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Nitrogen deposition reveals global patterns in plant and animal stoichiometry

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The elemental content of organisms links cellular biochemistry to ecological processes, from physiology to nutrient dynamics. While plant stoichiometry is thought to vary with climate and nutrient availability across latitudes, the consistency of these patterns across trophic groups and realms remains unclear. Using the StoichLife database, which includes nitrogen and phosphorus content data for 5443 species across 1390 sites, we examine how solar energy (temperature, radiation) and nutrients (nitrogen and phosphorus) influence stoichiometric variation. We find that plant stoichiometry in terrestrial and freshwater ecosystems is more strongly associated with environmental gradients, particularly nitrogen deposition, than animal stoichiometry. Contrary to expectations, temperature, radiation, and labile P show limited global effects. Latitudinal patterns in stoichiometry are more closely associated with species turnover rather than intraspecific variation. Given the strong links between stoichiometry and organismal performance, these findings underscore the need to predict the ecological consequences of anthropogenic disruption to global biogeochemical cycles.

The elemental content of living organisms, referred to as organismal stoichiometry, plays a crucial role in shaping biological processes, spanning from growth rates to consumer-resource interactions, eco-evolutionary dynamics, and global biogeochemistry[1–6]. Given its profound influence on how organisms respond to and interact with their abiotic and biotic surroundings, investigating large-scale patterns in organism stoichiometry can provide key insights into how climatic and biogeochemical conditions regulate local ecological and evolutionary processes worldwide[6–8]. These insights are particularly relevant in the context of human activities altering energy and nutrients in the environment[8–10].

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Research on geographic variation in organismal stoichiometry has consistently revealed that organismal nitrogen (N) and phosphorus (P) content tend to increase, while the N:P ratios decrease with increasing latitude[11–13]. However, most studies investigating these latitudinal patterns in organismal stoichiometry have focused on relatively narrow subsets of taxonomic groups, particularly plants or algae[11–14]. The limited availability of animal data has historically constrained the evaluation of their stoichiometric patterns at global scales. Growing interest in animal stoichiometry has led to several local-scale studies[e.g.15–18], which when integrated, create new opportunities to evaluate biogeographical and macroecological patterns in organismal stoichiometry. Nonetheless, a mechanistic understanding of how and why plant and animal stoichiometry vary along environmental gradients—especially across latitudes—remains incomplete.

Along latitudinal gradients, organismal stoichiometry is expected to respond to shifts in environmental conditions—such as temperature, solar radiation, and nutrient availability—through changes in the uptake, assimilation, storage, and excretion of nutrients[12,19]. Spatial environmental variation influences processes across multiple levels of ecological organization, from individuals to ecosystems[20]. However, the magnitude and direction of these effects are unlikely to be uniform across taxa and ecosystems, owing to differences in stoichiometric homeostasis and the physiological roles of these elements[10,21].

Three primary mechanisms have been proposed to explain latitudinal variation in organismal stoichiometry and its underlying environmental drivers: temperature, radiation, and nutrients (Supplementary Fig. 1). Each general mechanism (G) corresponds to one or two specific hypotheses. The first mechanism, "Temperature-Dependent Physiology", G_{T°, is rooted in the universal effects of temperature on metabolic processes. Two contrasting hypotheses emerge from this mechanism: the "hotter is better" and the alternative "metabolic cold adaptation" hypotheses. The "hotter is better" hypothesis posits that organisms in warm, low-latitude environments exhibit accelerated metabolic rates and, consequently, increased synthesis of N-rich proteins and P-rich RNA molecules. This enhanced biosynthetic activity leads to elevated N and P contents in organisms inhabiting warmer climates. Notably, because RNA synthesis is more temperature-sensitive than protein synthesis, P content is expected to increase more steeply than N content, resulting in a lower N:P ratio in warmer, low-latitude environments[22,23]. In contrast, the "metabolic cold adaptation hypothesis" proposes that ectothermic organisms—both within and among species—inhabiting cold, high-latitude environments evolve elevated metabolic rates to compensate for thermally constrained rates of biochemical reactions at low temperatures[24,25]. This adaptation is thought to involve physiological changes such as increased mitochondrial density and higher concentrations of RNA and protein, which together enhance metabolic enzyme production and energy-generating capacity[19,23,26]. While the "metabolic cold adaptation hypothesis" does not explicitly predict changes in elemental content, it supports mechanistic predictions about organismal stoichiometry in cold environments. Specifically, it implies that colder environments may be associated with increased organismal N and P contents due to elevated investment in protein and RNA to sustain higher metabolic processes. Given that ribosomes (which are P-rich) are more sensitive to temperature than proteins (which are N-rich)[27,28], this mechanism further suggests that P content should increase more steeply than N content as temperature declines. Consequently, this would lead to a decreasing N:P ratio in organisms toward cooler, high latitude environments[19,29].

The second proposed mechanism centers on the influence of solar radiation on physiological processes—"Radiation-Dependent Physiology", G_R—encompasses two hypotheses: the "growing season length" and the "UV-dependent" hypotheses. According to the "growing season length hypothesis", shorter growing seasons impose a strong selection pressure on organisms to maximize growth rates within a limited timeframe[30–32]. This demand promotes increased RNA synthesis, leading to a lower protein:RNA ratio and, consequently, a reduced N:P ratio alongside elevated organismal P content[1,2,19,33]. Alternatively, the "UV-dependent hypothesis" posits that increased UV radiation stimulates the production of N-rich UV-defense compounds (e.g., melanin) or P-rich UV-DNA repairing mechanisms, thereby elevating organismal N and P contents[34–36]. Under this hypothesis, organismal N and P contents are expected to increase with higher UV irradiance, typically associated with lower latitudes.

The third mechanism, "Nutrient-Dependent Physiology", G_N, attributes variation in organismal stoichiometry to latitudinal differences in nutrient availability, which can directly affect organismal physiology, fitness, and species interactions[11,12]. Within this framework, the "stoichiometric plasticity hypothesis" suggests that organisms in nutrient-rich environments (e.g., elevated N or P availability) exhibit higher N and P contents, mirroring environmental nutrient conditions. Autotrophs are expected to exhibit greater stoichiometric plasticity than heterotrophs because of their capacity for nutrient storage[1,2,37,38]. Given global nutrient gradients, where highly weathered, ancient tropical soils are often P-limited and younger, temperate soils are typically N-limited[39,40], one should expect that an increase in organismal P content and a decrease in organismal N content from low to high latitudes, or along nutrient availability gradients.

