

Ratios Matter

Volume 8 Issue 1

March 2024

WOODSTOICH 5!

CALL FOR APPLICATIONS

Announcing Woodstoich 5! We are seeking enthusiastic early career scientists from across the biological sciences for five days of peace and stoichiometry. We invite applications to participate in the Woodstoich 5 Workshop to be held **September 30 - October 4, 2024** at the Biologische Anstalt in Helgoland, Germany.

Woodstoich is a collaborative, product-driven event that connects early career scientists from diverse backgrounds to produce a novel piece of research expanding the use of ecological stoichiometry (see page 4 for more on the history and inter-workings of Woodstoich). There will be five working groups (full details available at www.woodstoich.org/research-groups), each covering a cutting-edge topic integrated with ecological stoichiometry. Working groups will meet remotely on a weekly/biweekly basis to produce a complete first manuscript draft prior to the in-person event on Helgoland. At the in-person event, manuscripts will be finalized and undergo rapid peer review in *Frontiers in Ecology and Evolution*.

Prior research in ecological stoichiometry is not mandatory (though basic familiarity with ecological stoichiometry theory is strongly suggested), we encourage anyone with an interest in the biological significance of elemental ratios of organisms and the environment to apply. Enthusiasm for the working group topic is the most important trait in a potential group member. Thus, we encourage people to apply for the project(s) that most interests you.

Required qualifications: We are seeking applications from current PhD candidates and postdocs, but applications from other early career scientists (e.g., assistant professors) will also be accepted. Applicants should have no prior participation in earlier Woodstoich workshops.

Expectations: Group members should expect to commit to working with their group starting in April 2024. During the months leading up to the workshop, working groups will advance their projects with the strongly-stated goal of arriving at the workshop with a fully written draft of their product. *Continued on next page.*



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Did you know?

Some termites species build large and long-lasting mounds that can be >9 m in diameter and over 4000 years old. In a recent paper, Jouquet & Brouand (2023) hypothesize that the building of termite mounds could have a stoichiometric explanation as well! The paper suggests that termites obtain sodium from soil in deeper horizons as the upper horizons are sodium deficient. This could explain why they bioturbate the soils and create the spectacular mounds seen in many tropical regions.

Jouquet, P. & A. Brouand. 2023. Bioturbation as a means to circumvent sodium limitation by termites? Suspected processes and ecological consequences. *Biology and Fertility of Soils*: 59:567-570



Source: <https://www.flickr.com/photos/93452909@N00/3491333666>

Woodstoich 5- Continued from page 1.

Application Materials: To apply, complete the application page at www.woodstoich.org/apply. In this form, please submit a curriculum vitae, contact details of two references, and a letter of interest (1-page maximum) as a single PDF file **by 27 March 2024**. The letter of interest should outline your experience and/or interest in ecological stoichiometry, your specific interest in your preferred project(s), and how your training/background and skills would contribute to the project.

Logistics: There are no registration fees for this event, and accommodation and food on Helgoland will be covered. Participants will need to cover their own transportation costs to Helgoland, which is accessible by a daily ferry from Cuxhaven and Hamburg.

Diversity: We encourage applications from all interested candidates, especially individuals who will contribute to the diversity of the workshop. We welcome early-career applications without regard to age, race, national origin, disability, religion, marital or parental status, protected veteran status, military service, genetic information, sexual orientation, or gender identity.

More information is available at www.woodstoich.org

Please direct any questions to the organizers via cedric.meunier@awi.de

One Fish, Two Fish, Elemental Shifts in Fish: Exploring Ontogenetic Stoichiometry

Nicole Wagner
Oakland University

As **stoichiometrists**, we know vertebrates have a high phosphorus (P) content caused by the formation and maintenance of bones. Additionally, we have a general understanding that as organisms grow from embryo to adult, their elemental composition can drastically change. However, the variability of ontogenetic stoichiometric changes among different species is relatively unknown. A recent study published by Downs et al. (2023) in *Ecology* examined the weekly changes in C, N, P, and Ca of 10 fish species from the embryo stage until 10 weeks of age. Data were analyzed by week and % of relative size at adulthood to account for the vast differences in growth rates.

