autocorrelation, host family, mistletoe species identity, and host-mistletoe species pair.

Our findings illustrate how combining **bioconcentration ratios** with measures of **stoichiometric regulation** provides a more complete understanding of trophic stoichiometric relationships than either metric alone. Beyond mistletoes, this framework provides a general approach for understanding terrestrial consumer-resource interactions. By moving beyond carbon, nitrogen, and phosphorus to consider the broader ionome under natural conditions, we can better uncover the physiological mechanisms linking trophic interactions, evolution, and ecosystem functioning.

From the Paper: *"By linking elemental imbalances across individual, community, and ecosystem levels, our results highlight the integrative role of stoichiometric theory in understanding the biology of parasitic plants and their ecological consequences.*"

Santiago-Rosario, L.Y., K.E. Harms and S. Mathews. 2026. Stoichiometric mismatches between Australian showy mistletoes and their hosts: You are what you assimilate. Ecosphere 17: e70717. https://doi.org/10.1002/ecs2.70717

Communicated by: **Charlotte Narr**

A *LOT* of Stoichiometry at the Extremes: Building the Limiting, Optimal, Toxic Continuum

Angie Peace
Virginia Tech

What if we could predict how aquatic life responds to essential-toxic elements across the entire concentration spectrum from nutrient limitation to lethal toxicity? To tackle this challenge, our working group, led by David Costello (Kent State), Angela Peace (Virginia Tech), Elizabeth Herndon (ORNL), and Travis Schmidt (USGS), brought together ecologists, ecotoxicologists, geochemists, and applied mathematicians from academic, federal, and national laboratory institutions. Supported by the USGS John Wesley Powell Center for Analysis and Synthesis with additional funding from the Consortium of Universities for the Advancement of Hydrologic Science, Inc. (CUAHSI), our team gathered in Fort Collins for our second meeting in June 2026.

Together, we advanced our new framework: the Limiting, Optimal, Toxic (LOT) Continuum. Building on classic subsidy-stress theory, the LOT Continuum bridges the historical divide between nutrient limitation research and ecotoxicology into a single continuous framework. We identified 13 essential-toxic trace metals and metalloids central to this effort: arsenic, boron, cadmium, chromium, cobalt, copper, iron, manganese, molybdenum, nickel, selenium, vanadium, and zinc. Our goal is to use process-based models to link molecular, physiological, organismal, and community-level stress responses, empowering researchers to quantify bioavailable element concentrations and characterize limiting and toxic thresholds across diverse taxa. Moving beyond single thresholds gives regulators and managers a tool to evaluate both elemental deficiency and excess in restoration planning, risk assessment, and environmental policy. Beyond the conference room, our team had great opportunities to collaborate outside while taking in the Colorado scenery, including a group hike in the Rocky Mountains and bicycle rides around Fort Collins. Stay tuned as we work towards finalizing our manuscripts!