Importantly, the magnitude and direction of these mechanisms are likely modulated by trophic group (T)—autotroph versus heterotroph—and realm (R)—freshwater versus terrestrial. For example, autotrophs and freshwater organisms tend to be more sensitive to radiation [T_R, R_R[41,42];] and exhibit lower stoichiometric homeostatic regulation, allowing greater nutrient storage under fluctuating nutrient conditions (T_N, R_N) than heterotrophs and terrestrial organisms[2,21]. Conversely, heterotrophs exhibit stronger sensitivity to temperature (T_{T°, R_{T°) than autotrophs[43,44]. These differences in physiological sensitivities should result in distinct latitudinal and environmental responses in elemental content across taxa (Supplementary Fig. 1). Moreover, these mechanisms are not mutually exclusive and may act simultaneously across spatial scales.

All three mechanisms—temperature, radiation, and nutrient availability—capture both intraspecific and interspecific sources of stoichiometric variation. Intraspecific variability in organismal stoichiometry, via phenotypic plasticity or local adaptation, is more responsive to fine-scale, short-term environmental changes[45–47]. In contrast, interspecific differences driven by species turnover are more likely to underlie broader-scale, long-term ecological patterns[48]. Accordingly, we expect that (i) species exposed to greater environmental heterogeneity will exhibit greater intraspecific stoichiometric variation (hereafter I_{NTRA}) and (ii) large-scale patterns will be predominantly shaped by species turnover (hereafter I_{NTER}).

Here, we test these hypotheses using a global dataset of plant and animal elemental content—StoichLife[49]—comprising N, P, and N:P ratios across freshwater and terrestrial realms, spanning from 60° S to 80° N (Fig. 1A). The dataset integrates environmental information for 998 georeferenced sampling sites, including temperature, solar radiation, N deposition, and labile P. In this study, we used atmospheric N deposition as a proxy for environmental N availability and limitation, acknowledging both its strengths as a globally consistent metric and its limitations relative to local soil and water nutrient supply. These sites collectively capture substantial global environmental space, covering 41.6% of the temperature-phosphorus gradient and 75.5% of the temperature-radiation gradient (Fig. 1B). Across sites, latitude was strongly negatively correlated with temperature and radiation, while associations with N deposition and labile P were weaker (Fig. 1C).

In this study, we show that global variation in the elemental content of plants and animals is more consistently associated with nutrient availability, particularly nitrogen deposition, than with temperature or solar radiation. Across terrestrial and freshwater realms, P content (but

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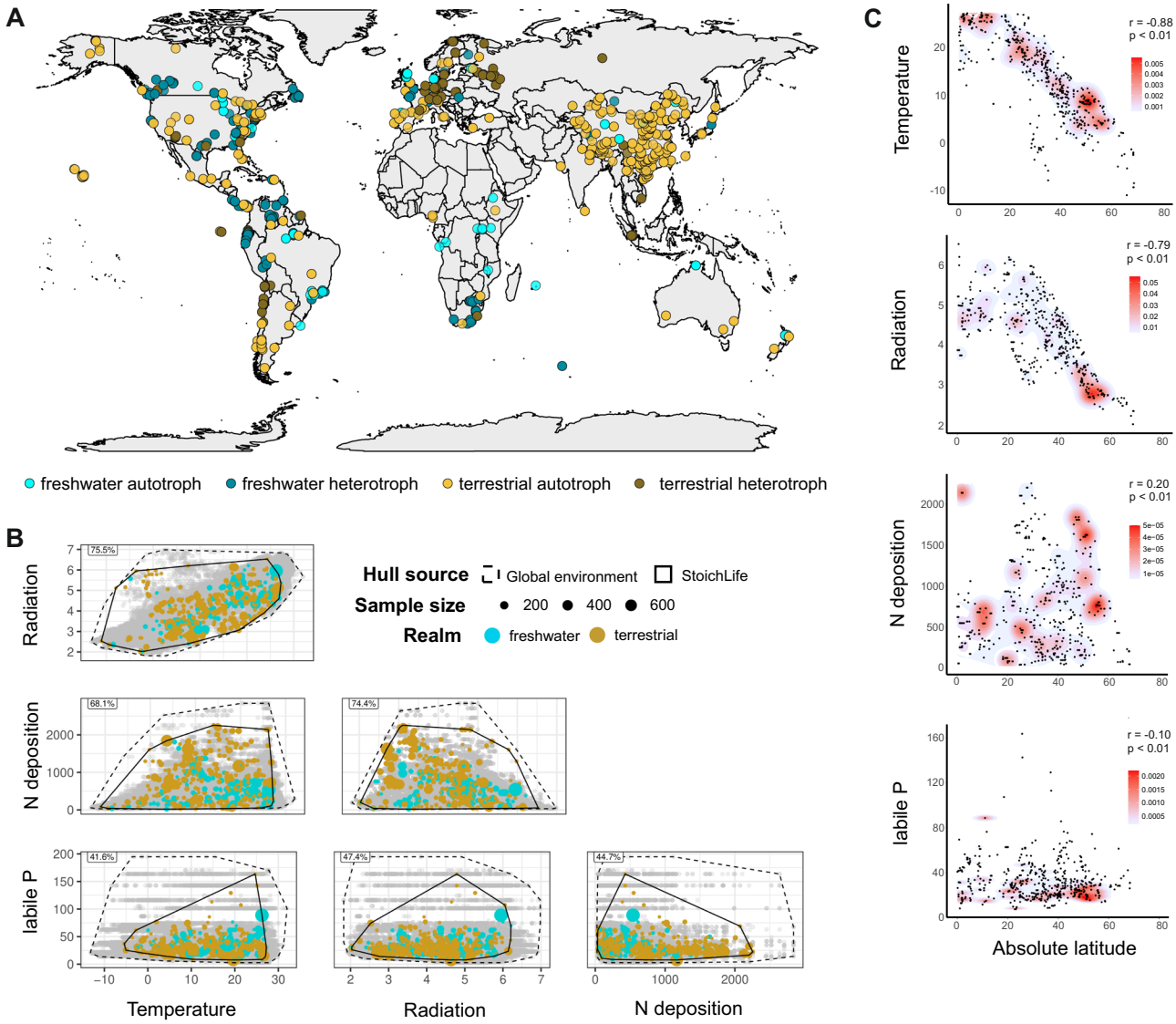

Fig. 1 | Global distribution of sampling sites and environmental drivers. A Map of 998 sampling locations in the database, including autotrophs (freshwater: light blue circles; terrestrial: light brown circles) and heterotrophs (freshwater: dark blue circles; terrestrial: dark brown circles). **B** Environmental space coverage of our dataset (StoichLife; $n = 336$ freshwater locations in blue, $n = 697$ terrestrial in brown; solid hull) compared with global environmental space coverage (Global Environment; $n = 47{,}500$ random locations, representing 95% of available data; dashed hull). Circle size reflects the number of samples per location. **C** Variation in main environmental predictors across absolute latitude. Gradients indicate the density of sampling locations. Temperature (°C) was positively correlated with radiation (W/m^2; two-sided Spearman's r = 0.74). Neither variable showed strong correlations with N deposition (kg N km^{-2} y^{-1}; two-sided Spearman's r = −0.20 and two-sided Spearman's r = −0.51, respectively) or labile P (g P m^2 y^{-1}; two-sided Spearman's r = 0.05 and two-sided Spearman's r = 0.18, respectively). N deposition was not strongly correlated with labile P (two-sided Spearman's r = −0.38). All correlations were significant ($P < 0.0001$, asymptotic tests).

not N content) tends to increase with latitude, resulting in declining N:P ratios, especially in autotrophs. These stoichiometric patterns reflect contributions from both intraspecific variation and species turnover. Because stoichiometry underpins ecological performance, our findings highlight nutrient deposition as a key correlate of global stoichiometric patterns and stress the need to anticipate ecological impacts of human-driven biogeochemical change.

