

Review

Exploring Nutrient Stoichiometry in Inland Waters: A Bibliometric and Ecological Review of C:N:P Ratios in Freshwater Ecosystems

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Abstract

Nutrient stoichiometry, particularly the balance of carbon (C), nitrogen (N), and phosphorus (P), plays a fundamental role in regulating freshwater ecosystem dynamics, primary production, and biogeochemical cycling. This study presents one of the first dedicated reviews to combine bibliometric mapping with ecological synthesis of C:N:P ratios in inland waters, drawing on 1004 publications indexed in the Web of Science Core Collection (2000–2025), comprising peer-reviewed articles and review articles refined by document type, language, and research area. Bibliometric mapping using VOSviewer (version 1.6.20) identified exponential growth in publications after 2010, with phosphorus dynamics and eutrophication emerging as the most-cited themes, while recent years have shown increasing attention to C:P ratios as reliable ecological indicators. Four dominant thematic clusters were identified: Nutrient Cycling and Biogeochemistry; Phytoplankton and Food Web Dynamics; Eutrophication and Water Quality; and Climate Change and Ecosystem Responses. Ecological synthesis demonstrated substantial deviations from the canonical Redfield ratio (106C:16N:1P), with pronounced stoichiometric variability across trophic states, latitudes, and ecosystem types. Case comparisons revealed high C:P ratios in Arctic and alpine lakes linked to dissolved organic carbon inputs, low N:P ratios in tropical waters that promote cyanobacterial dominance, and stable, low phosphorus concentrations in deep African lakes. These findings emphasize the significance of flexible stoichiometry in predicting ecosystem tipping points, managing harmful algal blooms (HABs), and guiding nutrient restoration strategies. By integrating bibliometric and ecological evidence, this study identifies C:P ratios as a promising candidate indicator that merits further field validation for freshwater management, while underscoring persistent research gaps in microbial stoichiometry, cross-scalar modeling, and policy uptake in the Global South.



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1. Introduction

Stoichiometry in ecology describes the balance of chemical elements—principally carbon (C), nitrogen (N), and phosphorus (P) that constrain organismal growth, food-web interactions, and ecosystem processes [1]. The elemental ratios of C:N:P therefore provide a simple yet powerful lens for assessing the biotic and abiotic controls on freshwater ecosystems. While originally developed in marine ecology, the classical Redfield stoichiometry (106:16:1 for C:N:P) has served as a conceptual baseline [2]. However, freshwater systems typically exhibit far greater stoichiometric variability due to catchment influences, episodic hydrology, and anthropogenic nutrient enrichment [3].

From a nutrient-cycling perspective, C:N:P ratios reflect the relative supply and processing rates of organic carbon and mineral nutrients across the water–sediment interface. These balances mediate decomposition, denitrification, and internal phosphorus release, ultimately determining whether ecosystems function as nutrient sinks or sources [4]. Such processes influence downstream water quality and the global carbon budget, highlighting why stoichiometry is central to both local ecosystem management and Earth-system science [5].

From an ecological standpoint, cellular and community-level elemental composition shapes growth rates, competitive hierarchies, and trophic transfer efficiency [6,7]. Under phosphorus limitation, many phytoplankton reduce their P quota while storing excess C and N, producing seston with elevated C:P ratios. This stoichiometric mismatch reduces food quality for grazers, disrupting zooplankton dynamics and cascading to fish populations [8]. Conversely, in nitrogen-limited systems, N-fixing cyanobacteria often dominate, altering oxygen dynamics, toxin regimes, and ecosystem resilience [9].

Deviations in C:N:P ratios are now recognized as practical early-warning indicators of eutrophication, harmful algal blooms (HABs), and hypoxia [10]. Long-term monitoring has shown that sustained high C:P ratios can signal phosphorus scarcity and successful reoligotrophication, whereas persistently low C:P or N:P ratios are associated with continued nutrient enrichment and a risk of blooms [11,12]. Climatic drivers, including temperature, precipitation, and monsoon cycles, further modulate stoichiometric variability across latitudes and seasons [13,14]. Anthropogenic drivers exacerbate these natural gradients, as catchment land use, fertilizer application, and wastewater inflow consistently disrupt elemental balances, leading to eutrophic conditions and biodiversity loss [15,16].

Sedimentary archives provide an additional long-term record of C:N:P dynamics, preserving historical nutrient loading, ecological thresholds, and regime shifts [17]. Despite the abundance of case studies, research on freshwater stoichiometry remains fragmented. Studies are often restricted to particular lakes, taxa, or regions, and methodological heterogeneity complicates synthesis across studies [18]. Global trends in freshwater stoichiometry are therefore insufficiently synthesized, limiting the capacity to embed stoichiometric theory into predictive management models.

To address this gap, bibliometric analysis offers a reliable and reproducible approach. By systematically mapping scientific output, bibliometrics quantify trends in publication growth, author collaborations, thematic clusters, and geographic contributions [19,20]. This approach has been widely used in environmental sciences to trace conceptual evolution, identify research hotspots, and reveal underexplored areas [21].

Despite the long history of stoichiometric theory, no dedicated bibliometric synthesis has yet to map the structure, growth, and thematic evolution of freshwater C:N:P research as a distinct field. Such a synthesis is needed for three reasons. First, the volume of publications has grown rapidly since 2000, making it increasingly difficult for researchers and managers to identify dominant themes, key contributors, and underexplored areas without systematic mapping. Second, freshwater stoichiometry is a genuinely cross-disciplinary

field spanning limnology, biogeochemistry, ecology, and water quality management, and bibliometric analysis is well-suited to reveal how these disciplines interact and where integration is weak. Third, translating stoichiometric knowledge into operational management tools, particularly for HAB prediction and eutrophication control, requires clarity about what the research community has established and where the evidence base remains thin. The study period begins in 2000 rather than 1963 (when the foundational Redfield ratio paper was published) for a deliberate and practical reason: the Web of Science Core Collection provides reliable, consistent, and electronically searchable metadata for journal articles from approximately 2000 onwards, ensuring reproducibility and completeness of the bibliometric dataset. Pre-2000 literature, while foundational, is inconsistently indexed and would introduce substantial retrieval bias into a quantitative bibliometric analysis. The conceptual contributions of Redfield and other pre-2000 authors are fully acknowledged in the Introduction and Discussion and are incorporated into the ecological synthesis, even though they fall outside the formal bibliometric window.

The aims of the present review are fourfold: (1) to quantify temporal and spatial trends in freshwater C:N:P stoichiometry research between 2000 and 2025; (2) to identify thematic hotspots including phosphorus dynamics, eutrophication, and phytoplankton adaptation through bibliometric mapping; (3) to synthesize ecological evidence for C:N:P variability across regions and trophic states; and (4) to highlight research gaps and policy-relevant implications, particularly the emerging potential of C:P as an operational early-warning indicator for freshwater monitoring and management.

