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DATA ARTICLE

Limno-STOICH: A comprehensive database linking the elemental stoichiometry of organisms with inland aquatic habitats

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Scientific Significance Statement

All living things are made of the same building blocks: elements like carbon, nitrogen, and phosphorus. Based on decades of scientific research, we know that the ability for organisms to get these elements from their environment or their food can have profound impacts on organismal growth, biodiversity, and overall ecosystem production. Yet, much of this earlier work has been done at the small scale: within a lake or forest in a specific environment. To support studies to understand the larger scale regional and global constraints of elemental cycles on ecosystems, we have built the Limnology Stoichiometric Traits of Organisms in their Chemical Habitat (Limno-STOICH) database. The database contains information on the elemental contents of over 50,000 organisms or living material found in lake, river, wetland, and other inland aquatic ecosystems. These data represent all seven continents and over 190 distinct data sources, complemented by extensive spatial, temporal, taxonomic, and water chemistry information.

Abstract

All organisms contain carbon, nitrogen, and phosphorus in widely ranging amounts and proportions. Integrating existing datasets enables quantification of this variation at global scales. Such efforts could leverage ecological stoichiometry theory, the study of elemental supply and imbalances in ecological interactions, to connect ecological drivers and taxonomic constraints to ecosystem structure and function. Towards this goal, we developed the Limnology Stoichiometric Traits of Organisms In their Chemical Habitats (Limno-STOICH) database. The Limno-STOICH database includes 51,576 observations of organismal elemental stoichiometry from >3100 rivers, lakes, wetlands, and other aquatic ecosystem sites on seven continents, derived from 190+ sources. It also includes extensive spatial and temporal metadata to link elemental stoichiometry with ecosystem type, trophic status, etc., and information on organismal data (body size, taxonomic classifications, stable isotope composition) and water physicochemical parameters. The Limno-STOICH database sets the stage for significant applications across food web ecology, evolutionary ecology, biogeochemistry, and other disciplines.

Background and motivation

All organisms require carbon (C), nitrogen (N), phosphorus (P), and other elements for cellular structures, metabolism, and growth. Supply of any of these biologically essential elements can limit process rates from biogeochemical transformations to organismal growth and reproduction to community assembly (Urabe and Watanabe 1992; Elser et al. 2007a; Schade et al. 2011; Tromboni et al. 2018; Liu et al. 2023). Ecological stoichiometry (ES) theory, the study of the balance of multiple chemical elements and energy in ecological systems (Sterner and Elser 2002), informs our understanding of the drivers and implications of organismal elemental ratio and supply in ecological systems. The ES framework links questions across biological levels of organization because it characterizes interactions between organisms and their environment using a common currency (i.e., chemical elements) grounded in the first principles of conservation of mass and energy (e.g., Hillebrand et al. 2014). While ES theory derived from limnology (Hessen et al. 2013), it has since been applied to study various topics including the toxicity of marine and freshwater cyanobacterial blooms (Van De Waal et al. 2014; Wagner et al. 2023), recovery of biogeochemical processes following fires (Butler et al. 2018), large mammalian control of savannah vegetation dynamics (Sitters and Olde Venterink 2018), and even tumor growth in human cancer (Elser et al. 2007b; Kareva 2013). While meta-analyses have provided greater insight into our mechanistic understanding of ES theory (e.g., Hillebrand et al. 2013; Halvorson et al. 2019; Thomas et al. 2022), our understanding of ecological stoichiometric principles at broad spatial scales remains limited by our ability to coordinate organismal data collection across regional to continental scales (Van De Waal et al. 2018).

We developed the Limnology Stoichiometric Traits of Organisms In their Chemical Habitat (hereafter, “Limno-STOICH”) database to provide a public resource to be used to understand broad-scale patterns in the ecological stoichiometry of organisms and their resources in inland aquatic ecosystems (lakes, rivers, streams, wetlands, etc.). In building Limno-STOICH, we compiled elemental composition data for field-collected organisms from inland waters together with information about different environmental attributes. Our database complements other synthetic efforts that compile stoichiometric data of basal resources (e.g., living autotrophs and/or decomposing organic matter; Robbins et al. 2023), organismal traits (e.g., stoichiometry of fish excretion; Vanni et al. 2017) or across taxonomic domains (e.g., stoichiometry of aquatic and terrestrial animals; González et al. 2025; or marine plankton; Liu et al. 2025). However, Limno-STOICH uniquely connects stoichiometric observations across multiple taxonomic groups and ecosystem components. Limno-STOICH will expand our capacity to address macroscale questions about ecological stoichiometry across biological domains ranging from biogeochemical properties to food web dynamics to organismal ecology and evolution.

Data description

Spatial and temporal distribution of Limno-STOICH

The Limno-STOICH database (v.20250910) contains stoichiometric information about 50,696 organisms from 3112 sites across seven continents (Fig. 1). In the database, the widest spatial coverage across longitudinal and latitudinal gradients and ecosystem types occurs in North America, representing 74% of all sites (2320) and 86% of all sampling events (40,123). Over 42% of the organismal samples have concomitantly collected water chemistry information ($n = 21{,}835$), representing 1706 sites. Notably, Antarctica has a limited number of unique sites (46) but possesses the second-highest number of sampling events (4220), primarily due to the inclusion in the database of extensive time-series data obtained from eight lakes between 1993 and 2022 (Priscu 2022). In terms of ecosystem types, streams are most represented, at 32.4% of unique sites and 34% of sampling events, respectively. Reservoirs, while comprising only 0.9% of unique sites, are represented in a disproportionately high number of sampling events (19.7%), attributable to the long-term monitoring studies in the database (Vanni et al. 2022a).

The earliest records of organismal stoichiometry in the Limno-STOICH database are C : N ratios from 1915 (Birge and Juday 2022). Records for organismal N : P and C : P ratios in Limno-STOICH begin in 1926 (Birge and Juday 2022) and 1992 (Sterner and George 2000; Vanni et al. 2022), respectively; though this is a reflection of data availability at the time of publication rather than scientific progress per se (see Baudouin and Ravera 1972; Olsen et al. 1986; Andersen and Hessen 1991) when observations of organismal N : P and C : P ratios began to be reported, respectively. Over a third of our data contributions come from collections during summer months in the Northern hemisphere (June, July, August). Other temporal trends include basal resource samples peaking in the 1920s and again in the 2000s; and consumer samples peaking in the 1990s and 2000s. More than 100 sites have organismal data spanning more than 5 yr, with long-term data available for seston, periphyton, Mollusca, macrophyte, Insecta, Crustacea, Bryophyte, and detritus for at least one site. The longest datasets spanned 34 yr for the Emerald Lake in California, USA (1983–2016; Sadro 2018), followed by 33 yr for various springs in Florida, USA (since 1989; Briceno 2025), and 29 yr for Lake Bonney, Antarctica (1993–2022; Priscu 2022).