Results and discussion

Latitudinal patterns in plant and animal stoichiometry

Our analyses revealed that neither the N and P content of heterotrophs nor the N content of autotrophs exhibited consistent latitudinal trends across terrestrial and freshwater realms (Fig. 2, Supplementary Fig. 2, and Supplementary Tables 1 and 2). These findings contrast with previous studies reporting a significant, albeit weak, increase in the N content of plants[11,12,50] and microbes[51,52] at high latitudes. In line with earlier work, however, we observed a significant increase in P content with latitude in freshwater and terrestrial autotrophs[11,12,50] and across terrestrial organisms as a whole (Fig. 2A,B, and Supplementary Table 1). Given the absence of a latitudinal trend in N content alongside a clear increase in P content, variation in N:P with latitude appears to be more strongly related to P content. Notably, these patterns were largely associated with terrestrial autotrophs (predominantly plants), which exhibited, on average, a 173% increase in P content (back-transformed scale) from 0° to 80° absolute latitude (Fig. 2C and Supplementary Table 1). Consistent with our predictions, terrestrial organisms as a group showed a decline in N:P with increasing latitude (Fig. 3A and Supplementary Table 1), largely reflecting the increase in autotroph P content (Fig. 2A, Fig. 3B and Supplementary Table 1). This latitudinal decrease in the N:P ratio of terrestrial autotrophs, also reported in previous studies[11,12,50], reflects a steeper and significant increase in P content (slope coefficient = 1.3e-02) relative to a smaller, non-

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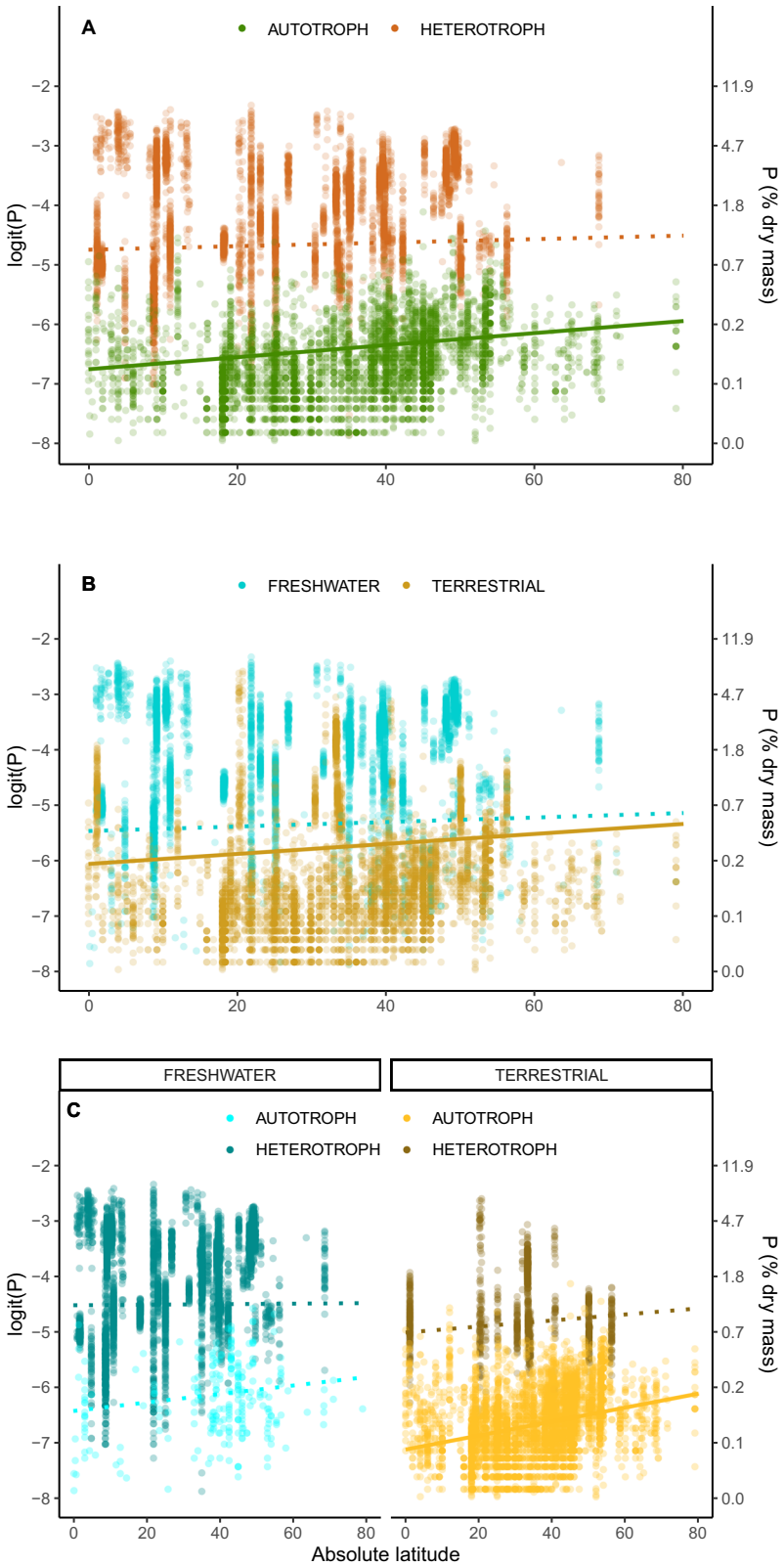

Fig. 2 | Estimated marginal effects of latitude on organismal P content. **A** Latitudinal patterns for autotrophs vs. heterotrophs, pooled across realms. **B** Latitudinal patterns for freshwater vs. terrestrial organisms, pooled across trophic groups. **C** Latitudinal patterns for freshwater and terrestrial autotrophs vs. heterotrophs. Model fit lines indicate significant (solid; $P < 0.05$) or non-significant (dotted; $P > 0.05$) relationships from linear mixed-effect models. Data points and estimates are shown on the logit scale and back-transformed to % dry mass. *P* values are from two-sided tests with permuted t-statistics and were adjusted for multiple comparisons. Supplementary Table 1 for slope coefficients on the logit scale and exact *P* values.