2. Materials and Methods

This study conducted a focused bibliometric analysis of C:N:P research in freshwater ecosystems between 2000 and 2025 using the Web of Science (WoS) Core Collection. Rather than restricting the corpus by journal quartile, the search was refined by database, document type, language, and research area, a strategy chosen to capture the disciplinary core of freshwater stoichiometry while maintaining a reproducible, electronically indexed dataset [22]. This design does not screen for journal ranking; consequently, high-quality regional or applied studies published in lower-indexed or non-English outlets, and relevant work outside the WoS Core Collection, are underrepresented. This is a recognized limitation of single-database, English-language bibliometrics and is carried through the interpretation of all geographic and thematic patterns below [23].

A systematic search was conducted using the following Web of Science Topic Search (TS) query, applied to titles, abstracts, author keywords, and indexed terms: TS = (("C:N:P ratio" OR "Carbon Nitrogen Phosphorus" OR "C/N/P" OR "C:N:P stoichiometry" OR "Elemental Stoichiometry" OR "Ecological Stoichiometry" OR "Nutrients Ratio" OR "nutrient cycle") AND ("freshwater ecosystem" OR "lakes" OR "river" OR "stream" OR "reservoir" OR "wetland" OR "freshwater phytoplankton" OR "phytoplankton Stoichiometry" OR "eutrophication" OR "inland water")). The query deliberately pairs a broad set of stoichiometric terms with a broad set of freshwater-habitat terms and imposes no mandatory process-specific term as an intersecting requirement, ensuring that microbial, benthic, sediment, dissolved-organic-matter, and food-web studies are retained, provided they address freshwater elemental stoichiometry. Results were then refined to the WoS Core Collection, limiting document types to Article and Review Article, English-language records, and the Environmental Sciences and Ecology research-area group (including Marine and Freshwater Biology, Water Resources, Biodiversity Conservation, and related categories). Data extraction was completed in July 2025, yielding 1004 records spanning ecology, limnology, biogeochemistry, and environmental science. Records were exported as full records and deduplicated in R and Excel. Keyword co-occurrence analysis used author-supplied key-

words; because the export did not include a separate Keywords Plus field, the two keyword types were not combined. The complete list of analyzed records, identified by DOI, is provided as Supplementary Material to ensure full reproducibility of the corpus [19].

The analytical workflow, summarized in Figure 1, involved the following sequential steps: (1) database query and full-record export from WoS; (2) data cleaning and deduplication in R (version 4.4.1: R Core Team, Vienna, Austria) and Microsoft Excel (Microsoft Corporation, Redmond, WA, USA); (3) conversion to formats compatible with VOSviewer (version 1.6.20; Centre for Science and Technology Studies, Leiden University, Leiden, The Netherlands); (4) construction of a keyword co-occurrence network and a country-level co-authorship and citation network; (5) computation of citation metrics, publication trends, and thematic clusters; (6) visualization of networks, trends, and thematic clusters; and (7) ecological synthesis and interpretation, in which the bibliometric patterns are integrated with the broader limnological literature. For the keyword co-occurrence network, only terms occurring at least five times were retained, a conventional threshold that suppresses idiosyncratic single-study terms while preserving recurring concepts. This multistage process ensured rigorous filtering, reproducibility, and transparent data handling.

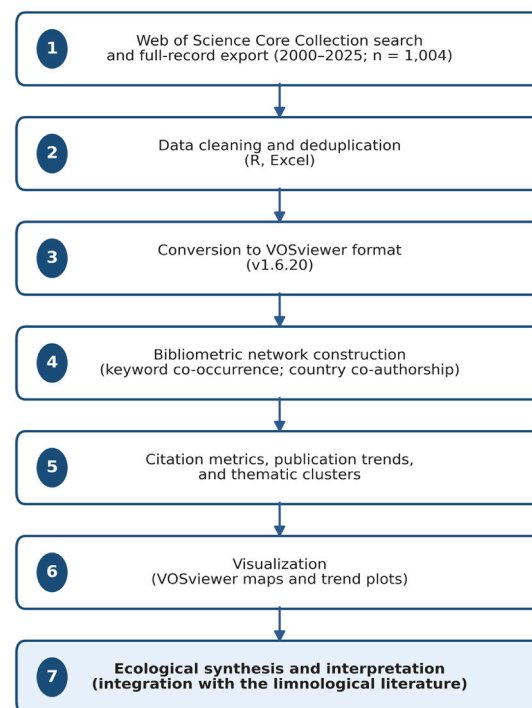


Figure 1. Flowchart of the data extraction, bibliometric analysis, and ecological synthesis workflow. The final stage integrates the bibliometric patterns with the broader limnological literature. Note: Limitations- The analysis is restricted to English-language records in the WoS Core Collection and was refined by document type and research area rather than by journal quartile; it therefore omits influential regionally oriented or non-English literature and work outside the Core Collection. These constraints are reflected in the interpretation of geographic patterns throughout this review.

The methodology integrates quantitative bibliometric mapping (publication trends, keyword co-occurrence, author and country networks) with qualitative ecological synthesis (case comparisons, stoichiometric ranges, and management implications), enabling examination of both the scholarly landscape and its alignment with empirical ecosystem realities [24]. An important methodological limitation should be noted: keyword co-occurrence frequencies reported here are raw counts and were not normalized against total annual publication output in ecology or environmental science. As a result, observed increases in keyword frequency may partly reflect the overall growth in scientific pub-

lishing rather than genuine field-level shifts in research focus. Interpretations of keyword trends should therefore be read as indicative patterns rather than definitive evidence of changing research priorities [21]. A further limitation concerns geographic interpretation in particular. Because the corpus is confined to English-language records in the Web of Science Core Collection, the apparent dominance of North American, European, and Chinese output and the near-absence of African and most South American systems partly reflect indexing and language coverage rather than the true global distribution of freshwater stoichiometry research. Studies published in regional or non-English journals, in gray literature, or in outlets outside the Core Collection are systematically underrepresented. The geographic and collaboration patterns reported here should therefore be read as the structure of the internationally indexed, English-language literature rather than a complete census of global research effort, and country-level comparisons are best treated as relative rather than absolute.

3. Results

3.1. Publication Trends and Citation Growth

Figure 2 presents the annual publication counts and cumulative citation trajectory in freshwater C:N:P stoichiometry research across the 25-year study period. Publication output remained modest between 2000 and 2009, then grew substantially after 2010. This growth coincided with, but cannot be causally attributed to, increasing global attention to freshwater quality and nutrient management. Peak annual output occurred in 2020–2022 (2022, $n = 81$; 2021, $n = 77$; 2020, $n = 75$). Although this period overlapped with intensified international environmental commitments such as the UN Sustainable Development Goals (United Nations, 2015) and expanded national monitoring programs, the present data document the publication trend itself and do not establish its drivers; such associations are offered as plausible context rather than demonstrated causes [25]. The citation curve followed a parallel trajectory, confirming both increasing publication volume and the growing scientific influence of the field. The rise in citations between 2010 and 2024 indicates that foundational publications are increasingly referenced in applied contexts, reflecting a maturation of the field from theoretical to management-oriented inquiry. It should be noted that citation and publication counts for 2025 are substantially lower than preceding years, as data extraction was completed in July 2025 and therefore captures only a partial year of output. The 2025 data point should be interpreted with this limitation in mind and does not represent a genuine decline in research activity or scientific interest in the field.