Generally, from the embryo stage until the fish reach about 5 to 8 % of their adult length, their body %C decreases, while their body %N and %P increase. The variation/plasticity in the stoichiometric niche of C, N, C:N, and N:P decreased as the fishes grew. Thus, as fishes age, interspecific competition may increase if the fish have similar diets. While larva fish are hard to identify, excluding this most elementally plastic life-stage in nutrient storage or excretion estimates could under or over estimate the extent that fish populations serve as nutrient sources or sinks.

Downs, K.N., P.T. Kelly, A. Ascanio and M.J. Vanni. 2023. Ontogenetic variation in the ecological stoichiometry of 10 fish species during early development. *Ecology* 104:e1476 <https://doi.org/10.1002/ecy.4176>

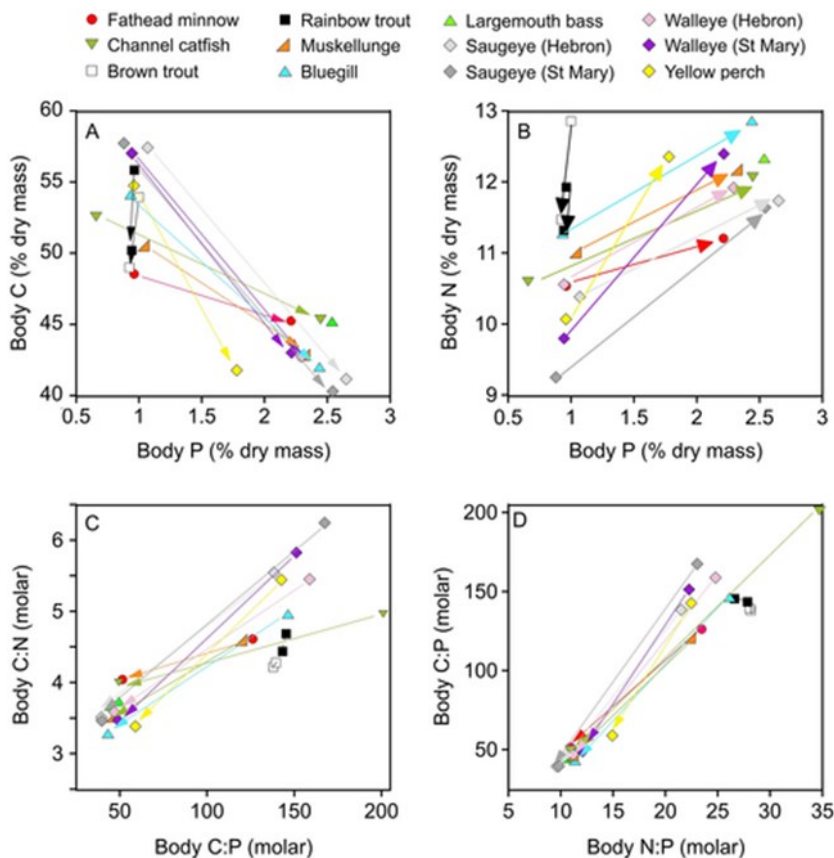


Figure 5 from the paper: “Stoichiometric niche plots. Each species is represented by two points, which is a mean for that species. The arrows show the change in concentration or ratio from the embryo stage (start of arrow) to a relative size of 5%–8% (end of arrow) for that species.”

More about Woodstoich 5

Five Days of Peace and Stoichiometry

Kimberley Lemmen¹ and Robert Buchkowski²

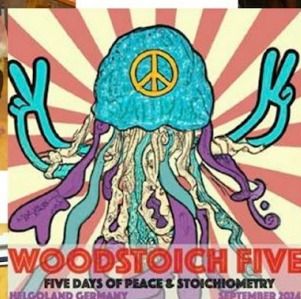
¹University of Zurich

²Western University

Woodstoich is a product-based workshop that has been held every five years since 2004. It aims to expand the use of stoichiometric theory in novel research areas. The workshop provides a space for early career researchers interested in stoichiometry to connect with like-minded peers and write a manuscript that can help improve our understanding of stoichiometry or apply stoichiometric theory to a new research area. The **fifth Woodstoich workshop will be held this September at the Biologische Anstalt in Helgoland, Germany (see page 1).**