Organismal representation and stoichiometry

We categorized our organismal samples within Limno-STOICH first by type (zooplankton, periphyton, etc.) and then further identified them as either basal resources (living or dead autotrophs) or consumers (heterotrophs), representing 69% and 31% of samples, respectively (Figs. 2, 3). Across resource

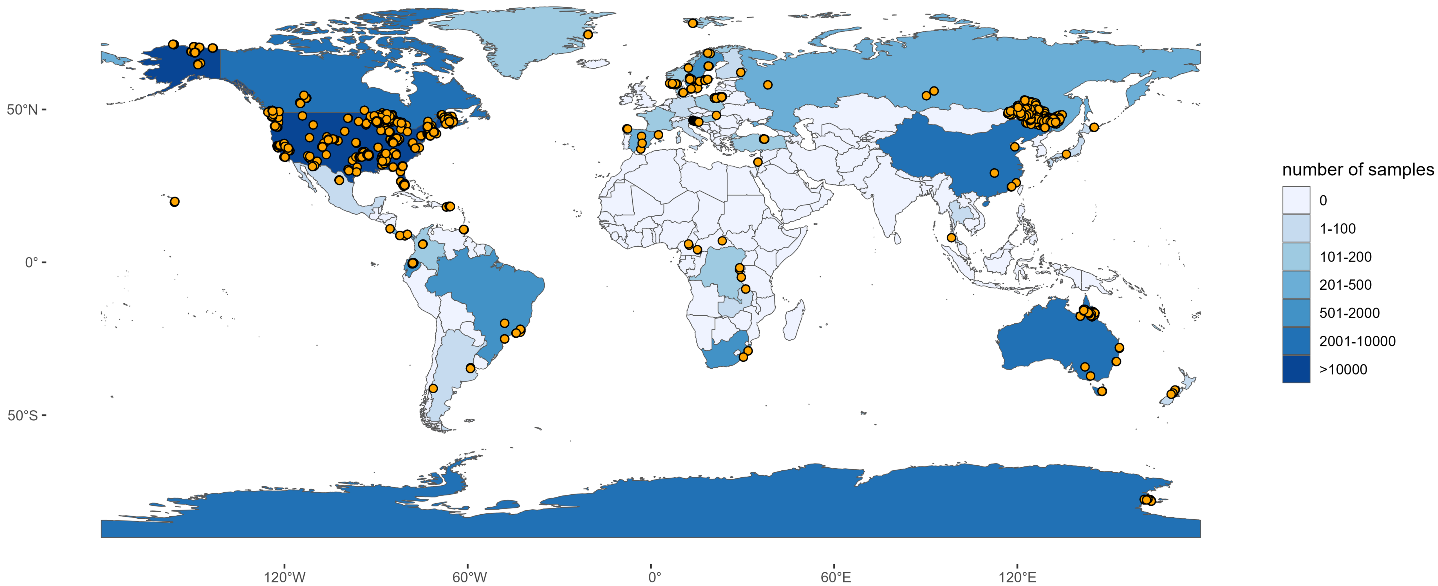

Fig. 1. Geographic distribution of data included in the Limnology Stoichiometric Traits of Organisms In their Chemical Habitat (Limno-STOICH) database. Shading represents the number of organismal samples within each country (darker shading corresponds to more samples), and orange points indicate site locations.

and consumer types, stoichiometric values from seston ($n = 14{,}075$), fine particulate organic matter (FPOM, $n = 5633$), and Insecta ($n = 6667$) are most represented in the database (Fig. 3). Fifty-four taxonomic orders are represented by more than 25 samples, with Trichoptera ($n = 1368$), Poales ($n = 1079$), and Diptera ($n = 1055$) most represented. Additionally, 117 families are represented by more than 25 samples and 218 genera by more than 10 samples. *Dreissena*

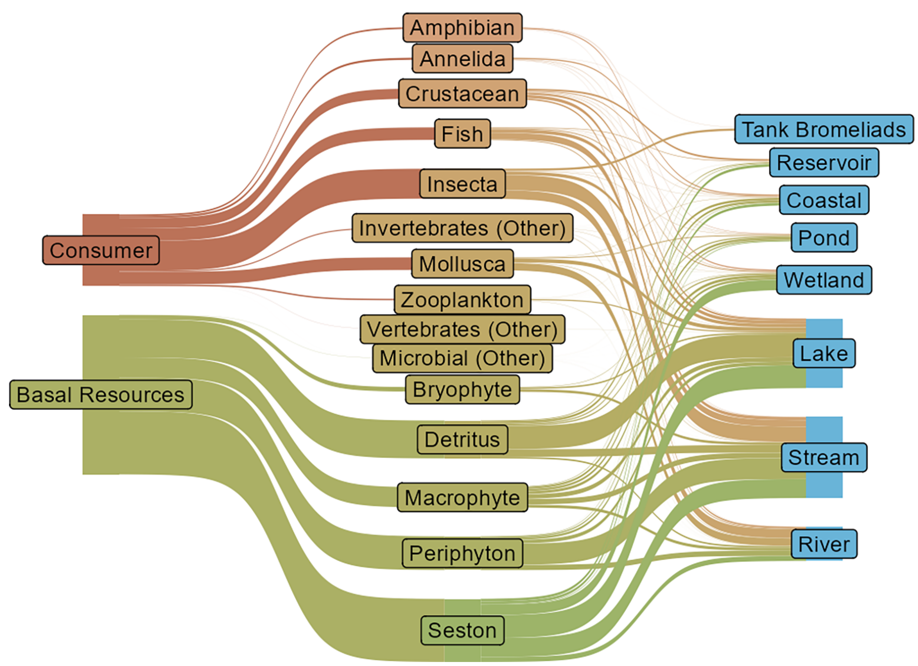

Fig. 2. Sankey diagram describing the diversity of consumers and basal resources across inland water ecosystem types in the Limnology Stoichiometric Traits of Organisms In their Chemical Habitat (Limno-STOICH) database, with each line representing a single organism type. Line thickness correlates to the number of samples represented by each group.

polymorpha (zebra mussels) and *Cyclonaias* spp. are represented by 656 and 371 sample points in Limno-STOICH, respectively, largely from Naddafi et al. (2012a).

Carbon-to-nitrogen ratios are the most frequent of the three ratios reported, with 95.6% of organisms in Limno-STOICH having C : N ratios but only 45.4% or 48.8% having C : P or N : P ratios, respectively, and 44.7% having all three. Carbon-to-nitrogen and C : P ratios of consumers tend to be lower than those of resources, while N : P ratios are more similar (Fig. 3). Consistent with Cross et al. (2005), across nearly all types of organisms and stoichiometries, basal resource ratios are more variable than consumer ratios (Fig. 3).