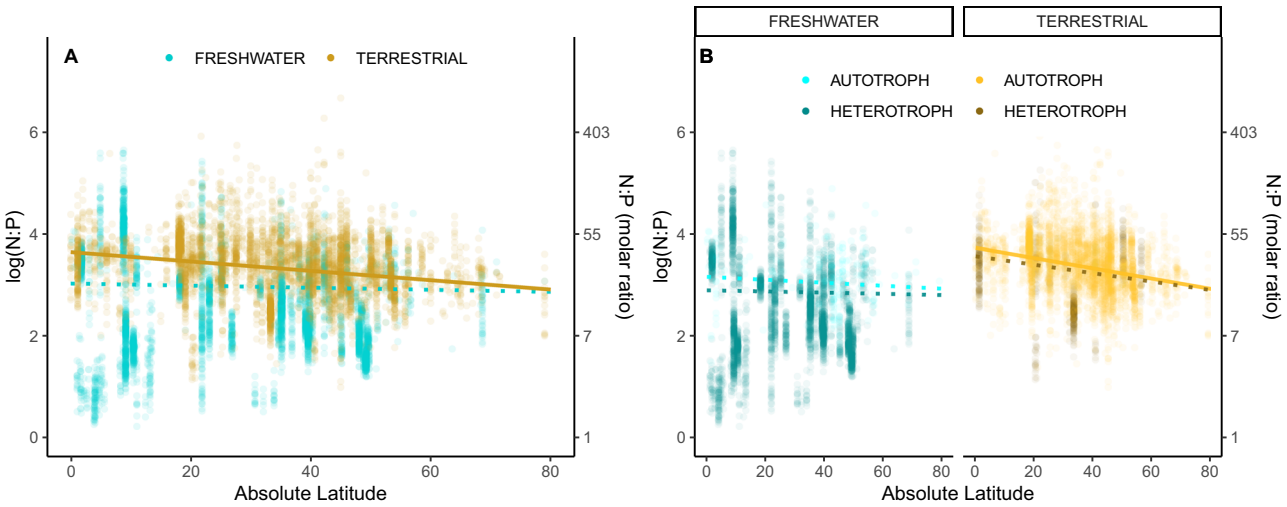

Fig. 3 | Estimated marginal effects of latitude on organismal N:P ratios. **A** Latitudinal patterns for freshwater vs. terrestrial organisms, pooled across trophic groups. **B** Latitudinal patterns for freshwater vs. terrestrial autotrophs vs. heterotrophs. Model fit lines indicate significant (solid; $P < 0.05$) or non-significant (dotted; $P > 0.05$) relationships from linear mixed-effect models. Data points and estimates are shown on the log scale and back-transformed. *P* values are from two-sided tests with permuted t-statistics and were adjusted for multiple comparisons. See Supplementary Table 1 for slope coefficients on the log scale and exact *P* values.

significant increase in N content (slope coefficient = 4.0e-03; Supplementary Table 1). The observed decline in N:P has often been attributed to the greater environmental sensitivity of P-rich ribosomes compared to N-rich proteins[53,54], consistent with the "growth rate hypothesis"[33]. While this metabolic explanation is plausible, alternative mechanisms may also contribute. For example, nutrient supply constraints, such as low soil P availability in highly weathered tropical soils and strong binding of P to iron (Fe) and aluminum (Al) oxides[55], could reduce autotroph P content at low latitudes. In addition, differences in nutrient storage capacity, lineage-specific allocation strategies, or species turnover along environmental gradients could also alter %N, % P, and N:P ratios independently of protein/RNA synthesis demands. Together, these explanations remain consistent with all three hypothesized mechanisms (temperature, radiation, and nutrients). Supporting the role of nutrient availability, the predicted mean N:P for terrestrial autotrophs declined markedly from 41.7 (39.2–44.5, 95% CI) near the equator to 15.3 (13.6–17.1, 95% CI) at higher latitudes. An N:P above 20 has been proposed as indicative of strong P limitation for plant growth and biomass production[56], suggesting that terrestrial autotrophs are more likely to experience P-limitation in low-latitude environments[40].

Environmental predictors of plant and animal stoichiometry

Further analyses of environmental drivers of organismal stoichiometry revealed potential mechanisms underlying these latitudinal patterns. We observed a positive relationship between organismal N content and N deposition (Fig. 4A and Supplementary Table 1), particularly in autotrophs (Fig. 4B, Supplementary Table 1) and freshwater organisms (Fig. 4C and Supplementary Table 1). In contrast, the N content of terrestrial organisms, especially heterotrophs, showed no significant response to N deposition (Fig. 4B, C and Supplementary Table 1). Among different trophic groups within realms, freshwater autotrophs exhibited the strongest association with N deposition, while terrestrial heterotrophs showed the weakest; terrestrial autotrophs and freshwater heterotrophs showed intermediate sensitivities (Fig. 4D and Supplementary Table 1). These patterns align with extensive evidence indicating that heterotrophs generally exhibit lower stoichiometric plasticity than autotrophs[2,7,37]. Autotrophs, by contrast, often display greater plasticity in their elemental content, including elevated N content in N-rich environments through enhanced N uptake[21]. Freshwater organisms—autotrophs and heterotrophs—also exhibited stronger associations with nutrient availability than their terrestrial counterparts (Fig. 4C, D), likely reflecting physical, physiological, and morphological differences in nutrient uptake and allocation strategies[2,10,57]. For example, aquatic autotrophs tend to invest less in structural biomass than terrestrial autotrophs[57,58], and they typically possess higher maximum relative growth rates and a greater capacity for the luxury uptake of non-limiting nutrients[59]. Similarly, the observed increase in the N:P ratio of freshwater heterotrophs under high-N deposition (Fig. 4E, F) likely reflects differential uptake rates of N and P[60].

Although our models incorporating environmental variables explained between 10% to 84% of the variance in organismal N and P contents (Supplementary Table 2), temperature, solar radiation, and labile P showed weak or non-significant associations with elemental content of plants and animals (Supplementary Tables 1, 3–5). These results challenge previously reported effects of temperature and radiation on the elemental content of plants[11,12,61] and microbes[13,52], often interpreted as consequences of enhanced metabolic rates, nutrient uptakes, and growth rates under warmer and more light-rich conditions[33,62]. Our findings therefore provide limited support for the "Temperature-Dependent Physiology" and "Radiation-Dependent Physiology" mechanisms (Supplementary Table 5). The consistent latitudinal patterns in plant P content and N:P ratio in this study and prior work[11,12,50,63] suggest global-scale mechanisms in autotroph stoichiometry. In contrast, the lack of consistent responses in plant N content may reflect the influence of local factors, such as soil or water fertilization or land-use variation, which can blur broader biogeographical patterns.