History: Woodstoich was first held in Norway in 2004 and is named after the infamous Woodstock music festival in 1969. Both events are gatherings of young people hoping to revolutionize their respective worlds. Following the inaugural event, further Woodstoichs were held in Japan (2009), Australia (2014) and the USA (2019). In total, Woodstoich has brought together over 100 early career researchers (including several of the RM editors) and has thus far produced 23 scientific papers which have been cited nearly 1350 times. Notable papers include contributions on cryosphere stoichiometry (Ren et al. 2019), spatial stoichiometry (Sitters et al. 2015), comparisons between autotrophs and heterotroph stoichiometry (Persson et al. 2010), and physiological constraints (Frost et al. 2005).

How does it work? After members are selected, teams will meet regularly in the months leading up to the workshop to write a manuscript. The goal is to arrive at the workshop with an almost-finished draft. During the first two days of the workshop, teams will complete the manuscript based on feedback from their mentors. At the end of the second day, the manuscript will be submitted to *Frontiers in Ecology and Evolution*. On the third day, all participants partake in a grande adventure - while reviewers read and provide feedback on the submissions. By the morning of day four, everyone will have comments and it will be time to work on the revisions. The goal is to resubmit a revised manuscript by the end of day five.



Who can apply? Early-career ratio enthusiasts are encouraged to apply to become a working group member - prior stoichiometric research is not required. Applications from current PhD students and postdocs will receive priority consideration, but applications from other early career scientists (e.g., assistant professors) will also be accepted. There will be five groups at Woodstoich 5 working on topics that have already been selected by the leader of each group who were selected earlier this year. Applicants will rank the topics they would like to work on. See page 2 for more information on applying.

For more information on Woodstoich 5, visit: www.woodstoich.org

Ren, Z., N. Martyniuk, I.A. Oleksy, A. Swain and S. Hotaling. 2019. Ecological stoichiometry of the mountain cryosphere. *Frontiers in Ecology and Evolution* 7: 360

Sitters, J., C.L. Atkinson, N. Guelzow, P. Kelly and L.L. Sullivan. 2015. Spatial stoichiometry: cross-ecosystem material flows and their impact on recipient ecosystems and organisms. *Oikos* 124: 920-930

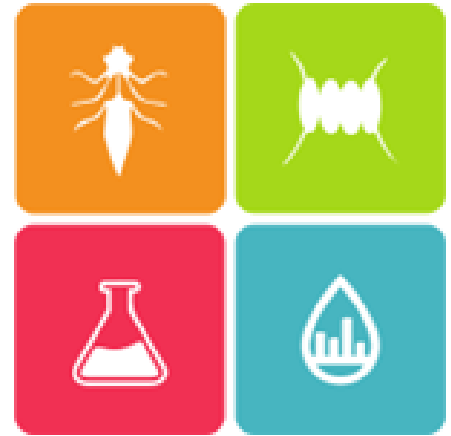
Persson, J., P. Fink, A. Goto, J.M. Hood, J. Jonas and S. Kato. 2010. To be or not to be what you eat: regulation of stoichiometric homeostasis among autotrophs and heterotrophs. *Oikos* 119: 741-751

Frost, P.C., M.A. Evans-White, Z.V. Finkel, T.C. Jensen and V. Matzek. 2005. Are you what you eat? Physiological constraints on organismal stoichiometry in an elementally imbalanced world. *Oikos* 109: 18-28

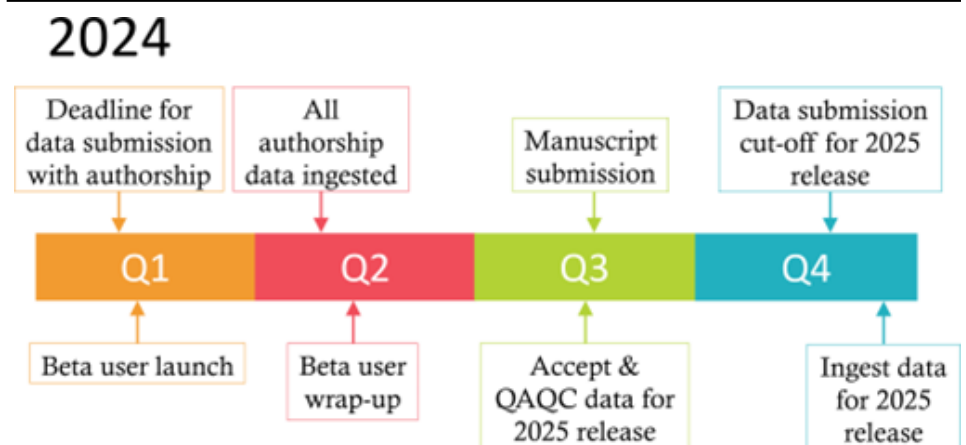
An introduction to the **STOICH** project

