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EDITED AND REVIEWED BY  
Stefano Colazza,  
University of Palermo, Italy

\*CORRESPONDENCE  
Cédric L. Meunier  
✉ cedric.meunier@awi.de

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# Editorial: Advances in ecological stoichiometry

Cédric L. Meunier<sup>1\*</sup>, Robert Buchkowski<sup>2</sup>, James J. Elser<sup>3,4</sup>,  
Cecilia Laspoumaderes<sup>5</sup>, Geneviève S. Metson<sup>2</sup>,  
Lienne R. Sethna<sup>6</sup> and Maarten Boersma<sup>7,8</sup>

<sup>1</sup>Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung, Biologische Anstalt Helgoland, Helgoland, Germany, <sup>2</sup>Department of Geography and Environment, Western University, London, ON, Canada, <sup>3</sup>Flathead Lake Biological Station, Division of Biological Sciences, University of Montana, Polson, MT, United States, <sup>4</sup>School of Sustainability and Global Futures Laboratory, Arizona State University, Tempe, AZ, United States, <sup>5</sup>Instituto de Investigaciones en Biodiversidad y Medioambiente (INIBIOMA), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET)-Universidad Nacional del Comahue, Bariloche, Argentina, <sup>6</sup>St. Croix Watershed Research Station - Science Museum of Minnesota, Marine on St. Croix, MN, United States, <sup>7</sup>Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung, Wattenmeerstation, List auf Sylt, Germany, <sup>8</sup>Department of Biology and Chemistry, University of Bremen, Bremen, Germany

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## Editorial on the Research Topic

### Advances in ecological stoichiometry

All living things are subject to the law of mass balance across multiple chemical elements. Furthermore, living things cannot form biomass in arbitrary combinations of chemical elements - they are constrained by the chemical composition of major biomolecules (such as nucleic acids, proteins, lipids, and carbohydrates). These fundamental “rules of life” form the basis of the wide-ranging theory of ecological stoichiometry, the study of the balance of energy and multiple chemical elements in ecological interactions (Sterner and Elser, 2002), and of the broader framework of biological stoichiometry, which takes the same perspective and applies it to all levels of biological organization while integrating it into an evolutionary framework (Elser, 2006). Ecological stoichiometry is a highly interdisciplinary field of research, and stoichiometric theory has been increasingly applied across a variety of habitats, organism types, and levels of organization during the past two decades. The stoichiometric approach is becoming increasingly widespread, which suggests that there is ample material becoming available for integration and synthesis in order to consolidate the insights gained during recent years.

Synthesis and integration is especially important for stoichiometric approaches given their exceptionally wide breadth and scope. Accomplishing this synthesis and integration requires a special kind of training that equips emerging scientists with skills and perspectives that allow them to assimilate information from a broad range of disciplines, recognize patterns of commonality, and collaboratively innovate in finding new applications and ways to test new ideas. This training builds on existing insights and paradigms while remaining open to new ways of thinking and innovation. It emerges from an environment of open dialogue and rigorous exchange of ideas and methods. Such

approaches are especially well-suited to early career scientists whose ways of working are not locked into place by tradition or professional obligations. Indeed, bringing early career scientists into an intensive and open environment where their ideas can emerge without the undue influence of senior investigators provides a model for the development and articulation of novel ideas. These are foundational concepts of the Woodstoich workshops on ecological stoichiometry.

Woodstoich seeks to accelerate transformational improvements in our understanding of ecological and evolutionary interactions by engaging the creative energies of early career scientists. The vision of this workshop is to empower early career scientists to invigorate interdisciplinarity by improving and expanding the use of stoichiometric theory. To achieve its ambitious goals, the workshop participants are organized in groups led by late stage PhD candidates, postdoctoral scholars, or very early career researchers who, early in the process, conceptualize each group's project focus and decide on the type of product that will be produced (e.g. meta-analysis, review paper, opinion paper, data product). During the months leading up to the workshop, the groups advance their projects with the goal of finalizing and submitting their manuscripts during the Woodstoich workshop. Each group receives rapid (<24 h for the first round) peer review during the workshop, previously arranged with a large group of international experts. The workshop is organized every five years, and took place in Norway in 2004 (Hessen and Elser, 2005), in Japan in 2009 (Urabe et al., 2010), in Australia in 2014 (Sterner et al., 2015), and in the USA in 2019 (Evans-White et al., 2019). In 2024, Woodstoich 5 took place in Germany at the Biologische Anstalt Helgoland of the Alfred-Wegener-Institut, Helmholtz-Zentrum für Polar- und Meeresforschung.