The absence of global stoichiometric responses to temperature and radiation across taxa and realms may reflect scale-dependence. At local scales, for instance, darker individuals with high N-rich melanin content can gain thermoregulatory advantages in colder environments, while lighter phenotypes avoid overheating in warmer environments[64,65]. At broader scales, however, the mismatch between coarse climatic variables and the microenvironment experienced by organisms may weaken trait-environment associations[66]. Our findings suggest that stoichiometric responses to energy-related variables (temperature and radiation) are more scale-dependent than responses to nutrient-related drivers, with N deposition emerging as the most consistent predictor at global scales.

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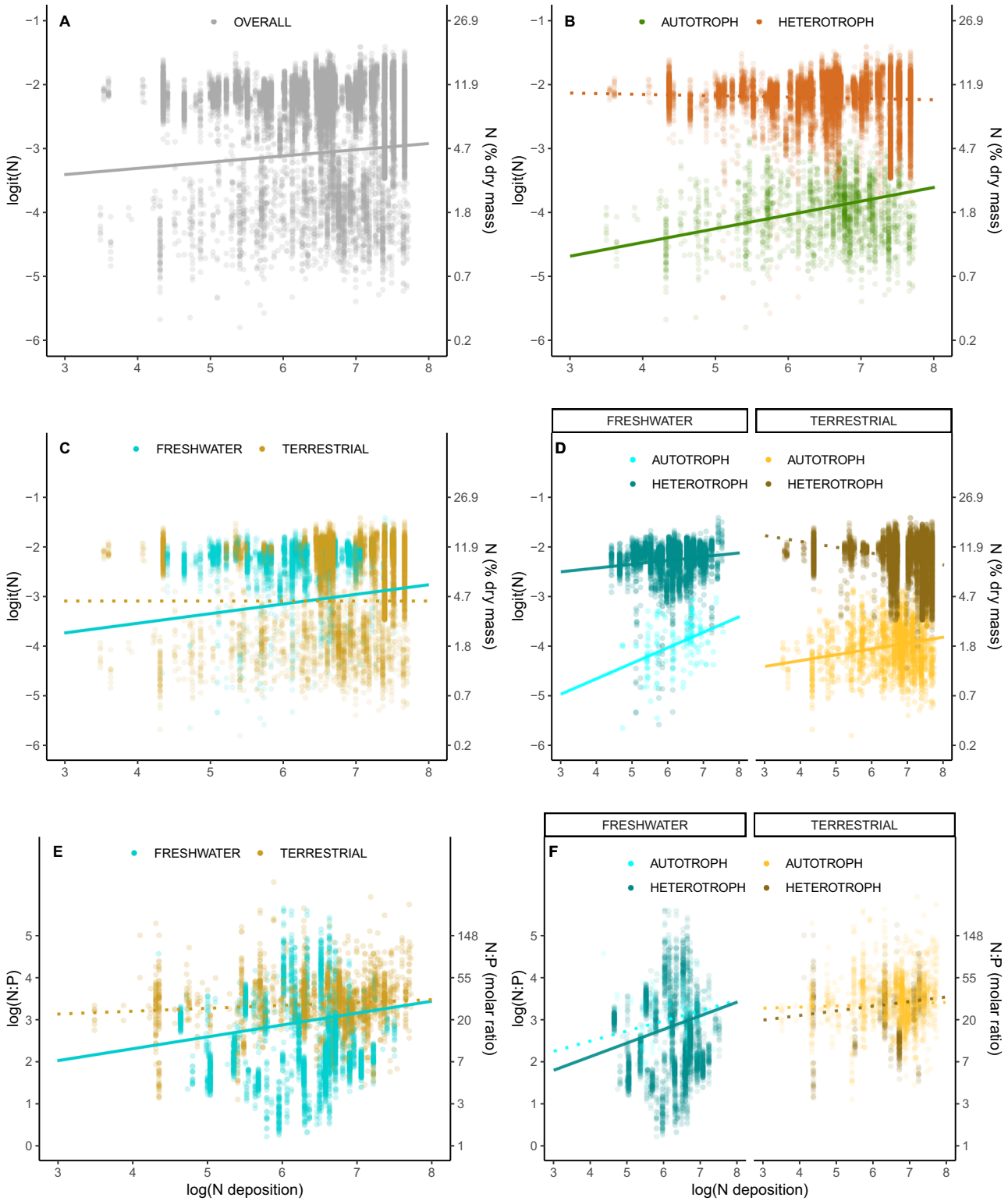

Fig. 4 | Estimated marginal effects of log-transformed N deposition on organismal N content and N:P ratios. A Overall responses of organismal %N, pooled across realms and trophic groups. **B** Responses in %N of autotrophs vs. heterotrophs pooled across realms. **C** Responses in %N of freshwater vs. terrestrial organisms, pooled across trophic groups. **D** Responses in %N of freshwater and terrestrial autotrophs vs. heterotrophs. **E** Responses in N:P ratios of freshwater and terrestrial autotrophs vs. heterotrophs. **F** Responses in N:P ratios of freshwater and terrestrial organisms, pooled across trophic groups. Model fit lines indicate significant (solid; $P < 0.05$) or non-significant (dotted; $P > 0.05$) relationships from linear mixed-effect models. Data points and estimates for %N are shown on the logit scale and back-transformed to % dry mass, while N:P ratios are shown on the log scale and back-transformed. *P* values are from two-sided tests with permuted t-statistics and were adjusted for multiple comparisons. See Supplementary Table 1 for slope coefficients on the logit and log scales, and exact *P* values.

To better evaluate how environmental factors influence organismal N content, it is important to consider both direct and interactive effects of temperature, nutrient availability, and other abiotic conditions. While our primary analyses did not detect strong main effects of temperature or radiation on organismal N content, these factors may still interact with nutrient availability[62]. Indeed, we found that temperature and labile P together modestly strengthened the relationship between organismal N content and N deposition (Supplementary Table 4), although these interactions explained only 1% of additional variance (Supplementary Table 2). These results highlight that while energy-nutrient interactions can influence organismal stoichiometry, their contribution is minor compared to the broad-scale signal of N deposition. These findings are consistent with previous studies pinpointing the context-dependent effects of environmental drivers on organismal elemental content[67,68] while emphasizing the dominant role of N deposition in shaping global stoichiometric patterns. Finally, we emphasize that N deposition was used here as a proxy for environmental N availability and limitation. This proxy provides globally consistent coverage and captures large-scale enrichment patterns, but it does not necessarily reflect local variation driven by soil chemistry, microbial processes, or land-use history. The fact that N deposition nonetheless emerged as the strongest environmental predictor highlights both its utility as a broad-scale indicator and the need for complementary, finer-scale measures of nutrient availability in future work.