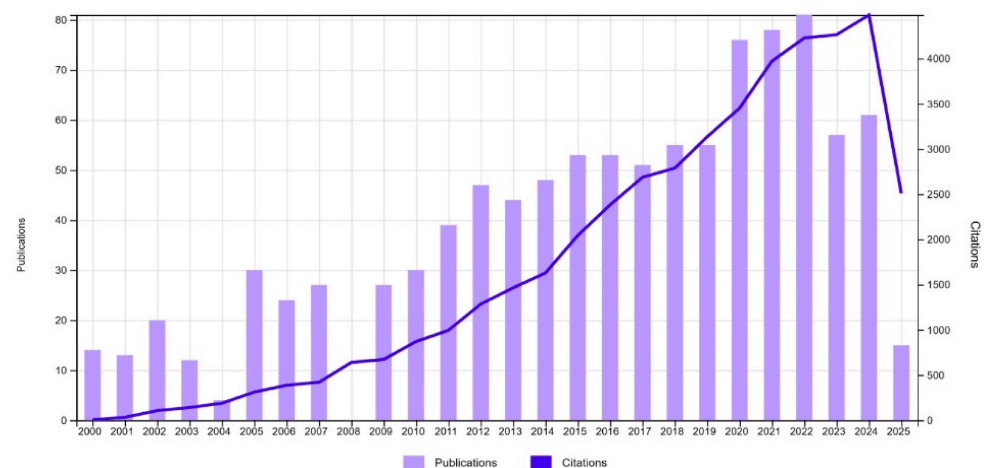


Figure 2. Temporal trends in publications and citations on freshwater C:N:P stoichiometry (2000–2025).

3.2. Keyword Co-Occurrence Network and Thematic Clustering

To visualize the conceptual evolution of the field, VOSviewer was employed to generate a keyword co-occurrence network (see below Figure 3) [20]. Only keywords appearing at least five times were included. Prominent terms such as Eutrophication, Nitrogen, Phosphorus, Periphyton, and Pelagic Zone formed dense thematic clusters, reflecting their critical roles in freshwater C:N:P dynamics. Clustering was based on modularity optimization, grouping keywords with stronger internal linkages into coherent thematic areas. Emerging terms such as Wetland, Geomorphology, and Permafrost have appeared in recent years, indicating expanding thematic boundaries toward climate-mediated nutrient processes.

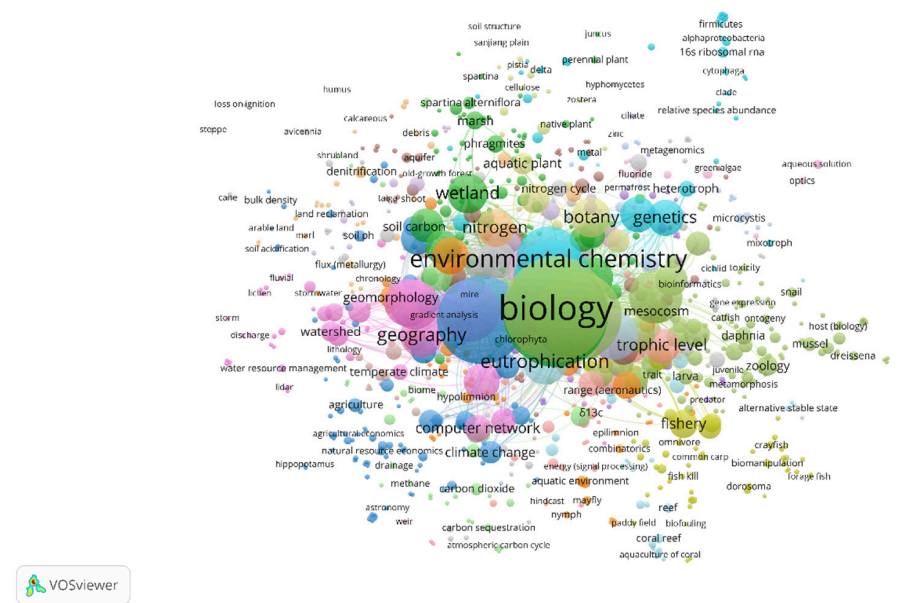


Figure 3. Keyword co-occurrence network (2000–2025) showing four thematic research clusters, visualized in VOSviewer. Red = Nutrient Cycling and Biogeochemistry; Green = Phytoplankton and Food Web Dynamics; Blue = Eutrophication and Water Quality; Yellow = Climate Change and Ecosystem Responses.

Four dominant research clusters were identified: (1) Nutrient Cycling and Biogeochemistry (Red Cluster) anchored by carbon, nitrogen, phosphorus, and C:N:P ratio, highlighting foundational stoichiometric work and biogeochemical theory; (2) Phytoplankton and Food Web Dynamics (Green Cluster) centered on phytoplankton, zooplankton, algal blooms, and primary production, reflecting research on how stoichiometric imbalances propagate through aquatic food webs; (3) Eutrophication and Water Quality (Blue Cluster) incorporating eutrophication, phosphorus limitation, lake management, and water quality, emphasizing applied research connecting stoichiometric imbalances with ecosystem degradation; and (4) Climate Change and Ecosystem Responses (Yellow Cluster) integrating warming, temperature, Arctic lakes, and climate change, capturing how global environmental change modifies nutrient ratios and ecosystem resilience. Strong co-occurrence links between the C:N:P ratio and eutrophication bridge theoretical stoichiometry and applied management, while links between phytoplankton and climate change signal growing interest in interactive stressors.

3.3. Geographic Distribution of Research Output

Figure 4 illustrates the international landscape of scholarly influence based on co-authorship and citation networks. By publication output, the United States (372 records)

and China (316; aggregating records indexed as Peoples R China and China) lead by a wide margin, followed by the United Kingdom (approximately 97, aggregating England, Scotland, Wales, and Northern Ireland), Germany (88), Canada (84), Spain (60), France (41), and Australia (40). In the co-authorship and citation network, the United States, China, and Canada occupy the most central positions, linked by dense collaboration ties; Canada's centrality reflects its high co-authorship connectivity rather than raw output, in which it ranks fifth. Peripheral contributors, including Germany, the United Kingdom, Australia, and Sweden, bridge collaborations across Europe, North America, and Asia. The dispersed arrangement of smaller nodes representing developing countries suggests emerging but limited integration into the global research network. The geographic analysis identifies a pronounced underrepresentation of African and South American freshwater systems: South Africa (10 records) is the only African country in double figures, with all other African nations appearing in only one or two records each (approximately 20 country appearances in total), while South American output is concentrated in Brazil (35) and Argentina (21). Because the corpus is confined to English-language WoS Core Collection records, this pattern reflects indexing and language coverage as well as genuine research activity and should be interpreted partly as a database artifact rather than solely as scientific scarcity. Even allowing for this caveat, the limited representation of these regions of high ecological variability, climate vulnerability, and intensifying nutrient pressures indicates a clear gap in the globally indexed evidence base.