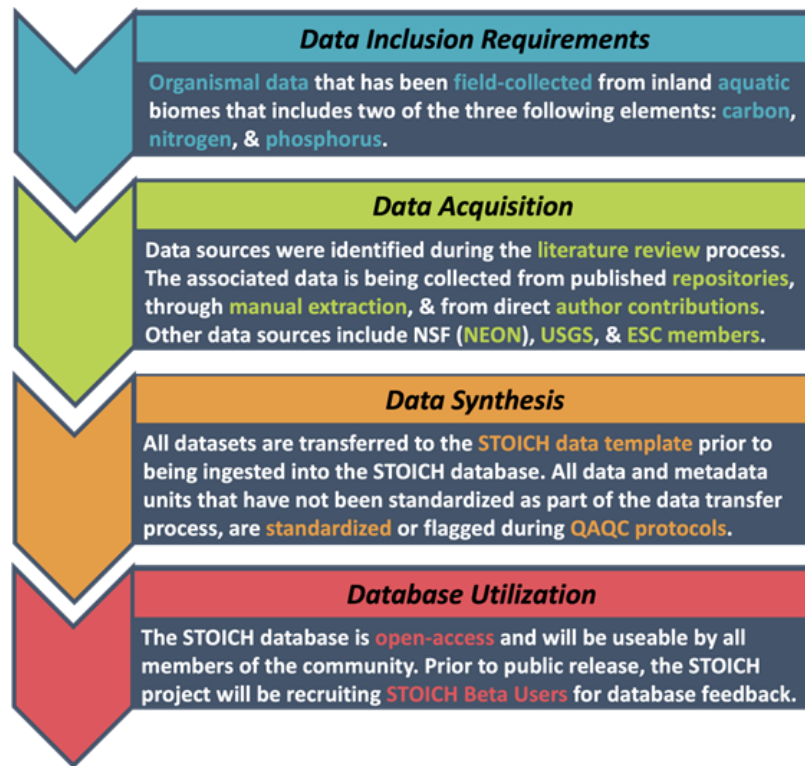
Jessica Corman, Casey Brucker, and Chad Petersen
University of Nebraska

Much of the work on ecological stoichiometry (ES) has happened at the local scale: manipulative experiments in a stream, coordinated bioassays across a lake district, or nutritional studies in a lab. This approach has led to fundamental insights into the role of carbon, nitrogen, and phosphorus in ecological interactions. However, the ES community has been limited in our ability to scale ecological stoichiometry principles beyond the local level due to the inherent difficulties coordinating data collection across regions to continents. This is where the Stoichiometric Traits of Organisms in the Chemical Habitat (STOICH) project has come to help.



The team* behind the STOICH project is leading an effort to build an open-source database compiling information on environmental bioelement concentrations and organismal stoichiometry across lakes, streams, and other inland aquatic ecosystem types. There are three main data sources: published data, contributed data, and newly acquired data from a collaboration with the National Ecological Observatory Network (NEON). To identify published and contributed data, we have spent the last two years looking for relevant literature and data repositories. This search has included the review of over 20,000 journal articles! Datasets that were not already available in public repositories were sought out by contacting authors and making data requests (perhaps you have received one of these requests?). Additionally, we are collaborating with NEON to acquire macroinvertebrate samples for elemental analysis and inclusion in STOICH.





We are currently doing a “soft launch” of our database, a process we call the “Beta User” phase. The multi-step Beta User phase fosters collaboration between project members and potential collaborators by having a select group of engaged students and scientists use the STOICH database. The process walks Beta Users through the STOICH project’s research goals and the use of the beta version of STOICH, introducing them to the STOICH-utilities R package. Simultaneously, the Beta Users will provide our metadata committee with feedback at each step, allowing for revisions prior to the public launch of STOICH in early 2025.