Reported methods to determine C, N, and P content varied somewhat. Of 46,838 reported organismal C values, 45.5% entries specified the method of analysis: 99.9% were measured using elemental analysis techniques, and the remainder were measured with alternative methods such as a total organic carbon (TOC) analyzer or loss on ignition. Similarly, for 48,722 values reporting organismal N, 43.6% specified a method, with 99.4% of N values measured using elemental analysis and the remaining 0.6% determined using a TOC analyzer, Kjeldahl analysis, or an unspecified digestion method. The database includes 24,852 values for organismal P content, and 57.6% specified a method for P analysis. We classified the 10 unique methods into colorimetric methods (2.0%), Inductively Coupled Plasma Mass Spectrometry (ICP-MS, 34.2%), Inductively Coupled Plasma Atomic Emission Spectroscopy/Optical Emission Spectroscopy (ICP-AES/OES, 0.8%), and unspecified acid digestion methods (63%, Supporting Information Table S5).

Most elemental values were from single organisms, but some values were pooled from multiple observations: 23.3% of entries indicated whether the observation was statistically pooled or not. Among these, 79.8% represent a single independent measure of an organismal sample, while the remainder summarizes multiple observations.

Methods: Data components and acquisition

We used three strategies to assemble the data for the Limno-STOICH database. First, we partnered with the US National Ecological Observatory Network (hereafter, "NEON"; Nagy et al. 2021) to build a dataset of the stoichiometry of benthic macroinvertebrate, resource, and water from ongoing NEON sampling at aquatic field sites. Briefly, NEON is funded by the US government to collect ecological data from 24 wadeable stream sites, three non-wadeable river sites, and seven lake sites across North America, with sites selected to represent the full breadth of terrestrial biomes and regions across the continent. Previous to our project, NEON did not collect benthic macroinvertebrate samples in a manner that permitted stoichiometric analysis but for 2 yr, they partnered with our project to collect samples for stoichiometric analysis. Once we received benthic invertebrate samples from NEON, we identified, processed, and analyzed them for C, N, and P content. Information about water, primary producers, and resources such as seston were acquired directly from NEON. Second, we conducted a literature review to incorporate relevant stoichiometric data from published manuscripts and repositories. Finally, we collaborated with stoichiometry researchers to add unpublished investigator datasets into our database. The details of our approach for compiling these data sources follow:

Benthic invertebrate sampling and analysis

Community samples of benthic macroinvertebrates were collected from the 34 aquatic sites monitored by NEON in 2021 and 2022. At each site, one community sample was collected from the dominant habitat, according to NEON standard operating procedures (Parker 2023), was frozen and shipped to Middlebury College (Middlebury, VT, USA) for identification and stoichiometric analysis. To target taxa not present at the NEON sites, additional collections occurred in Vermont and Arizona (USA) following the same procedures as NEON. Standard benthic invertebrate sampling collection took place three times per year with some exceptions (e.g., COVID-19 travel restrictions, lack of surface water to sample, and natural disasters). Prior to stoichiometric analyses, samples were thawed, identified to the lowest practical taxonomic level (typically genus), and dried at 60°C for 48 h. All identifications were cross-checked against finalized site- and sampling event-specific taxonomic data from NEON. Discrepancies in identifications were reviewed with specimen photographs or, if photographs were not available or ambiguous, specimen identifications were left at the lowest agreed upon taxonomic level. To determine P (body) content, samples were combusted at 550°C for 4 h, digested in HCl, and then analyzed using ICP-MS at Middlebury College (Costanza-Robinson et al. 2025). To determine C and N (body) content, samples were analyzed using an elemental analyzer at the University of Wyoming Stable Isotope Facility. When possible, individual organisms were prepared separately for analysis, but in many cases, low body mass required pooling multiple individuals from the same community and sampling event into a composite sample to achieve minimum detection limits. A maximum of five replicate samples of each taxon from each community sample were analyzed for P, C, and N, but in many cases, insufficient biomass in community samples limited replicates. This work ultimately generated 984 individual C and N samples and 1483 individual P samples encompassing 185 genera in 93 families.

Literature review, data repositories, and contributed datasets

We conducted literature searches to find published stoichiometric data on May 26, 2021 and July 14, 2022 using Web of Science v. 5.35 with the search terms: TOPIC: (((lake OR stream OR wetland OR river OR freshwater) AND ((carbon AND nitrogen) OR (carbon AND phosphorus) OR (nitrogen