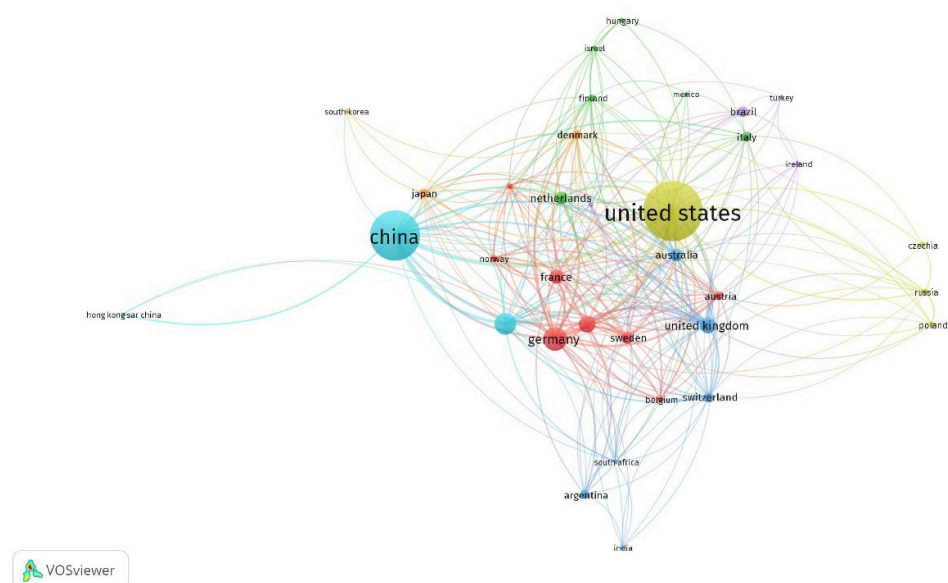


Figure 4. Country-level collaboration and citation map showing leading nations in freshwater C:N:P stoichiometry research (2000–2025). Node size reflects publication output and link strength.

4. Discussion

The bibliometric and ecological synthesis presented here offers a 25-year panoramic view of freshwater C:N:P stoichiometry research, revealing both the intellectual maturation of the field and the persistent empirical and policy gaps that constrain its application in water management. The following subsections integrate bibliometric trends with ecological evidence to build a coherent interpretive framework. Throughout, we distinguish bibliometric findings, publication, keyword, and country-level patterns derived from the 1004-record corpus, from ecological interpretations, which draw on broader primary literature and therefore extend beyond the formal bibliometric dataset.

4.1. C:P Ratios and Phytoplankton Community Structure

The carbon-to-phosphorus (C:P) ratio is a key determinant of phytoplankton community composition and nutrient cycling dynamics in freshwater ecosystems [26]. Changes in C:P ratios can alter community structure, fuel the development of harmful algal blooms, and modify food web efficiency [27]. Phosphorus limitation is tightly coupled to carbon dynamics via dissolved organic carbon (DOC) and inorganic carbon (DIC): in Chinese Loess Plateau reservoirs, high DIC and total nitrogen (TN) favored Bacillariophyta, whereas low TN:TP ratios promoted Cyanophyta dominance [28]. Extremely high sestonic C:P ratios sometimes exceeding 500 in summer in nutrient-loaded European lakes indicate severe phosphorus depletion, reducing algal productivity and zooplankton grazing efficiency and facilitating the competitive advantage of bloom forming cyanobacteria [29].

Stoichiometric flexibility in bloom-forming cyanobacteria is well documented: *Cylindrospermopsis raciborskii* can thrive under variable N:P regimes, and CO₂ concentration, light availability, and temperature can override strict nutrient-driven competitive rules [30]. Elevated CO₂ and nitrogen concentrations increase microcystin production in *Microcystis aeruginosa*, establishing a direct link between atmospheric carbon chemistry and toxin expression [31]. Rising atmospheric CO₂ can further strengthen cyanobacterial competitive advantage by alleviating carbon deficiency, suppressing green algae, and shifting nutrient competition toward nitrogen and phosphorus limitation [32,33], a climate-change interaction of critical management relevance.

Figure 5 visually summarizes how varying C:P ratios shape phytoplankton community composition. Broader ecosystem studies corroborate this: in Lake 227 (Canada), shifts in C:P ratios through stimulated *Daphnia* grazing catalyzed a collapse of nitrogen-fixing cyanobacteria [34], sediment records of Yunnan Plateau lakes document historical phytoplankton transformations associated with decreasing sedimentary C:P driven by anthropogenic eutrophication [35]. Stoichiometric balances are further regulated by food web dynamics, as *Daphnia* grazing can moderate cyanobacterial dominance by redistributing phosphorus in favor of edible phytoplankton taxa [36].

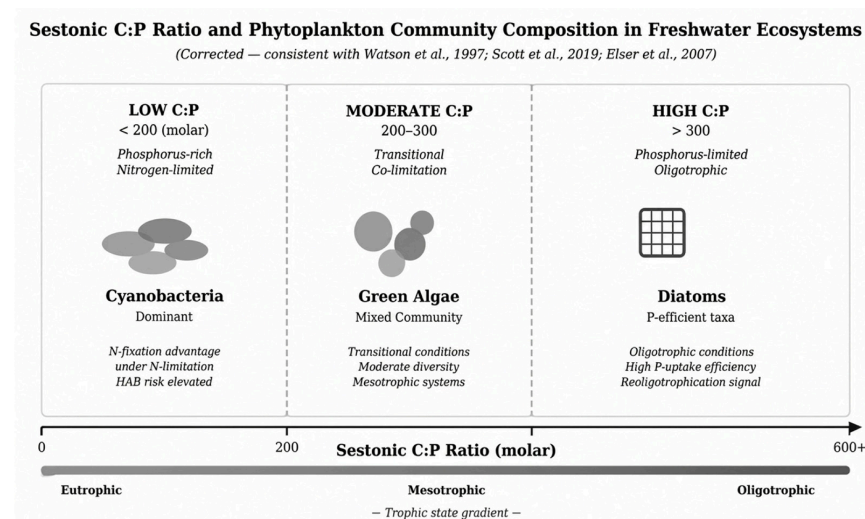


Figure 5. Corrected conceptual diagram illustrating how sestonic C:P ratios relate to phytoplankton community composition. Low C:P (<200, molar) reflects phosphorus-rich, often nitrogen-limited conditions that favor nitrogen-fixing cyanobacteria; moderate C:P (200–300) is associated with transitional nutrient conditions supporting mixed communities including green algae; high C:P (>300) reflects strong phosphorus limitation typical of oligotrophic systems where P-efficient taxa such as diatoms are competitively favored. This revised depiction is consistent with established limnological theory [37–39], and corrects a prior version that misclassified cyanobacteria as high C:P (phosphorus-limited) conditions.