If you’re interested in becoming involved in the STOICH project, you can contact the STOICH Project PI, Dr. Jessica Corman (jcorman3@unl.edu), to discuss research collaborations or reach out to other project members by finding them on the STOICH project website (STOICHproject.org). For more information on the STOICH database structure, how to use the database or how to contribute data, please see SNR-STOICH.unl.edu.

*Project investigators include scientists from the University of Nebraska-Lincoln (Jessica Corman), Middlebury College (Eric Moody), University of Central Arkansas (Hal Halvorson), University of Alaska-Anchorage (Erin Larson), and University of Wyoming (Sarah Collins, Amy Krist, and Catherine Wagner).

What is *Chlamydomonas* made of?

Jana Isanta-Navarro

University of Copenhagen

How does variation in growth rate and resource limitation influence cell morphology, macromolecular composition, and elemental stoichiometry of a **primary producer**? To answer this question, our research explored phenotypic plasticity of elemental and macromolecular pools in *Chlamydomonas reinhardtii*, a green alga. We grew *Chlamydomonas* under controlled chemostat conditions and manipulated growth rate, 20% and 80% of the maximum growth rate, as well as light (limiting or saturating) and N:P ratios (balanced, low N:P and high N:P).

Our research found significant **changes in cell morphology based on growth rate**. Faster growth rates led to smaller cell sizes, and the effect was consistent across different resource limitations. However, low light conditions resulted in even smaller cell sizes compared to slow growth under standard light conditions. This observation aligns with the idea that, under resource limitation, cells may undergo morphological acclimations to optimize nutrient acquisition, as smaller cells are more efficient in light harvesting.

We also delved into **macromolecular composition**, measuring carbohydrates, lipids, proteins, RNA, DNA, chlorophyll, and ATP. Carbohydrates, lipids, and proteins were identified as dominant macromolecular pools, collectively accounting for a significant portion of cell dry weight. The composition of these pools varied with both growth rate and resource limitation, suggesting a dynamic cellular response to changing environmental conditions.

Elemental composition analysis focused on carbon (C), nitrogen (N), and phosphorus (P). We normalized these elements to both cell dry weight and cell abundance to assess variations in elemental stoichiometry. Carbohydrates, lipids, and proteins explained a substantial portion of biomass carbon, while RNA was a major contributor to biomass nitrogen. Phosphorus was primarily associated with RNA, but we noted a potential contribution from unmeasured pools, such as phospholipids and polyphosphates.

Naturally, given the senior author of the paper, we discussed the implications of our findings in the context of the **growth rate hypothesis (GRH)** (Figure 1). The GRH posits that variations in organismal stoichiometry (C:P and N:P ratios) are driven by growth-dependent allocation to P-rich ribosomal RNA.