Intra and interspecific stoichiometric responses

While organismal stoichiometry exhibited responses to environmental factors—most consistently with N deposition—the observed variation in elemental content among plants and animals reflected contributions from both intraspecific variation (I_{NTRA}) and species turnover (I_{NTER}). The magnitude of intraspecific variation depended on species identity and the environmental gradient considered, but overall contributed only moderately to broad-scale patterns. This is supported by the limited differences between main models and those based on species-mean values (Supplementary Tables 2 and 6). A focused analysis along the N deposition gradient revealed a significant positive association between environmental N deposition and the range of species-level N content (Supplementary Fig. 3). Consistent with hypothesis I_{NTRA}, species exposed to broader environmental gradients in N deposition tended to exhibit greater intraspecific variation in N content—potentially conferring greater ecological tolerance and performance, as reported for other functional groups[69]. Given the established links between organismal stoichiometry, ecological performance, and evolutionary processes[4,37], understanding the scope of these responses is essential for predicting the impacts of global environmental change—particularly those arising from nutrient enrichment[37].

Alongside intraspecific plasticity, we observed relatively high species turnover along the N depositional gradient. Most species occupied only narrow portions of the total N deposition range (Supplementary Fig. 4), and assemblages in high-deposition environments were increasingly composed of N-rich species (Supplementary Fig. 3), supporting hypothesis I_{NTER}. While the relative contributions of intraspecific variation and species turnover remain partially confounded—due to incomplete species distribution data in the StoichLife dataset—our results align with prior work suggesting that species turnover often dominates broad-scale stoichiometry patterns[12,46,70]. Furthermore, the parallel responses of intraspecific variation and species turnover responses to N deposition suggest common principles structuring stoichiometric variation at global scales (Supplementary Table 6 and Supplementary Figs. 2–5).

From these analyses, we identified seven key limitations that future studies should address: First, our dataset analysis is based on non-exhaustive community samplings. It is thus possible that species with unique stoichiometries or those restricted to specific microhabitats (e.g., extremophiles) may not shift along environmental gradients, even when community-wide stoichiometry does.

Second, grouping organisms with contrasting life histories likely weakened stoichiometric patterns. Our heterotroph data, for example, included fast-growing taxa (e.g., Culicidae) and slow-growing taxa (e.g., Odonata), as well as chitin-rich invertebrates and vertebrates with P-rich skeletal tissues. These biological differences may modulate responses depending on taxon-specific ways.

Third, although our findings support the "Nutrient-Dependent" mechanisms, N deposition alone explained less than 2% of the variation in organismal N content (upper limit of CI of the partial R^2; Supplementary Table 3). This aligns with prior analyses of plants and microbes[11–13,61,63] and may reflect cross-scale ecological and evolutionary processes—including plasticity, local adaptation, phylogenetic constraints, and lineage turnover—that obscure broad-scale trait-environment relationships.

Fourth, evolutionary constraints such as phylogenetic conservatism may limit the responsiveness of elemental traits to environmental variation. While closely related taxa may respond more similarly to environmental conditions, divergence among distantly related species with distinct life strategies may weaken observed trait-environment relationships. Due to the absence of a unified phylogeny encompassing all organisms (plants and animals) in our dataset, we could not explicitly evaluate phylogenetic effects.

Fifth, our analyses did not account for how environmental drivers may alter resource quality—either indirectly influencing animal stoichiometry or propagating effects through food webs[2]. Recent evidence suggests that water and soil chemistry shifts resulting from elevated N deposition could trigger plant community turnover and subsequently affect consumer stoichiometry[70].

Sixth, we acknowledge that unmeasured environmental variables—particularly precipitation—likely play a critical role in shaping the elemental content of terrestrial autotrophs (Figs. 2 and 3). In particular, long-term P leaching under high rainfall in weathered tropical soils, coupled with strong binding of P to Fe and Al oxides, may underlie the consistently low P content of tropical autotrophs observed here and in other studies (Nutrient-Supply Hypothesis[2,11,50]). Future research should examine how interactions between organismal stoichiometry and water availability influence food web dynamics, especially in light of intensifying anthropogenic alterations of global water cycles.

Seventh, our analyses were limited to N and P, reflecting the availability of data. Because elemental content is expressed as percentages of dry mass, values are bounded to 100%, and unmeasured elements are implicitly represented as "other." This means that variation in %N or %P may partially reflect reallocations relative to other elements (e.g., carbon, potassium, calcium). While this does not undermine the robustness of our findings, it constrains mechanistic interpretation. Broader multi-element data would allow evaluation of covariation and trade-offs among elements, providing a more complete view of organismal stoichiometry across realms. Although multi-element datasets remain limited, smaller-scale studies already highlight the value of multi-element approaches. Incorporating such data in regional or taxon-specific contexts represents a feasible step toward testing multidimensional stoichiometric predictions and informing the gradual expansion of global databases.

In conclusion, our findings indicate that N deposition is consistently associated with global variation in plants and animal stoichiometry, whereas latitude, temperature, radiation, and labile P show comparatively weaker or inconsistent effects. Although N deposition itself reflects underlying climatic and environmental processes—including precipitation-driven leaching, temperature-mediated decomposition rates, soil properties, and biological nitrogen fixation—its broad-scale influence on organismal stoichiometry emerges as particularly robust. Expanding stoichiometric analyses to include elements beyond N and P will be critical for refining interpretations of how environmental drivers

structure global patterns. In the near term, regional syntheses and taxon-specific studies can help bridge the gap until broader global coverage is achieved. Future progress will benefit from multidimensional stochiometric frameworks (e.g., stoichiometric[71,72] and biogeochemical niches[73,74]), which conceptualize elemental content in a multivariate trait space and enable assessment of covariation, trade-offs, and environmental sensitivity across scales. Such integrative approaches, coupled with expanded global datasets linking organismal and resource stoichiometry, will improve predictions of how human-driven changes in nutrient inputs and climate affect the elemental content of life and, ultimately, multiple dimensions of biodiversity.