4.2. C:N Ratios and Nutrient Limitation Dynamics

Carbon-to-nitrogen (C:N) ratios are primary determinants of nitrogen availability and ecosystem productivity [40,41]. A high C:N ratio signals nitrogen limitation, in which microbial decomposition and nutrient regeneration become inefficient, particularly in allochthonous systems [42]. In nitrogen-limited subarctic lakes, consumer-driven nutrient recycling cannot fully compensate for stoichiometric imbalances arising from high C:N organic matter inputs [43]. In the Yangtze River basin, elevated DOC:DON ratios under baseflow conditions were associated with increased phytoplankton nitrogen limitation, demonstrating that hydrological regimes directly modulate stoichiometric nutrient control [44]. Land degradation in alpine streams similarly elevated C:N ratios by increasing DOC concentrations more than TN or TP, altering microbial and biofilm stoichiometry [45].

Lake browning and warming-induced DOC inputs shift ecosystems toward greater nitrogen limitation, favoring nitrogen-fixing cyanobacteria over diatoms [46], a pattern with direct implications for predicting community shifts under continued climate warming. Urban nitrogen loading intensifies C:N imbalances in downstream freshwater systems, as TN loads scale with urban density and climate scenarios [47]. Long-term N and P additions have reduced stoichiometric flexibility in stream ecosystems, increasing systemic vulnerability to environmental disturbance [48]. Collectively, C:N ratios serve as a dynamic integrator of ecosystem processes, linking land-derived inputs, climate drivers, and trophic responses into a single measurable parameter.

4.3. Phosphorus Dynamics and Stoichiometric Thresholds

Phosphorus (P) is the primary driver of freshwater productivity, and its speciation and threshold concentrations govern ecological outcomes [49]. Soluble reactive phosphorus (SRP) is the most biologically available fraction, while total phosphorus (TP) includes organic and particulate fractions of lower immediate bioavailability [50]. This discrepancy can distort eutrophication risk assessments, as elevated TP does not necessarily reflect available P for biological uptake [51]. Dissolved organic phosphorus (DOP) plays an important supplementary role under P-limiting conditions through alkaline phosphatase (APA)-mediated hydrolysis, and APA activity serves as a sensitive enzyme indicator of phosphorus limitation in stratified lakes [52].

Figures 6 and 7 provide schematic conceptual illustrations of threshold transitions in phosphorus dynamics; both figures are qualitative in nature and are not derived from statistical modeling of the bibliometric dataset. The threshold values shown are approximations drawn from the broader limnological literature and vary substantially among lake types, latitudes, and trophic histories. C:P and N:P ratios serve as practical indicators of nutrient limitation: in temperate ecosystems, $N:P > 20$ indicates phosphorus limitation, while $N:P < 10$ indicates nitrogen limitation or risk of cyanobacterial dominance [53]. Tropical systems experience longer, more persistent sediment P regeneration than temperate lakes, which exhibit greater seasonal variability in internal P dynamics [54]. Table 1 summarizes key C:N:P stoichiometric thresholds and their ecological interpretations.

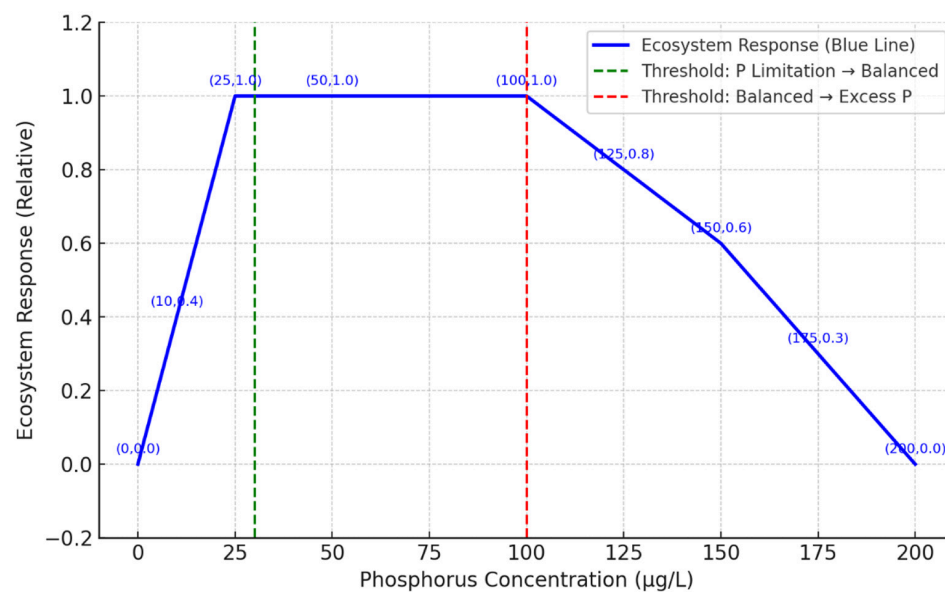


Figure 6. Schematic conceptual diagram of phosphorus dynamics and ecosystem response in freshwater ecosystems. The y-axis “ecosystem response” refers qualitatively to the level of biological activity, including primary production, algal biomass, and nutrient cycling rates. Under phosphorus limitation (total phosphorus < 30 µg/L), ecosystem productivity is constrained by phosphorus availability; under balanced conditions (30–100 µg/L), productive but diverse phytoplankton communities typically develop; under phosphorus excess (>100 µg/L), eutrophication and HAB events become more likely [39,55]. This figure is a schematic conceptual illustration only. Threshold values are approximate and vary substantially among lake types, latitudes, and seasons. The figure does not represent empirical data or a fitted statistical model and should not be used to predict ecosystem responses for specific water bodies without site-specific assessment.