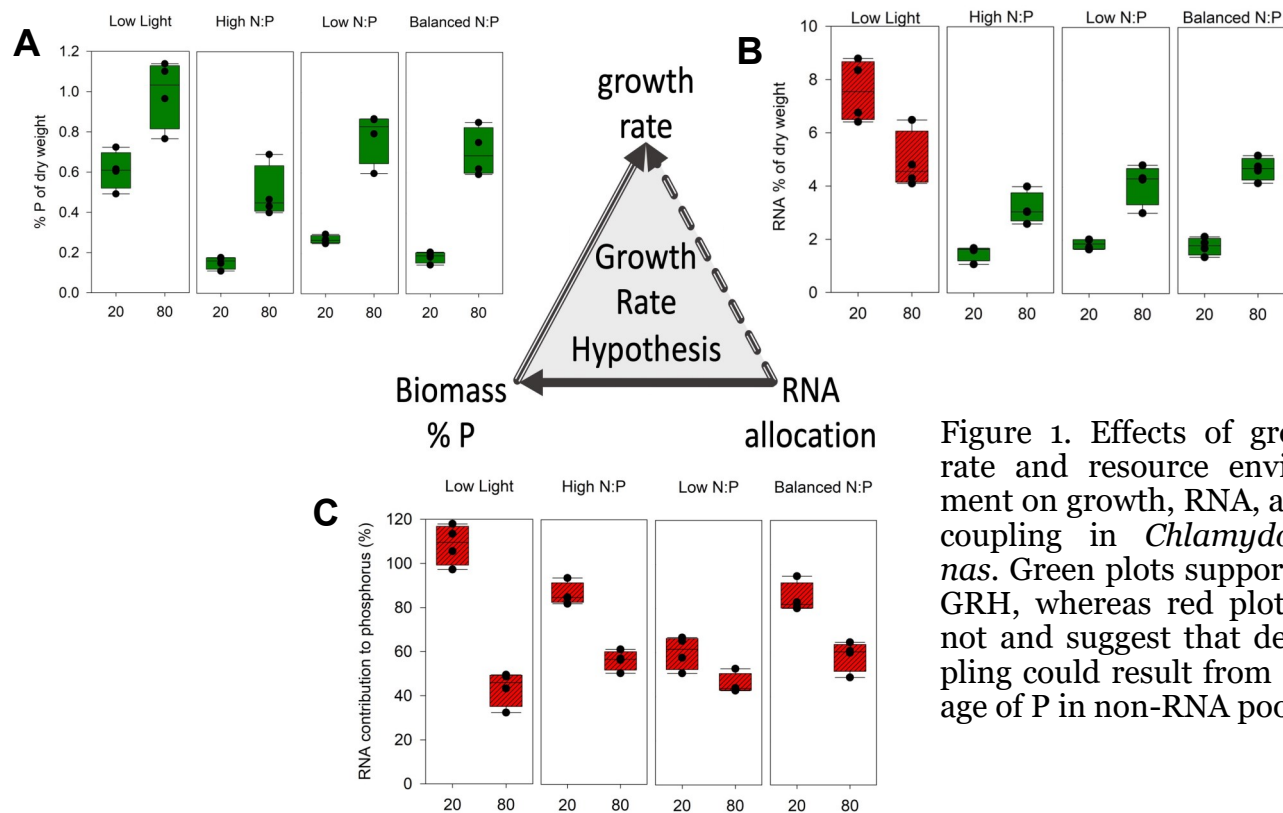


Figure 1. Effects of growth rate and resource environment on growth, RNA, and P coupling in *Chlamydomonas*. Green plots support the GRH, whereas red plots do not and suggest that decoupling could result from storage of P in non-RNA pools.

While our study confirmed an increase in biomass phosphorus content with faster growth (Figure 1a), contrary to the GRH predictions, the contribution of RNA to biomass phosphorus pools did not increase (Figure 1c). This discrepancy suggests that *Chlamydomonas reinhardtii* accumulates phosphorus in unmeasured intracellular pools, potentially storage molecules like polyphosphates.

In conclusion, our publication is for everyone who is looking for a reference of “What is *Chlamydomonas* made of?” under a variety of different environmental conditions and of course for every stoichiometry lover. We provide valuable insights into the complex interplay between growth rate, resource availability, and cellular composition in *Chlamydomonas reinhardtii*. The observed phenotypic plasticity highlights the adaptability of this green alga to varying environmental conditions, and the study underscores the need for a nuanced understanding of ecological stoichiometry, particularly in the context of the growth rate hypothesis.

From the Paper: “The GRH is most robust under high N:P and performs worst under low light conditions, helping to identify the domain of conditions under which the GRH holds or fails to hold.”

Isanta-Navarro, J., L.M. Peoples, B. Bras, M.J. Church and J.J. Elser. 2024. Elemental and macromolecular plasticity of *Chlamydomonas reinhardtii* (Chlorophyta) in response to resource limitation and growth rate. *Journal of Phycology*: 00, 1-14. doi.org/10.1111/jpy.13417

Body size is a better predictor of **intra- than inter-specific variation of animal stoichiometry** across realms

Angélica González

Rutgers University

The size scaling of animal elemental content is generally poorly understood, despite its potential relevance to the structure and function of animals and its impacts on ecosystem functioning. While theoretical research has provided evidence for the size dependence of body phosphorus content, across unicellular and multicellular animals, empirical research on the size scaling of animal stoichiometry, at both inter- and intra-specific levels is still limited. Therefore, we still lack a thorough understanding of the size dependency of animal elemental content. This gap in our understanding is relevant because the existence of general scaling relationships may indicate shared fundamental physiological, physical, and evolutionary constraints governing animal stoichiometry, across realms. Furthermore, due to the potential for body size evolution in response to environmental changes, understanding the link between body size and stoichiometry can be crucial for the predicting the functioning of ecosystems in a rapidly changing world.