Methods

Terrestrial and freshwater autotrophs and heterotrophs

We used a subset of the extensive global trait database we assembled, StoichLife[49], which encompasses 28,049 geo-referenced measurements of individual-level multicellular autotroph (fresh leaf elemental content for terrestrial autotrophs) and heterotroph (animals) tissue or bulk stoichiometry data from terrestrial, freshwater, and marine realms. The StoichLife database assembly involved integrating published and unpublished data on organismal elemental content. Note that all unpublished data included in this study are fully described in the data paper accompanying the StoichLife database, where methodological details are explicitly documented. The methods employed in these unpublished sources follow established protocols widely used in animal and plant stoichiometry research. The subset of the database used here focuses only on terrestrial and freshwater taxa and includes 24,598 geo-referenced measurements from 1390 sampling sites, each with latitude or latitude-longitude coordinates; of these, 998 sites include both latitude and longitude information. Autotroph and heterotroph data were compiled from independent studies and were not necessarily collected at the same locations.

Terrestrial and freshwater realms are represented in 697 and 336 sites, respectively, with 35 sites reporting organisms from both terrestrial and freshwater realms. To maintain consistency, we classified organisms based on their primary habitat (freshwater or terrestrial realm) according to the original source of information, such as databases, templates, and papers provided by the authors. For example, insects with larval stages were categorized as freshwater or terrestrial depending on whether the larvae or the winged adult were sampled. Although the StoichLife database includes data on marine organisms (2282 entries), we excluded them from the analyses due to challenges retrieving comparable environmental data across different realms. Additionally, we excluded birds and mammals due to the limited number of data points (17 and 50 for birds and mammals, respectively), which were also geographically restricted. Finally, we excluded data from a specific study (34 entries[75]) due to concerns about comparing N and P content values with the rest of the database. It is important to note that data on the elemental content of plants represent leaf or shoot tissue, while for animals, only whole-body data was included. The database includes information on bulk N and P content (% of dry mass, %N, %P), molar N:P ratio, geographic location (latitude and longitude), taxonomy at the level of morphospecies (the latter referring to taxa, not identified to a taxonomic species), realm (freshwater, terrestrial), and trophic group (autotroph, heterotroph). Only records with both %N and %P were retained, as these values were required to calculate N:P. As a result, the dataset contained no missing values for these variables.

The dataset analyzed in this study encompasses a wide taxonomic range, including 5 phyla, 15 classes, 80 orders, and 273 families of autotrophs, totaling 3133 species or morphospecies. In terrestrial realms, the %N of autotrophs ranges from 0.09 to 8.00, %P content from 0.01 to 1.6, and N:P from 0.17 to 789. In freshwater realms, these values range from 0.18 to 4.97 for %N, 0.02 to 1.03 for %P, and 4.42 to 133 for N:P ratio (Supplementary Fig. 6). Moreover, the dataset includes 9 phyla, 25 classes, 90 orders, and 472 families of heterotrophs (animals), comprising 2310 species or morphospecies. For heterotrophs in terrestrial ecosystems, the %N content ranges from 1.16 to 19.50, %P content from 0.12 to 7, and N:P ratio from 3.14 to 192. In freshwater ecosystems, %N varies from 0.38 to 19.50, %P from 0.02 to 8.88, and N:P ratio from 1.25 to 284 (Supplementary Fig. 6). Terrestrial autotrophs are dominated by three main classes—Magnoliopsida (76%), Liliopsida (13%), and Pinopsida (6%)—while aquatic autotrophs are mainly represented by, Liliopsida (44%), Ulvophyceae (21%), and Florideophyceae (19%; in percent of all terrestrial or aquatic autotrophs, respectively). In turn, the three main classes of terrestrial heterotrophs are Insecta (32%), Arachnida (27%), and Collembola (17%), and aquatic heterotrophs are represented by Insecta (42%), Actinopterygii (27%) and Anthozoa (8%; in percent of all terrestrial or aquatic heterotrophs, respectively).

Environmental data

To test our hypotheses, we gathered independent data on mean annual temperature (G_{T°: Temperature Dependence), radiation (G_R: Growing Season Duration or UV defense), and environmental nutrient availability (nitrogen deposition and labile phosphorus; G_N: Nutrient Supply) at each location where plant or animal samples were collected. In our analyses, nitrogen deposition (N deposition) was treated as a proxy for environmental nitrogen availability. Using the geographic coordinates of sampling sites, we downloaded the mean annual temperature at 10 m above the soil (in °C; T10M; 0.5° × 0.5° resolution) and solar radiation data (ALLSKY_SFC_SW_DWN: All Sky Insolation Incident on a Horizontal Surface; 1° × 1° resolution; in W / m^2) directly from the NASA Power Project repository. Both temperature and radiation data were averaged annually from 1981 to the present (https://power.larc.nasa.gov/), providing time-integrated conditions for a site. For N deposition, we used global deposition data from[76], which provide information on inorganic N deposition (kg N / km^2 / $year^1$) from 1984 to 2016 at a spatial resolution of 2° × 2.5°. For phosphorus, we used labile P data (in g P / m^2) from the Oak Ridge National Laboratory Distributed Active Archive Center (ORNL DAAC) for Biogeochemical Dynamics. Although these data lack specific temporal coverage, they nominally cover the pre-industrial period (ca. 1850). To obtain labile phosphorus values for the sampling locations of terrestrial and freshwater organisms included in our database, we averaged the labile P across values from a 2°longitude × 2°latitude window centered on the latitude and longitude coordinates of each data point. We acknowledge that these proxies might not perfectly represent nutrient availability, especially in regions with high N deposition rates (i.e., influencing N availability) or with contrasting soil mineralogy, pH, and microbial activity (i.e., influencing P availability). However, they remain the most comprehensive data available for the global scope of terrestrial (e.g., grasslands, forests, shrublands) and freshwater (streams, ponds, lakes, rivers, phytotelmata) ecosystems included in our analyses. We believe that the potential use of improved N and P availability data would not change our main conclusion that organismal stoichiometry responds more strongly to nutrient availability (N deposition or labile P) than to energy-related variables (temperature and radiation).

Statistical analyses

To test hypotheses G_{T°, G_R, and G_N (Supplementary Fig. 1), we employed linear mixed effects models (LMM; lme4-package[77]). The response variables in all models were %N, %P, or N:P ratios. To account for the bounded nature of %N and %P data between 0% and 100%, we logit-transformed these data and log-transformed the N:P ratios. Continuous predictors included absolute latitude and four selected environmental drivers: temperature, solar radiation, and both N deposition and labile P. Prior to analyses, N deposition and labile P were log-transformed. Categorical predictors comprised the realm (terrestrial vs. freshwater) and trophic group (autotroph vs.

heterotroph). Interactions between continuous and categorical predictors and between the realm and trophic groups were included in all models. We modeled the species or morphospecies identity as a random intercept, as we expect species or morphospecies to vary in their elemental contents. In total, we built six models, each with varying numbers of observations (models with latitude / environmental drivers): logit-transformed %N ($N = 22{,}467$ / $N = 19{,}040$), %P ($N = 11{,}200$ / $N = 8479$), and log-transformed N:P ratios ($N = 9253$ / $N = 6777$).