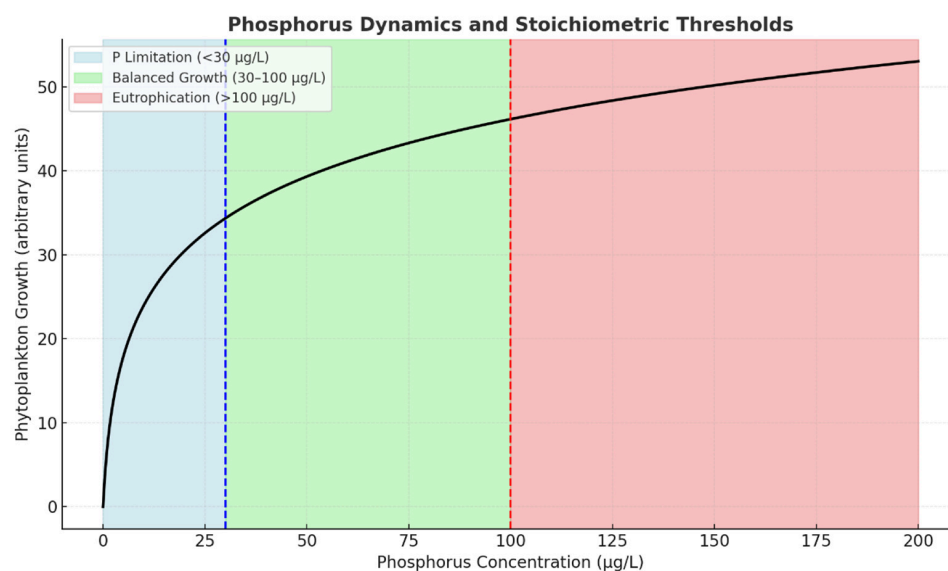


Figure 7. Schematic conceptual diagram of the phosphorus threshold continuum from limitation to excess in freshwater ecosystems, illustrating progressive transitions toward eutrophication as phosphorus loading increases. The blue dotted vertical line marks the 30 µg/L threshold separating phosphorus-limited conditions from balanced growth, and the red dotted vertical line marks the 100 µg/L threshold separating balanced growth from eutrophication, consistent with the thresholds described in the main text and in Figure 6. This figure is a conceptual illustration based on established limnological principles and is not derived from a primary statistical analysis of the bibliometric dataset. It is intended to provide a qualitative interpretive context for the stoichiometric thresholds discussed in the text.

Table 1. Summary of key C:N:P stoichiometric thresholds in freshwater ecosystems.

Threshold (Molar Ratio)	Ecological Implications	Key References
C:N ≈ 7.8–10.5	Balanced organic matter production; deviations suggest shifts between phytoplankton and heterotrophic dominance	[56,57]
N:P ≈ 16 (Redfield)	Benchmark for nutrient sufficiency; values < 16 indicate N-limitation; values > 16 indicate P-limitation	[58–60]
C:P < 200	High P availability; favors fast-growing phytoplankton; potential for bloom formation	[26,39]
C:P > 300	Strong P-limitation; reduced primary production; intensified competition for P among phytoplankton	[61]
N:P > 30	Risk of P-driven eutrophication; cyanobacterial dominance in temperate lakes	[62,63]
Variable C:N:P across latitudes	Lower N:P in tropical lakes, higher ratios in temperate systems; climatic modulation of limitation patterns	[26,64]

Note: All threshold values are expressed as molar ratios. These thresholds are approximate and context-dependent: they vary substantially among lake types, latitudes, trophic histories, hydrological regimes, and organic-carbon loadings, and should be treated as interpretive reference points rather than universally applicable cut-offs.

4.4. Synergistic Interactions and Functional Stoichiometry

Functional stoichiometry models treat C:N:P ratios as predictors of biological interactions, community structure, and process activity across the climatic and latitudinal spectrum [65]. Changes in C:P and N:P ratios influence phytoplankton taxon dominance and species-specific traits, including cell size and nutrient acquisition efficiency [26]. Phosphorus limitation typically prevails under high light, whereas low light increases nitrogen limitation, generating resource-dependent community switches with cascading effects on lake metabolism and food-web energy flow [8,66].

Ecosystem warming combined with nutrient enrichment favors smaller, faster-growing phytoplankton taxa with higher nutrient requirements and reduced internal C:P ratios [67]. Non-additive interactive effects between temperature and nutrient stressors on stoichiometric ratios across trophic levels further complicate prediction and management [66]. Internal cellular stoichiometry does not always reflect ambient nutrient conditions, as phytoplankton may exhibit homeostatic regulation or stoichiometric plasticity depending on growth stage and nutrient saturation [5,68]. Regional discrepancies in sediment C:N:P ratios, largely driven by fertilized lake catchments, further illustrate the role of organic matter and redox dynamics in controlling nutrient delivery and microbial bioavailability [69].

4.5. The Redfield Ratio as a Baseline and Its Freshwater Limitations

The Redfield ratio (106C:16N:1P) was derived for marine plankton and open-ocean conditions and has long served as a familiar reference point in aquatic nutrient-limitation theory, though it was never proposed as a universal benchmark for inland waters [2]. Modern ecological stoichiometry has long treated elemental ratios as flexible, so the pronounced deviations observed in freshwater are expected consequences of catchment inputs, residence time, and internal recycling rather than departures from a normative standard. Although the bibliometric corpus is bounded to 2000–2025 to ensure consistent Web of Science metadata, the ecological synthesis developed here rests on the foundational pre-2000 literature. Redfield’s identification of a characteristic marine elemental ratio [2], together with subsequent whole-lake nutrient-enrichment experiments and comparative analyses of nitrogen and phosphorus limitation in lakes (e.g., the work of Schindler and of Guildford and Hecky), established the conceptual basis on which the modern freshwater stoichiometry literature builds. The 2000–2025 trends mapped in this review, therefore, represent the continuation and quantitative refinement of this earlier theoretical lineage rather than

an independent point of departure. While marine phytoplankton often approximates this stoichiometry, freshwater environments deviate significantly due to heterogeneous catchment inputs, variable residence times, and internal recycling dynamics [70]. Seston and particulate C:N:P in lakes diverge substantially from Redfield proportions, often exhibiting elevated C and highly variable N:P [71]. Cyanobacteria exhibit high C:P and flexible N:P, whereas diatoms maintain lower C:P and distinct element allocation strategies [53].

In Lake Erie, seston under phosphorus limitation often exceeds 400:40:1, far beyond Redfield proportions [72]. In Lake Taihu (China), persistently high N:P ratios associated with nitrogen-rich agricultural runoff drive the dominance of nitrogen-fixing cyanobacteria [73]. Our bibliometric mapping confirms that, while Redfield-based assumptions still frequently serve as a baseline, publications emphasizing deviations from Redfield expectations have grown substantially since 2010, indicating a field-wide shift toward flexible, ecosystem-specific stoichiometric models. Fixed-ratio models fail to capture the complex interactions of eutrophication, warming, and altered precipitation on nutrient stoichiometry [74,75]. Extreme events such as deep-water nutrient upwelling in Lake Tanganyika [76], storm-triggered P releases in Lake Okeechobee [77], and severe C:N:P fluctuations following flood-drought cycles in Australian reservoirs all illustrate the inadequacy of fixed-ratio assumptions. Replacing Redfield assumptions with flexible, region-specific, climate-sensitive stoichiometric modules is a critical methodological priority [78].

4.6. Global C:N:P Patterns and Regional Case Highlights

Freshwater C:N:P ratios exhibit substantially greater variability than marine systems: C:N ratios range from 8 to 30, C:P from 100 to 1000, and N:P from 10 to 60 across global lakes, rivers, and reservoirs [26]. Arctic and alpine lakes exhibit high C:P ratios (often >600), driven by limited phosphorus availability and large DOC inputs from warming permafrost and glacial melt [79,80]. Tropical lakes and rivers tend toward low N:P ratios (<15), which promote nitrogen-fixing cyanobacterial dominance [81]. East Asian water bodies, subjected to intensive aquaculture and agricultural phosphorus loading, show tighter N:P coupling and persistent eutrophication [82]. The African Great Lakes, such as Victoria, Tanganyika, and Malawi, are characterized by unusually stable, low phosphorus concentrations and distinct stoichiometric regimes that support unique microbial communities and carbon burial dynamics [83]. Scandinavian oligotrophic lakes exhibit elevated C:N variability due to peatland DOC inputs, while phosphorus scarcity maintains low productivity [84].