To help fill this gap in our understanding, Nessel et al. (2024) recently analyzed close to 10,000 individuals belonging to 1,500 invertebrate and vertebrate species from terrestrial, freshwater, and marine realms; data soon to be released in the “StoichLife database”. They found that body size is a better predictor of intraspecific than interspecific elemental content (N, P, and N:P) of invertebrates and vertebrates. In fact, body size alone explained a substantial fraction of the variance in intraspecific elemental content in both invertebrates (average 42% variance) and vertebrates (average 45% variance). Further, their results revealed that the N content of small marine invertebrates tends to be higher than that of small freshwater and terrestrial invertebrates, and that larger marine invertebrates have lower N content than larger freshwater invertebrates. Contrary to what we predicted from stoichiometric principles of structural allocation, aquatic vertebrates have higher P content than terrestrial vertebrates at an equivalent body size, but scaling relationships did not vary in a predictable manner among terrestrial, freshwater, and marine organisms. Finally, vertebrate and invertebrate species from different realms did not differ in their scaling slopes.

Overall, the expanded taxonomy in this study across terrestrial, freshwater, and marine realms highlights that neither body size nor realm alone are good predictors of the large observed variation in N, P, and N:P across animal species. Furthermore, the substantial variation in scaling relationships within and among animal lineages contrast with other biological attributes such as metabolic rate, which scales strongly with body size across taxonomic groups. This suggests that animal stoichiometry may be more dependent on unique nutrient allocation strategies. The important role of taxonomy in this study, suggests that evolutionary history may play a fundamental role in underlying animal stoichiometry and its size scaling relationships. The strong intraspecific stoichiometric scaling observed for both vertebrates and invertebrates, however, could be attributable to differences in the developmental trajectories of species during ontogenetic growth. The specific underlying mechanisms behind these scaling relationships, however, demand further research.

From the Paper: “Based on the first comprehensive comparison of terrestrial and aquatic animals across vertebrate and invertebrate taxa, our study sheds light on the role of body size, realm, and taxonomy in driving variation in the elemental content of animals. Further research assessing how these scaling relationships vary within and among taxonomic groups, can help uncover the evolutionary and ecological drivers of stoichiometric diversity specifically for terrestrial vertebrates and non-arthropod invertebrates.”

Nessel, M.P., O. Dezerald, J. Merder, K. Andrzejek, U. Brose, M. Filipiak, M. Jackson, M. Jochum, S. Harpole, H. Hillebrand and S.J. Leroux, S.J. 2024. **Body size is a better predictor of intra- than interspecific variation of animal stoichiometry across realms.** *bioRxiv*, pp.2024-01. <https://www.biorxiv.org/content/10.1101/2024.01.22.576743v1.full>

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Are you attending **ASLO 2024**?

Once again, ecological stoichiometry will be on the menu at ASLO! If you are there, be sure to check out these special sessions:

SS14 Exploring nitrogen fixation along the freshwater-marine continuum: A joint ASLO-SFS endeavour.

SS23 Dynamics of reservoir ecosystems in the Anthropocene: Ecology, Biogeochemistry, and Physics

SS27 Highlighting the "bio" in biogeochemistry: Trait-based insights into aquatic ecosystem functioning and its response to global change.

SS31 Get STOICH-ed for ecosystems: ecological stoichiometry at the ecosystem-scale

SS37 Carbon and nutrient fluxes under climate change: Cycling, retention and impacts along the aquatic continuum from land to coastal ocean.

There will also be a special tribute session for stoichiometry's own Bob Sterner

TR01 Bob Sterner: Celebrating A Career Full of Stoichiometry, Lakes of Many Sizes, and Thoughtful Science

Hope to see you all there! Regular registration closes on June 1st.



**Adapting to a
Changing World**

**2-7 June 2024
Madison, Wisconsin USA**