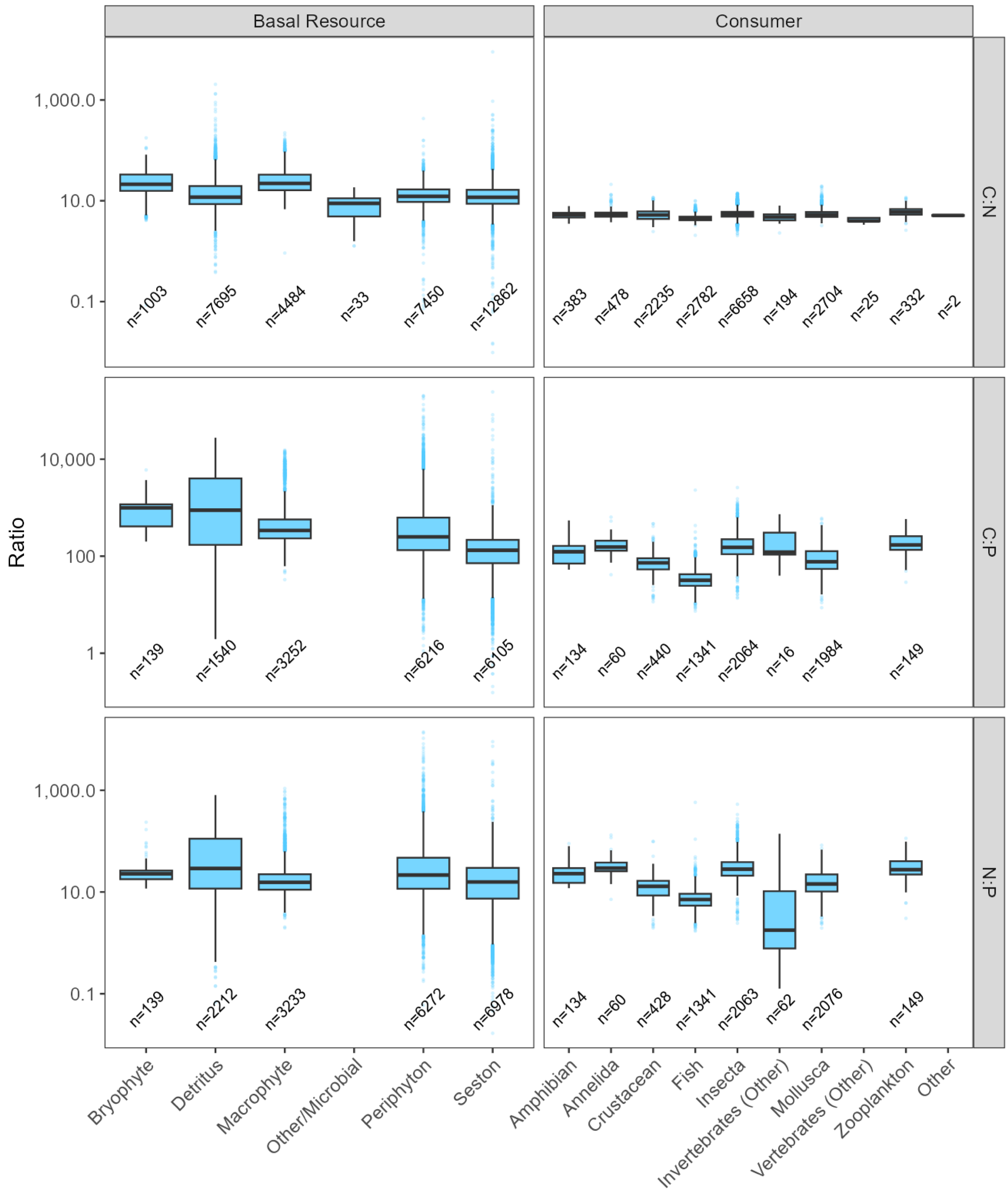

Fig. 3. Variation across basal resource and consumer stoichiometry in carbon to nitrogen (C : N), carbon to phosphorus (C : P), and nitrogen to phosphorus (N : P) molar ratios. For each boxplot, the middle line represents the median, the top and bottom of the box correspond to the first and third quartile values, and the whiskers represent the largest or smallest values, up to 1.5 times the interquartile range, respectively.

AND phosphorus)) AND (stoichiometr* OR ratio* OR nutri*))). From these searches, we identified 22,306 publications that were potentially useful for STOICH. Of these, we surveyed all publications for inclusion criteria (see "Dataset Inclusion Criteria" below). A total of 1154 papers (5.2%) were identified as meeting criteria for the database (see below). Of these, 44 had data available in online repositories or supplemental materials. Of the remaining papers (1110), all first authors and/or corresponding authors were contacted to solicit their raw data. Associated metadata were gained from authors or the associated publication(s). Plot digitizing software with manual extraction may be a useful tool for future expansions of the database (Jelicic Kadic et al. 2016; Aydin and Yassikaya 2022). Additionally, in May 2023, we searched for published repositories associated with online libraries including Dryad, DataOne, and Environmental Data Initiative (EDI; https://edirepository.org/) using the search terms "lake carbon nitrogen ratio" and "aquatic stoichiometry." These search terms were modified from the original search terms due to more limited search tools. After removing duplicate publications, these searches resulted in 5125 repositories. Of these, we identified 126 repository datasets as containing data that fit our requirements. In total, we added 180 published datasets (101 from author contributions and 79 from data repositories) included in data repositories into Limno-STOICH (Sarnelle 1992; Manca et al. 1994; Feijoó et al. 1996; Sterner and George 2000; Brazner et al. 2001; Cloern et al. 2002; Kiffney et al. 2002; Cross et al. 2003; Volk et al. 2003; Paszkowski et al. 2004; Steiner 2004; Descy et al. 2005; Hamilton et al. 2005; Jardine et al. 2005; Gladyshev et al. 2007; Hendrixson et al. 2007; Kanduč et al. 2007; Köster et al. 2008; Piola et al. 2008; Cremona et al. 2009; Elser et al. 2009; Walters et al. 2009; Hanisch et al. 2010; Hanson et al. 2010; Rachamim et al. 2010; Bode et al. 2011; Hossler et al. 2011; Sakamaki and Richardson 2011; Watson and Barmuta 2011; Giling et al. 2012; Jardine et al. 2012a, 2012b; Karube et al. 2012; Kohler et al. 2012; Kominoski et al. 2012; Morse et al. 2012; Naddafi et al. 2012; North et al. 2012; Spencer et al. 2012; Theissen et al. 2012; Volk and Kiffney 2012; Bonin 2013; Jardine et al. 2013; Kling 2013; Koshino et al. 2013; McKnight 2013; Sakamaki and Richardson 2013; Atkinson et al. 2014; Bellinger et al. 2014; El-Sabaawi et al. 2014; Feijoó et al. 2014; Johnson et al. 2014; Lau et al. 2014; Milanovich et al. 2014; Mooney et al. 2014; Peipoch et al. 2014; Zadereev et al. 2014; Georgia Coastal Ecosystems LTER Project and Alber 2015; Gladyshev et al. 2015; Halvorson et al. 2015a, 2015b; Jaffe and Pisani 2015; Kaymak et al. 2015; Liu et al. 2015; Mozsár et al. 2015; Mulholland 2015; Ortega-Cisneros and Scharler 2015; Pringle 2015; Santa Barbara Coastal LTER and Melack 2015; Wang et al. 2015; Biederman et al. 2016; Corman et al. 2016; Díaz Villanueva et al. 2016; Kling and Cory 2016; Kling and Luecke 2016; Knoll et al. 2016; MacAvoy et al. 2016; Myers-Smith and Bonanza Creek LTER 2016; Neres-Lima et al. 2016; Showalter et al. 2016; Syväranta et al. 2016; Ball 2017; Cabrerizo et al. 2017; Chodkowski and Bernot 2017; Dionne et al. 2017; Dudley et al. 2017; Eberts et al. 2017; González et al. 2017; Halvorson et al. 2017; Kristensen et al. 2017; Melvin et al. 2017; Mischler et al. 2017; Neres-Lima et al. 2017; Takacs-Vesbach et al. 2017; Zandonà et al. 2017; Aranguren-Riaño et al. 2018; Diehl et al. 2018; Durston and El-Sabaawi 2018; Fritz and Whiles 2018; Halvorson et al. 2018; Johnson et al. 2018; Kohler 2018; Niwot Ridge LTER and Caine 2018; Sadro 2018; Sterner 2018; Valiela et al. 2018; Zhang et al. 2018; Крылов et al. 2018; Camilleri and Ozersky 2019; Díaz Villanueva 2019; Isanta Navarro et al. 2019; Kristensen et al. 2019; Moody et al. 2019; Pastor et al. 2019; Pearce et al. 2019; Rugema et al. 2019; Salonen et al. 2019; Williams 2019; Wollheim et al. 2019; Bergström et al. 2020; Gladyshev et al. 2020; Isles et al. 2020; Kattel et al. 2020; Pothoven and Vanderploeg 2020; Rojo et al. 2020; Shurin et al. 2020; Caine 2021a, 2021b, 2021c, 2021d, 2021e; Gao et al. 2021; Georgia Coastal Ecosystems LTER Project and Alber 2021; Hu et al. 2021b; Karpowicz et al. 2021; Knapp et al. 2021; Moe et al. 2021; Nocentini and Kominoski 2021; Olid et al. 2021; Price et al. 2021; Sadro 2021; Tonin et al. 2021; Williams 2021a, 2021b; Zandonà et al. 2021; Beck et al. 2022; Bergström et al. 2022; Briceno 2022; Elser 2022; Fogelman et al. 2022; Gao et al. 2022; Goetz and Johnson 2022; Harms et al. 2022; Machado-Silva et al. 2022; Morrison et al. 2022; Oliveira-Cunha et al. 2022; Priscu 2022; Santa Barbara Coastal LTER et al. 2022; Swanner et al. 2022; Vanni et al. 2022; Baruch et al. 2023; Beaufort Lagoon Ecosystems LTER 2023a, 2023b; Gaiser and Tobias 2023; Gotelli and Ellison 2023; Kling 2023; Kohler and McKnight 2023; National Ecological Observatory Network (NEON) 2023a, 2023b, 2023c; Sánchez González et al. 2023; Strickland et al. 2023; Yan et al. 2023; Finne et al. 2024).