According to Elser et al. (2007), eutrophic systems tend to have lower C:P and N:P values because they are phosphorus-rich, while oligotrophic systems maintain higher ratios due to nutrient scarcity [39]. Figure 8 illustrates global research intensity and eutrophication-prone hotspots, and Table 2 summarizes C:N:P ranges across major regions, ecosystem types, and trophic states.

Table 2. Representative ranges of freshwater C:N:P ratios across regions, ecosystem types, and trophic states.

Region/System	Ecosystem Type	Trophic State	Reported Ratios (C:N:P)	Source
Arctic/ Alpine lakes	Lakes	Oligotrophic	High C:P (>600), N:P ~ 20–40	[79]
Tropical lakes/ rivers	Lakes and rivers	Eutrophic–mesotrophic	Low N:P (<15), C:P ~ 200–400	[81]
Great Lakes (NA)	Large lakes	Variable	N:P ~ 20–40, C:P ~ 250–600	[1]
East Asia	Reservoirs	Eutrophic	N:P ~ 15–25, C:P < 300	[82]
African Great Lakes	Deep lakes	Oligotrophic	N:P ~ 30–50, C:P ~ 400–700	[83]

Note: All ratio values are expressed in molar units.

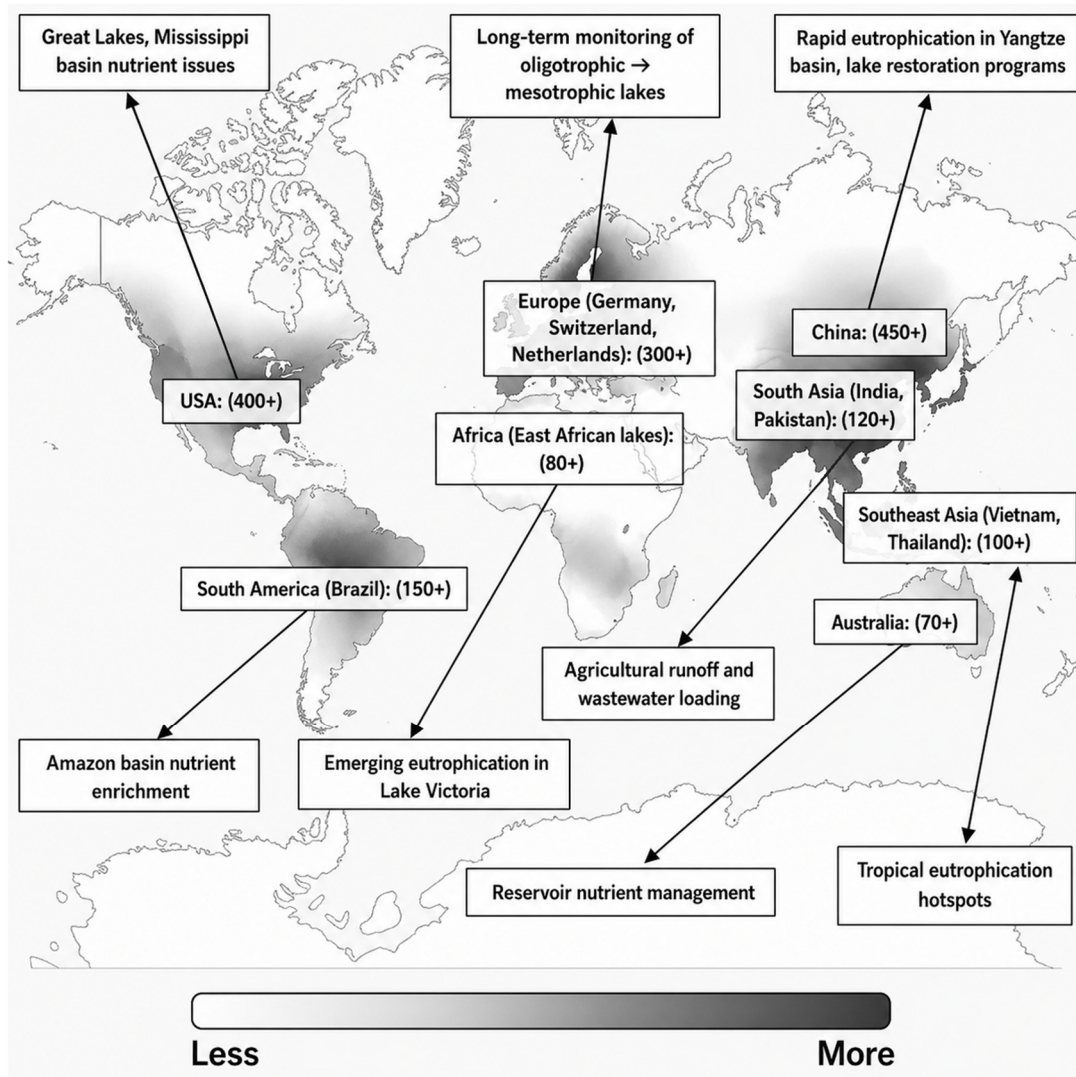


Figure 8. Global distribution of C:N:P stoichiometry research intensity (2000–2025) with eutrophication-prone hotspots highlighted [6,24,85].

4.7. C:P Ratios as an Emerging Management Indicator

A convergent finding from both bibliometric trends and ecological case studies is the growing research attention to the C:P ratio as a candidate decision-support indicator in freshwater management, recognizing that the bibliometric trend documents interest rather than validating any specific operational threshold. Unlike N:P ratios, which have historically dominated discussions of nutrient limitation, C:P provides a unified measure of the interplay between organic carbon dynamics and phosphorus cycling. High C:P reflects phosphorus limitation through shifts in phytoplankton community composition or increases in organic matter deposition, both of which are directly relevant to ecosystem restoration outcomes [24,86]. Critically, C:P ratios can serve as early warning signals of eutrophication or reoligotrophication before external manifestations such as oxygen depletion or HAB events become apparent [87]. In Lake Hallwil (Switzerland), sestonic C:P ratios rose progressively following cuts in phosphorus loading, providing a quantitative signal of ecosystem recovery before classical indicators responded. In contrast, the African Great Lakes, including Lake Victoria, have maintained persistently low C:P ratios consistent with long-term eutrophication under high phosphorus loading regimes. Bibliometric trends confirm a sustained rise in publications focused on C:P stoichiometry, aligning with this ecological shift toward applied management and HAB suppression rather than purely

theoretical Redfield-based models [64]. In practical terms, lake and reservoir managers can interpret sestonic or seston-based C:P ratios as follows. When C:P ratios fall below approximately 200 (molar), conditions are phosphorus-rich and ecosystems are at elevated risk of eutrophication and HAB development, warranting immediate investigation of external phosphorus loading sources and consideration of nutrient reduction interventions such as catchment best management practices or phosphorus-retaining constructed wetlands [53,55]. When C:P ratios are in the range of 200–300, the system is approaching phosphorus co-limitation, and managers should maintain monitoring frequency and avoid further phosphorus inputs. When C:P ratios exceed 300, the system is under strong phosphorus limitation, and sustained high C:P over multiple seasons can be interpreted as a signal of successful reoligotrophication following nutrient management measures [35,87]. These thresholds are not universal; they vary with lake trophic state, latitude, and organic carbon inputs and should be applied alongside complementary indicators such as total phosphorus concentrations, chlorophyll a, and Secchi depth. However, incorporating routine C:P monitoring into existing water quality programs would provide an additional early-warning layer that responds to ecosystem change before classical indicators deteriorate, enabling more proactive and cost-effective management responses [88].