Woodstoich 5 resulted in the publication of five scientific articles which focused on novel, and expanding fields in the framework of Ecological Stoichiometry. Through their breadth, these articles highlight the potential of ecological stoichiometry to advance our understanding of ecological and evolutionary phenomena at scales ranging from genes to ecosystems:

-Jones et al. focused on the fate of elements within phytoplankton cells, and the effect of external drivers on intra-cellular nutrient fluxes. They described the development of an integrative modeling approach that involves a stoichiometrically explicit model of Macromolecular Allocation and Genome-scale Metabolic Analysis (MAGMA) to improve our understanding of intra- and extracellular nutrient dynamics. This study indicates that the MAGMA modeling tool can be used to gain insights into the effects of resource supplies and other environmental drivers, especially temperature, on C:N:P demand, acquisition, and allocation at the cellular level.

-Olson et al. studied how phytoplankton stoichiometric traits connect resource availability to primary production via organismal metabolism. They used an existing database of

phytoplankton traits and lake ecosystem models to show that phytoplankton minimum quotas for nitrogen and phosphorus significantly influence predictions of lake gross primary production. In their model evaluation, Olson et al. emphasize that parameterization and calibration of phytoplankton stoichiometric traits are critical for obtaining better estimates of lake primary production.

-Schenone et al. conducted a systematic literature review to provide insights into the role of plankton mixotrophic metabolism and nutrient limitation in regulating cellular homeostasis, and community-scale responses to nutrient limitation. At the organismal scale, the review identified a stabilizing effect of mixotrophic metabolism on elemental composition, and that grazing may act as a compensation mechanism under stoichiometric imbalances. At the community scale, mixotrophs were found to increase in abundance relative to strict autotrophs and heterotrophs in nutrient-limited communities, and provide beneficial food for zooplankton grazers by maintaining relatively low and stable C:N:P stoichiometry.

-Bradley et al. developed a dynamic energy budget model to study the effects of stoichiometric imbalances on populations made up of individuals that have heterogeneous traits, and on feedbacks between consumer populations and environmental nutrient cycling. Using this case study, Bradley et al. demonstrated how heterogeneity in resource stoichiometry, and the ability of consumers to respond to such heterogeneity under nutrient limitation, can have variable effects on population dynamics and consumer-driven nutrient cycling.

-Reeves et al. reviewed the capabilities and limitations of optical remote sensing to quantify elements in terrestrial and aquatic systems. This approach enables the study of the elemental composition of Earth's surface over broad spatial extents by detecting reflected electromagnetic radiation. When applied under the framework of ecological stoichiometry, spatially and temporally explicit measurements of elemental composition can contribute to a better understanding of the drivers of ecological processes and variation over space and through time. Reeves et al. provide a practical guide for scientists to quantify elemental ratios, discuss remote sensing as an emerging tool in ecological stoichiometry and pose a set of emerging questions which integrate remote sensing and ecological stoichiometry is uniquely poised to address.

These publications highlight how the Woodstoich format offers a successful way to advance knowledge in a field. An emerging theme from the 2024 Woodstoich workshop was working across scales. Jones et al. and Schenone et al. explore how understanding internal cellular mechanisms can lead to larger-scale insights at community or ecosystem levels. Olson et al. and Bradley et al. explore, empirically and theoretically, how individual trait variation can help predict community and ecosystem level stoichiometry. Finally, Reeves et al. explores how measuring stoichiometry at

larger-scales can contribute to a finer understanding of how smaller-scale stoichiometric mechanisms play out. The success of this, and past Woodstoich workshops, is also due to the quality and diversity of its early-career participants. The Woodstoich format contributes to the development of a global community of scientists, which, as past workshop attendees indicate, will surely continue to collaborate into the future. Furthermore, the continued success of the Woodstoich workshops underscores the fundamental importance of ecological stoichiometry and demonstrates how applying this framework across diverse approaches is crucial for linking the elemental composition of organisms and their environment to ecological processes and nutrient dynamics across various biological and spatial scales.

## Author contributions

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