Lastly, we solicited contributions of unpublished stoichiometry datasets from stoichiometry researchers. We also encouraged data contributions during our correspondence with publication authors during the literature review (see above) and at scientific workshops and conferences attended by our group members. These solicitations resulted in 11 additional unpublished datasets contributed to Limno-STOICH for a total of 191 datasets.

Dataset inclusion criteria

Data included in the Limno-STOICH database had to meet several basic criteria. First, organisms must have been collected from inland aquatic ecosystems, including tidally influenced waters not extending beyond the coastline. We also included water-filled pools in plants, for example, tank bromeliads, as inland aquatic ecosystems because these pools are aquatic and host multiple trophic levels (González et al. 2011;

Benavides-Gordillo et al. 2019). Second, the organism must have been collected from the field, so any organisms that had been artificially manipulated in the field or spent significant time in a laboratory were excluded. Third, we only included samples of entire organisms; targeted tissues or muscle plugs were excluded. Basal food resources that were sampled as communities were included regardless if living (e.g., phytoplankton or periphyton) or non-living (e.g., leaf litter), if the sample was composed primarily of organic material (e.g., benthic sediments were excluded). Fourth, the samples must include organismal tissue measurements from at least two of the following three elements: C, N, or P. Finally, we only accepted datasets from primary sources to avoid duplication. Datasets meeting all these criteria were entered into the Limno-STOICH data template by a trained project technician and were included in the database (Supporting Information Table S1).

Methods: Database assembly

The Limno-STOICH database consists of seven tables: data entry information (InputFile), data source information (Contact and Source tables), Site, environmental information (SampleEvent and WaterChemistry tables), and OrganismStoichiometry (Fig. 4). The data template includes general information about each column within the tables (Supporting Information Table S2). The data were ingested into an SQL Server and exported into a comma-separated value (csv) file format. Each table uses a unique Id to identify and link entries in related tables.

InputFile Table

The InputFile table exists for data provenance purposes by tracking the status of the data transfer and if any updates to the data template were made during technical validation. The data templates were stored in a Google Drive during database construction, and this table ensures we can track updates from the Google Drive into the database.

Contact and *Source* Tables

The Contact and Source tables contain the list of all sources of data used to build Limno-STOICH with an associated unique identification code ("Id") for each data source. The Contact table includes the name and email of the data provider; most often the communicating author of the publication, but in some cases was another author or data curator. For the published NEON datasets, the contributor was listed as the Limno-STOICH data manager due to the work to prepare the datasets for ingestion and continual efforts to keep them updated in the Limno-STOICH database. The Source table includes information on whether the data were derived directly from a paper or data repository, contributed by the author, or unpublished. Associated bibliographic information (Title, First Author, Journal, Publication Year; Supporting Information Table S2) is included for published papers. In cases where data came from a repository or other source, identifying information is included about the Publisher or URL. If

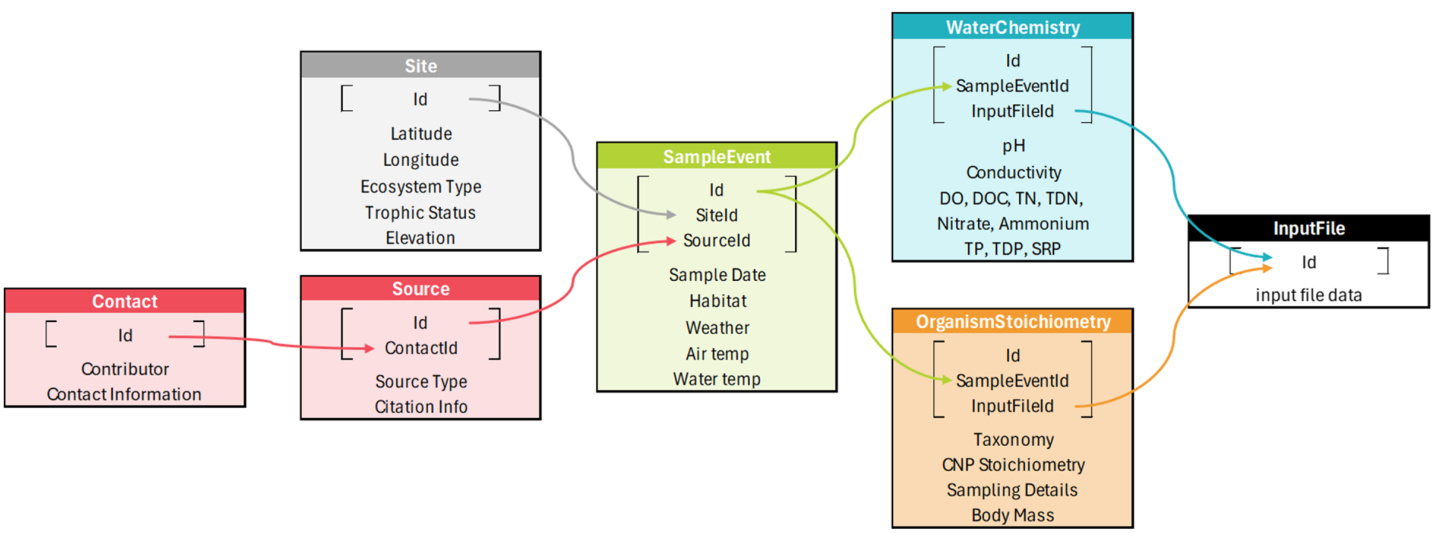

Fig. 4. General structure of the Limnology Stoichiometric Traits of Organisms In their Chemical Habitat (Limno-STOICH) database and connections between its seven tables. Data entry began with entering information about each data source and generating a unique shared Contact and Source Id. A separate table, InputFile, was also generated to track data provenance. Site information for each site within a data source was then entered into the Site table, and each site was given a unique SiteId. SiteIds and SourceIds were carried over into the SampleEvent, where information about the sampling event was entered and a SampleEventId was generated. Information about organismal stoichiometry and water chemistry characterization, along with any supporting data, was then entered into the OrganismStoichiometry or WaterChemistry table, respectively, linked by the Source Id and SampleEventId.

unpublished data were provided, the source is designated using the data curator's name or research group/lab as the author and either the year the data were received or the year the data were entered into the Limno-STOICH template for inclusion in the database.