4.8. Management, Policy Implications, and Research Gaps

The most actionable application of C:N:P stoichiometry is the prediction and management of HABs [89]. Low N:P ratios promote the dominance of nitrogen-fixing cyanobacteria because under nitrogen-limited, phosphorus-enriched conditions, cyanobacteria gain a competitive advantage through their ability to fix atmospheric nitrogen, which is unavailable to most other phytoplankton taxa [37,90,91]. Elevated N:P ratios, by contrast, are generally associated with oligotrophic or nitrogen-enriched conditions where cyanobacteria are not competitively dominant [38]. In subtropical Chinese reservoirs, cyanobacteria prevail when N:P falls below threshold values indicative of nitrogen limitation [92], emphasizing that relative nutrient ratios, not absolute concentrations, are the most reliable predictors of bloom risk.

Incorporating stoichiometric knowledge into integrated lake management through dual-nutrient management strategies that address both nitrogen and phosphorus simultaneously consistently outperform phosphorus-only approaches [55]. Sediment dredging, amendment capping, and phosphorus-retaining constructed wetlands have demonstrated measurable long-term reductions in algal biomass in shallow eutrophic lakes [93]. Stoichiometric modeling also enhances hydrological management: reservoir simulations in the South Saskatchewan River basin demonstrated how temperature and reduced flow interact with C:N:P dynamics to affect phytoplankton richness [94]. Embedding C:P monitoring within regulatory frameworks, such as the EU Water Framework Directive, would enable more adaptive and evidence-based responses to nutrient enrichment before irreversible ecological deterioration occurs [95,96].

Despite significant advances, several critical gaps constrain the field's predictive capacity and management application. First, tropical, subtropical, and African freshwater systems are dramatically underrepresented in the literature, despite being hotspots of nutrient-cycling complexity and climate vulnerability [97]. Second, microbial stoichiometry remains understudied relative to phytoplankton dynamics, despite bacteria and archaea mediating key biogeochemical transformations [98]. Third, mechanistic models incorporating flexible, region-specific, climate-sensitive stoichiometric parameters would be valuable for replacing fixed Redfield assumptions in operational management tools [74]. Fourth, standardization of C:P-based early-warning thresholds across monitoring networks would improve cross-study comparability and support adaptive management policy at regional

and global scales [88]. Fifth, advances in high-frequency remote sensing, autonomous in situ monitoring platforms, and machine learning offer transformative opportunities for real-time stoichiometric detection at the catchment scale [99].

5. Conclusions

This study provides a comprehensive bibliometric and ecological synthesis of global research on C:N:P nutrient stoichiometry in freshwater ecosystems over the 25-year period 2000–2025. The principal findings are as follows:

1. Publication output in freshwater C:N:P stoichiometry grew exponentially after 2010, driven by increased global policy attention to eutrophication, water quality management, and climate-nutrient interactions, with 2020–2022 recording peak annual volumes.
2. Bibliometric mapping identified four primary research clusters: Nutrient Cycling and Biogeochemistry; Phytoplankton and Food Web Dynamics; Eutrophication and Water Quality; and Climate Change and Ecosystem Responses—reflecting a conceptual evolution from foundational stoichiometric theory toward applied, management-oriented science.
3. The United States, China, and Canada dominate global research output and collaboration networks. Africa and South America remain significantly underrepresented despite their ecological importance, climate vulnerability, and rapidly intensifying nutrient pressures.
4. Ecological synthesis confirms substantial and systematic deviations from the canonical Redfield ratio across freshwater systems globally, with C:P ratios ranging from <200 in eutrophic tropical systems to >600 in oligotrophic Arctic lakes, driven by trophic state, latitude, catchment geology, and anthropogenic loading.
5. C:P ratios appear to be a promising candidate metric for freshwater management, with the potential to detect eutrophication and reoligotrophication before classical indicators such as dissolved oxygen or HAB occurrence respond; this potential is indicated by the literature synthesized here and requires site-specific field validation before operational use.

5.1. Study Contributions

This research makes three core contributions. First, it presents one of the first dedicated bibliometric syntheses of C:N:P stoichiometry in freshwater ecosystems, drawn from the Web of Science Core Collection and refined by document type, language, and research area rather than by journal quartile, with the resulting coverage limitations made explicit. Second, by combining bibliometric mapping with ecological synthesis, the study bridges scientometric trends with empirical ecosystem realities, offering a dual-perspective integration that strengthens interpretations. Third, it highlights C:P ratios as actionable decision-support tools for eutrophication control, HAB prevention, and lake restoration with direct relevance to water quality governance.

5.2. Future Research Priorities

Priority areas for future investigation include: (1) expanding empirical stoichiometric studies to underrepresented tropical, subtropical, and African freshwater systems; (2) developing flexible, region-specific mechanistic models that replace fixed Redfield assumptions with climate-sensitive stoichiometric parameters; (3) advancing microbial stoichiometry research to capture the full biogeochemical cycling role of bacteria and archaea in freshwater systems; (4) standardizing C:P-based early-warning thresholds across national and international monitoring networks for cross-system comparability; and (5) leveraging emerging

technologies including remote sensing, autonomous in situ sensors, and machine learning for real-time stoichiometric monitoring at catchment scale.

5.3. Policy and Management Implications

Embedding C:P monitoring into water quality frameworks such as the EU Water Framework Directive and regional watershed management plans can provide pre-emptive signals of eutrophication risk before catastrophic ecological deterioration. Recognizing the regional variability of N and P limitation patterns, management should adopt flexible stoichiometry-based nutrient controls rather than phosphorus-only approaches. Expanding stoichiometric monitoring to the Global South will enable more equitable and ecologically effective global water governance. As freshwater ecosystems face mounting pressures from climate change, agricultural intensification, and urbanization, integrating C:N:P ratios into monitoring and management frameworks offers a proactive pathway toward ecological resilience and sustainable water governance.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/hydrology13070164/s1>. The data supporting the findings of this study are available from the corresponding author upon reasonable request.

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