Non-linear effects of continuous predictors (e.g., raw latitude, quadratic effects, hump-shaped thermal responses) on transformed responses, and interactions between the four environmental predictors were not tested to focus on testing specific predictions and for maintaining the simplicity of the model structure. For each model, we explored the estimated marginal means of linear trends, representing the mean response of elemental content to a given predictor while keeping other predictors at their average values (emmeans-package[78]).

We estimated the significance of each marginal effect using a permutation procedure with 1000 iterations. In each iteration, we randomly permuted location identities, permuting absolute latitude or all environmental predictors together while keeping the relationship between elemental content and species identity. Then, we calculated the slope and standard error to generate a t-statistic distribution based on the permuted LMM results for each environmental parameter. By comparing the original and permuted t-statistics, we derived *P* values, which were then adjusted for multiple testing using the Benjamini-Hochberg procedure[79]. To ensure model assumptions were met, we examined QQ-plots and partial residuals against each predictor. Furthermore, we estimated explained variances by computing pseudo-R^2 coefficients for the entire models (piecewiseSEM-package[80]) and for each predictor (*partR2*-package[81]). Since proportions were modeled with a logit-normal (i.e., %N, %P) or log-normal distribution (i.e., N:P), we back-transformed the model outcomes to expected means using $e^y/(1+e^y)$ and e^y for elemental content and N:P, respectively, to improve visualization.

Because the observed patterns could be influenced by spatial locations (i.e., sets of environmental characteristics) or the identity of species/morphospecies (i.e., sets of elemental content), we conducted sensitivity analyses to assess the stability of our results. We aimed to determine whether the relationships between the elemental content of living organisms and the predictors remained consistent when using the main core of the data, defined as 95% of locations or species/morphospecies identities. To conduct these sensitivity analyses, we followed a similar procedure as described previously. However, in each iteration, we randomly removed five percent of locations (mean number of locations removed ($\pm$ SD) = 27.2 ± 11.7; mean percent of elemental records = $95.1 \pm 2.0\%$) or species/morphospecies (mean number of species/morphospecies removed ($\pm$ SD) = 101.2 ± 39.8; mean percent of elemental records = $95.0 \pm 1.6\%$). We then compared original and permuted t-statistics to establish the significance of a given predictor (i.e., *P* values). Overall, the observed trends in the elemental content of organisms along latitudes or environmental drivers, whether null, negative, or positive (Supplementary Table 1), remained robust to the random removal of 5% of either location or species identities (Supplementary Table 7). These results indicate that the environmental signature in organismal stoichiometry is preserved in the core of our database and that observed trends are resistant to minor changes in specific sets of locations or species. Importantly, these permutation and sensitivity tests also serve to evaluate robustness to potential measurement variation and uncertainty in environmental proxies, confirming that observed relationships were not artefacts of data structure.

Last, we acknowledge that our main models intentionally included two correlated predictors (i.e., temperature and radiation; Spearman's $r = 0.74$, Fig. 1). Excluding a predictor from a model may potentially result in omitted variable bias[82]; however, integrating two correlated predictors may lead to multicollinearity problems[83]. Regarding this double-edge issue and because of our hypothesis-testing approach, we were more concerned about omitted variables bias than multicollinearity problems and thus integrated the two correlated predictors into the main models. However, for the sake of statistical transparency, we decided to present additional models excluding either radiation or temperature. Using a procedure similar to the one described above to evaluate the significance of marginal effects, we aimed to determine any changes in estimates (e.g., gains or losses of significant relationships) in those additional models compared to estimates from the main models.

In comparison to the main models, removing radiation resulted in the emergence of five significant relationships: a negative effect of temperature on the N content of terrestrial autotrophs, as well as between the P content of heterotrophs (primarily influenced by freshwater heterotrophs) and N deposition. Additionally, we observed a positive effect between the N:P of all organisms (irrespective of the realm or trophic group) and that of heterotrophs (irrespective of the realm) and N deposition (Supplementary Table 5). Notably, all other predictors maintained similar effects (i.e., remained significant or non-significant, positive or negative) with the elemental content of organisms as estimated by the main models (Supplementary Tables 1 and 5). Similarly, excluding temperature resulted in the emergence of one significant relationship compared to the main models (i.e., the P content of freshwater heterotrophs against N deposition; Supplementary Table 5), which is also significant in the model excluding radiation, while only one relationship was not significant anymore (the N:P ratio of freshwater organisms against N deposition; Supplementary Table 5). The explained variance, both marginal and conditional, remained quantitatively consistent between the main models and those excluding radiation or temperature from predictors (Supplementary Table 2). In sum, these two additional models do not invalidate the key findings found in the main models. All statistical analyses and figures presented in this paper were conducted and generated using R 4.0.0[84]).

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

The StoichLife dataset analyzed in this study is archived in Dryad: González AL, Dézerald O, et al. *StoichLife: A global database of organismal stoichiometry*, Dryad, (https://doi.org/10.5061/dryad.3tx95x6r2) and described in González et al. (2025), *Scientific Data*[49] (https://doi.org/10.1038/s41597-025-04852-w).

Code availability

The RMarkdown notebook used to clean, analyze, and visualize the data is archived in Zenodo (https://doi.org/10.5281/zenodo.17064046).

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Author contributions

A.L.G. and O.D. wrote the first draft of the manuscript with inputs from the sBiomaps working group. O.D., J.M., and A.L.G. carried out most of the statistical analyses and the graph production. A.L.G. and O.D. compiled the sBiomaps database and obtained the iDiv funding that supported sBiomaps. A.L.G., O.D., K.A., U.B., M.F., H.H., W.S.H., M.C.J., M.J., M.P.N., R.E.O., G.L.W.P., R.P., M.St., A.R., E.S., J.Si., S.J.L., and E.Z. cleaned the database and compiled environmental data. G.L.W.P. and K.A. helped produce global environmental maps. A.L.G., O.D., J.M., K.A., U.B., M.F., H.H., W.S.H., M.C.J., M.J., M.P.N., R.E.O., G.L.W.P., R.P., A.Pe., M.St., A.R., E.S., J.Si., S.J.L., and E.Z. participated in one or more of the three sBiomaps workshops at iDiv, where the sBiomaps initiative was organized, and the evaluation of the data and first drafts were discussed. All other authors (A.M., S.B., H.D., N.E., V.F.F., J.H., P.K., C.L., E.K.M., M.E.P., A.Po., G.Q.R., J.M.R., S.S., N.S., J.Se., M.Ste., W.I.S., and A.T.) contributed data. All authors contributed to writing and editing the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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