SampleEvent Table

The SampleEvent table includes specific timing, location, and habitat information and condition for each observation. Sample dates were included in the Sample_Start_Date column when a single date was provided. When a date range was provided for a sample event, we used the Sample_Start_Date and Sample_End_Date columns to indicate the date range. Habitat_type and Depth_m columns further specify the habitat sampled, allowing us to distinguish sample events occurring on the same date. When pelagic samples were collected over a range of depths and numerical values were included, we included the average depth. When pelagic samples were taken at multiple depths, but numerical depth values were not included, sample events were characterized by the layer from which they were sampled ("Pelagic—epilimnion", for example). Air_temp, Water_temp, Cloud_cover, Canopy_cover, and Light columns were included to better characterize a sample event when provided. In instances when multiple water temperatures were provided for the same water chemistry or organismal chemistry data, these water temperatures were averaged. Only sample event rows with links to organismal stoichiometry or water chemistry observations were included in STOICH. However, in some instances, water chemistry observations were not collected on the same day as or were collected more frequently than the organismal stoichiometry data. In these scenarios, water chemistry observations were retained.

OrganismStoichiometry Table

The OrganismStoichiometry table includes metadata about organism taxonomy, body size and life stage, and elemental contents and ratios. First, we classified all organisms by their type which encompasses broad taxonomy- or origin-based classifications of Fish, Insecta, Mollusca, Annelida, Amphibian, Crustacean, Periphyton, Seston, Detritus (FPOM), Detritus (CPOM), Detritus (Other), Macrophyte, Bryophyte, Zooplankton, Invertebrates (Other), Vertebrates (Other), or Microbial (Other), where FPOM and CPOM denote fine or coarse particulate organic matter, respectively. We developed decision criteria to assist in applying these categorizations (Supporting Information Table S3). Next, to increase the spatial accuracy of each organism sampled within a given site, we designated the organism origin as Benthic, Sestonic, Epiphytic, Epixylic, Epipsammic, Epipelic, Epilithic, or Epizootic when such information was available. Then, we included an open entry for trophic mode for each organism. Finally, we included taxonomic levels of Kingdom, Order, Family, Genus, and Species. We did not include Phylum or Class to simplify our data submission process as these can be determined by the other taxonomic information provided. When taxonomic information was not provided (for example, to add Order identification when only Family and Genus were included), we used the National Center for Biotechnology Information (NCBI) taxonomy database, via the R package *taxize* (Chamberlain et al. 2012), to back-fill taxonomic information at higher levels. We also included annotations of "sp." and "spp." for species when provided by data sources, but we listed "NA" when the species was unknown.

For each organismal sample, we recorded whether the data provided represented a Single Individual, Multiple Individuals, or Subsample of a Composite (e.g., homogenized tissues). We also recorded whether a given observation represented an Independent measurement or an Aggregate of multiple samples, in which case we provided the sample size. We included sample sizes as interpreted and contributed by the source author, which typically entailed either the statistical sample number contributing to a mean or the number of individuals homogenized and included within a sample. If a range in the number of individuals was reported, the lowest value was included. We included annotations about developmental stage (open entry) and gut clearance (Cleared or Gut Removed) for each organism sample. We included measurements of organism mass with units. While we required whole organismal data for inclusion in STOICH, we did accept organismal data that represented the entirety of the organism but analyzed in parts, as for macrophytes. These samples are denoted Partial Organism and only represent above ground and below ground measurements. We also interpreted snails or mollusks with the shell removed as Whole Organisms given current conventions in the field. We included information on life stage, if provided; only about a fifth (20.8%) of macroinvertebrate samples contained this information. Even for those macroinvertebrate samples without this information, we expect that most will be in the juvenile stage as the aquatic stage is their juvenile life stage (some exceptions would be insects with aquatic adult life stages, like whirligig or riffle beetles).

Finally, for C, N, or P contents of each organism, we recorded the measurement of elemental content and its units (where we converted values into the following units when possible: percent, μg, μg L^{-1}, μg cm^{-2}), standard deviation of the measurement (when provided), and the method of measurement with supporting notes and links to method descriptions, when available. When the units of elemental contents were unclear, we excluded the data from the database. If elemental content was available for at least two of the elements, but the third element was below detection limit, the data that were below detection were coded as −999,999,999 (< 0.7% of all entries). We also report elemental molar ratios as provided by the data contributor. When not provided, we calculated them from individual elemental data. When provided, we reported the δ^{13}C and δ^{15}N isotopic composition and standard deviation (Supporting Information Text S1) and any measurement of chlorophyll and its units. We also annotated (Yes or No) if some measurement of quantity as standing stocks was associated with the organismal sample; whether other elemental data (beyond C, N, or P) were reported for that sample (designated as Yes or No); and any additional notes from the data provider.

Site Table

The Site table contains information about the location from which samples were taken. Each site was given a "Site Name," which the data contributor provided. Because of the individualistic nature of naming a location, Site Names may be unique to data sources and may not be associated with other sites within the same body of water. For example, both Toolik Lake (Kling 2013b; Johnson et al. 2014b) and Lake Superior (Bellinger et al. 2014; Camilleri and Ozersky 2019b) had multiple contributors. While we realize this decision may present certain challenges in using the database, it is a parsimonious way to synthesize many disparate data sources. When a site name was not provided, we entered one based on the latitude and longitude: "UNK_lat_long" using the decimal format.

Each site also includes information on latitude, longitude, elevation, country, state/province, and ecosystem type. If latitude and longitude were not available either from the source or provided by the authors, and if it was not possible to determine the sampling location from the source information, then the dataset was dropped. In some instances, location information was acquired using Google Earth based on study site information or figures. There were several instances in which data repositories used a bounding box; in this case, the coordinates of the centroid were entered. In both instances, the modification was noted or the rough coordinates were provided in the "Note_SampleLocation" column.

Ecosystem types provided by the researcher were standardized to the following list: Coastal, Lake, Pond, Reservoir, River, Stream, Tank Bromeliads, and Wetland. Generally, we did not provide quantitative distinctions among categories and defaulted to what was provided by the author contributor. When ecosystem type was not provided, we developed decision criteria to assist in applying these categorizations (Supporting Information Table S4). And, while we did not intentionally seek out coastal ecosystems (e.g., estuaries, marshes, tidal rivers), we did receive or encounter datasets with sites that were potentially marine. If the site was at least partly influenced by inland waters and/or resided at the ecotone on inland waters and marine waters, we retained this bycatch and categorized the ecosystem type as Coastal. However, database users interested in coastal or oceanic ecosystems should be aware that these ecosystems were not included in search terms and therefore are anticipated to be poorly represented in Limno-STOICH. For one dataset (i.e., Hu et al. 2021a), sites were reported collectively as "lakes, streams, rivers, or ponds." We assigned specific ecosystem types (pond, river, reservoir, stream, or wetland) to these 251 sites in northeastern China using their reported coordinates and a visual inspection of the ecosystem using Google Earth. Criteria included size, natural vs. man-made origin, altitude, and stream order. Notes about these site assignments were recorded in the "Notes" column. Users may want to consider carefully what is defined as a "Lake" or "Pond", or a "River" or "Stream" if the divisions are of interest.

WaterChemistry Table

The WaterChemistry table includes physical or chemical variables associated with the aquatic ecosystem from which the associated organismal sample(s) were collected (Supporting Information Table S2). This table includes non-particulate variables only, as seston, FPOM, and other particulates are considered basal resources and categorized in the OrganismStoichiometry table. Availability of these data varied widely among data sources. These data were either extracted from tables within data sources, data repositories, or provided by data contributors. Whenever possible, data were only entered as values for the sites and days that corresponded to the organismal collections. When multiple measurements were collected on the same day, data were averaged and inputted as a single value for each day. Multiple measurements over depth were only included if there was associated organismal data for those depths; otherwise, data not associated with an organismal collection were excluded. Information about statistical pooling, whether performed by data technicians or by data providers, is reported in the "Statistical_Pooling_Water" and "Sample_size_water" columns.

In some instances, water chemistry data were included at a site with dates prior to the organismal collections. However, we generally avoided this inclusion and encourage readers to link to more robust water chemical databases for this type of information (e.g., Water Quality Portal—Environmental Protection Agency and United States Geological Survey 2013; Waterbase—European Environment Agency 2024). The one exception of this is the NEON-derived data. NEON seldom collected aquatic organisms on the same day as water chemistry collections, sometimes up to 2 weeks apart. Depending on the interests of the data user, this time period may or may not be reasonable, so we left the data "unlinked" in Limno-STOICH. A function for linking these data is available in *stoichUtilities* Application Programming Interface (API; see below).

Water chemistry data were submitted in the reporting units and converted upon database inclusion to the standard units of μM C, N, or P, μg L^{-1} (dissolved oxygen), unitless (pH), or μS cm^{-1} (specific conductivity). If other variables were reported in the data source or repository, we included a comment in the "Other_elements_water" column. Some datasets reported nitrate concentrations as nitrate + nitrite; given the negligible concentrations of nitrite compared to nitrate in most surface waters, these concentrations were assumed to be primarily nitrate and reported as nitrate in Limno-STOICH. As decisions about handling records including negative values, zeros, or below detection limits (BDL) can lead to bias due to inconsistency in detection limits and reporting practices (Stow et al. 2018), we erred towards reporting data how they were reported in the original dataset. Hence, negative or zero values were entered without modification. If a BDL or non-detect was reported with no corresponding value, the concentration was entered as −999,999,999. If a value was reported, but flagged by the data contributor as a BDL, the value was entered without modification, but the BDL flag was noted in the "Notes_Water" column.

Technical validation

We employed manual and automatic checks in our technical validation of the Limno-STOICH database for quality assurance and quality control (QA/QC). After initial entry into the data template, a second trained project technician reviewed the data to ensure correct formatting, correct template version, and data completeness and accuracy. As described above, missing taxonomic data (e.g., Kingdom, Order, Class) were populated using the R package *taxize*. Then, a taxonomic expert assisted in correcting spelling errors and standardizing taxonomic classification (i.e., due to outdated classification). Taxonomic revisions can be found in Supporting Information Table S6.

Once the dataset passed this initial inspection, the dataset was reviewed through an automated check. The automated check first verified file contents for required columns, units, and proper case in text. Next, numeric values were converted to standardized units. Then, these values were automatically reviewed for expected or valid ranges and flags were created if values fell out of this range (Supporting Information Table S2). Expected ranges for organismal stoichiometry were also examined during this stage. We flagged samples with C or N contents below or above certain thresholds that were deemed out of the range of likelihood. Lower thresholds were C below 20% and N below 4% for animal tissues and C below 0.1% and N below 0.1% for resource samples. This QA/QC resulted in 1040 observations of C or N values being converted to −999,999,999. Upper thresholds were C above 80%C or samples where %C plus %N was greater than 90% or samples where %C plus %N plus %P was greater than 100%. All samples for P content were retained, but samples below the reported detection limit were recorded as −999,999,999. This QA/QC resulted in dropping 1.4% of samples (734 samples were removed representing 207 consumer and 527 resource entries) because they no longer included data from at least two elements after QA/QC.

If a dataset contained organismal C, N, and P contents in addition to C : N, C : P, and N : P ratios, the ratios contributed in the dataset were checked against the ratios derived from the contributed C, N, and P contents. While some differences between contributed and calculated C : N, C : P, and N : P ratios were expected (e.g., due to calculation of means, rounding errors, or differences in sample sizes in each reported elemental content), any difference greater than 9% was flagged to catch common errors (e.g., mass ratios mistakenly reported as molar ratios). Once numeric checks were complete, we reviewed the logs and either corrected minor issues with formatting or conducted further review, including contact with the original dataset author for data verification, cleaning, or rejection.

We conducted a final review of each dataset by examining distribution plots of numeric data, which allowed us to identify inconsistent units or auto-increments due to errors during copying and to check for missing data. Once a dataset was technically validated, a final check was done to ensure that the data were not duplicates of an existing entry. If multiple reports of sampling event information or water chemical characterization were found, individual values are stored in the "sample event" or "water chemistry" notes columns and averages are calculated in the data columns.

To conduct further QA/QC on the compiled database, we organized a remote beta testing program (recruiting participants from professional networks) along with five in-person workshops. These beta testing stages involved input from approximately 100 individuals. For the remote beta testing program, participants were challenged with various standardized and freeform activities related to database use through email communication. Additionally, we provided asynchronous instructions through video tutorials and instructional documentation with examples posted on a dedicated webpage and synchronous assistance through weekly office hours hosted by the Database Manager (C. Petersen). The workshops involved 10–25 individuals who tested example code, explored potential applications of the database, and assisted with targeted QA/QC. Beta testers and workshop participants reported issues directly to project PI's and database staff using a Google Form feedback tool. Over 40 submissions for errors and feedback were made, including typos, purported data errors, and R package documentation clarification. Recommended edits were brought to the database metadata committee and incorporated into subsequent beta versions of Limno-STOICH.

Associated API: STOICH-utilities

To facilitate the use of the Limno-STOICH Database, we created an application programming interface (API) in R called *stoichUtilities*. This package provides functions for loading, filtering, and joining tables in the Limno-STOICH Database (Petersen 2025). These functions allow users to load database tables and filter and join the tables using the Id for each table, reducing the burden for users by eliminating data type errors while loading and filtering data. The *stoichUtilities* package links to the most updated version of the Limno-STOICH Database (available from https://snr-stoich.unl.edu/get_data.htm).

Data use and recommendations for reuse

We anticipate that the Limno-STOICH database will be leveraged to address a wide variety of ecological and evolutionary questions and conservation or management concerns. In particular, the Limno-STOICH database can be used to study spatiotemporal scales of stoichiometric variation across levels of biological organization and determine when and where stoichiometric mismatches across trophic levels exist. Of course, any investigation into trophic mismatches will need to consider whether basal resources actually represent what are being consumed; the isotopic data within Limno-STOICH may help with this endeavor (Supporting Information Text S1). To help guide research inquiries, our group has developed a framework for investigating how stoichiometric diversity varies over time and space in biological communities (Moody et al. 2025) and explored how scaling-up ecological stoichiometry affects our understanding of ecological thresholds across space, time, and levels of biological organization with attention to patterns of freshwater biodiversity and evolution (Tumolo et al. 2025). And, while we attempted to be comprehensive in the information included in Limno-STOICH, we understand that all details may not have been addressed. For these scenarios, users are encouraged to dive into the source material (found in the *Contact* and *Source* tables) if there are aspects of the Limno-STOICH data that would be important to the questions they are asking but are not annotated within the database.

We also anticipate that linking Limno-STOICH to other existing databases and resources will further increase its impact. For instance, by linking Limno-STOICH to phylogenetic information from resources such as the Fish Tree of Life (Rabosky et al. 2018) or Open Tree of Life (Hinchliff et al. 2015), one can explore the extent to which stoichiometric traits are constrained by phylogeny, how much they evolve in different communities, and the relationships among community phylogenetic diversity, stoichiometric diversity, and basal resource stoichiometry. Additionally, by linking Limno-STOICH to existing databases on climate, land use/land cover, and other geographic variables (e.g., terrestrial ecoregions, Olson et al. 2001; HydroATLAS, Linke et al. 2019; Lehner et al. 2022), one can explore how ecosystem stoichiometries vary along climate, land use, and productivity gradients, how landscape alterations are reflected in stoichiometric changes of key species or communities, and how stoichiometric traits may interact with or mediate effects of climate change or other anthropogenic influences.

Our project would not have been possible without substantial funding. Specifically, our project employed a full-time database manager and a full-time database technician for most of the grant's duration, with additional full-time support staff hired to assist on a seasonal basis as needed. We also employed 45 undergraduate students across several institutions to conduct literature surveys, help add data into the database, and perform stoichiometric analysis of NEON samples, supplemented by graduate student support. Project faculty and graduate students served on database and metadata committees that discussed issues and solutions related to dealing with complex data syntheses and discussed ways to use the data in future papers.

We have made efforts to automate our data contribution processes for future datasets that could be included in Limno-STOICH in the hope that there will be future database updates. Future database updates will be critical for research and management of inland waters in the face of global change. We recognize that there are current gaps in the geographic, biome, and taxonomic coverage in the database (Figs. 1, 2). Furthermore, we acknowledge variation across methods used to collect and analyze samples (e.g., P analytical methods; Costanza-Robinson et al. 2025) and the temporal mismatch between water chemistry and organismal sampling at some field sites. To support the ease of database updates, we recommend standard protocols from NEON to those who may be collecting data that might be incorporated into Limno-STOICH. NEON provides extensive details on methods for sampling aquatic organisms and chemistry in lakes and streams. Among their protocols are details on sampling periphyton and phytoplankton (Parker 2025); aquatic macroinvertebrates (Parker 2023); aquatic plants, bryophytes, lichen, and macroalgae (Lafaver 2023); zooplankton (Parker 2024); and fish (Del Priore 2025). The protocols also include sampling surface waters for chemistry (Goodman et al. 2025) and depth profile sampling (Parker 2021). Standardized data collection, along with an eye towards data formatting previously described (Supporting Information Tables S1 and S2), will help ensure more useful, tractable, and timely updates to Limno-STOICH into the future.

Author Contributions

Amy C. Krist, Alexander L. Lewanski, Catherine E. Wagner, Eric K. Moody, Halvor M. Halvorson*, Jessica R. Corman*, Sarah M. Collins, and Steve Thomas contributed to the conceptualization and funding acquisition. Benjamin B. Tumolo, Casey Brucker*, Elise Ehlers*, Eli N. Wess, Gültekin Yilmaz, J. Harrison Edwards*, Halvor M. Halvorson*, Jessica R. Corman, Linnea A. Rock, Sarah M. Collins, and W. Reilly Farrell contributed to data curation and administration. Amina Mohamed, Benjamin B. Tumolo, Briante L. Najev, Binbin Wang, Cynthia Paszkowski*, Eric K. Moody, Gültekin Yilmaz, Halvor M. Halvorson, and Jessica R. Corman contributed to analysis and/or generation of visualizations. Amy C. Krist, Baker J. Angstman, Eric K. Moody*, Emma D. Neill, Elizabeth G. Peebles, Ella Roelofs, John S. Kominoski, Kayley Porter, Liza Toll, Molly S. Costanza-Robinson*, Natalie Montano, Qiting

Cai, Shuyi Lin, and Sophie Schuele contributed to NEON macroinvertebrate sample analysis. Chad Petersen*, Halvor M. Halvorson, and Jessica R. Corman contributed to code development. Amina Mohamed, Benjamin B. Tumolo, Briante L. Najev, Binbin Wang, Casey Brucker, Chad Petersen, Eric K. Moody, Gültekin Yilmaz, J. Harrison Edwards, Halvor M. Halvorson*, Jessica R. Corman*, Linnea A. Rock, Sarah M. Collins, and W. Reilly Farrell contributed to the writing of the manuscript. Amy C. Krist, Baker J. Angstman, Eric K. Moody, Emma D. Neill, Eli N. Wess, Elizabeth G. Peebles, Ella Roelofs, Halvor M. Halvorson, John S. Kominoski, Jessica R. Corman, Kayley Porter, Liza Toll, Molly S. Costanza-Robinson, Natalie Montano, Qiting Cai, Shuyi Lin, Sophie Schuele, and all other authors contributed data. All authors reviewed and provided edits for the final draft. Asterisks denote leads or co-leads of the different contributing efforts.

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Conflicts of Interest

None declared.

Data Availability Statement

Data are available in the Environmental Data Initiative repository at https://doi.org/10.6073/pasta/d63489af723aec3b4a608c54ba7d636d. The code that supports the analyses in this study is uploaded to Zenodo and is available at https://doi.org/10.5281/zenodo.18276533. Measurements: Organismal elemental content (carbon, nitrogen, phosphorus) and ecosystem attributes. Temporal range: Varies by location, 1922–2024. Frequency or sampling interval: Varies by location. Spatial scale: Global.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

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