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Original Research

From Methodological Foundations to Biodiversity Applications: A Comprehensive Analysis of Environmental DNA Research Trends (1992–2024)

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Abstract

Over the last decade, environmental DNA (eDNA)-based bioassessment has emerged as one of the most rapidly evolving and widely adopted methodologies in biodiversity research. In this context, we present a comprehensive overview of the eDNA research field based on a bibliometric analysis of 4524 documents published between 1992 and 2024. The journals with the most published articles on eDNA were Environmental DNA, PLOS ONE, and Molecular Ecology Resources. The countries with the most eDNA publications were the United States, China, and Japan. The structural topic modeling method employed allowed us to identify the main research topics, their interrelationships, and their temporal dynamics. Based on the temporal change in research topics, the application of eDNA research has shifted from methodological research to biodiversity and community research since 1992. The results were interpreted to provide insights into the current state of the eDNA research field, shedding light on the advancements, challenges, and potential applications of eDNA metabarcoding.

Keywords: environmental DNA, bibliometric analysis, structural topic modeling, temporal analysis, biodiversity

Introduction

Environmental DNA (eDNA) analysis is a transformative approach in molecular ecology that provides a non-invasive and highly efficient way to study biodiversity and ecosystem dynamics [1, 2]. Through

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meticulous analysis of DNA from environmental matrices (e.g., water, soil, and air), eDNA metabarcoding has become a cornerstone technique, as it enables species identification and offers insights into their distribution and abundance [3, 4]. According to Taberlet et al. [5], the term eDNA analysis was first introduced by Ogram in a 1987 publication, focusing on DNA extraction from sediments; subsequently, it has been applied to monitor phytoplankton blooms and understand their biomass regulation [6, 7]. Since the early 21st century, cloning-based metagenomics and metagenomic sequencing have gained widespread use in microbiology research [8, 9]. This sequencing has drastically changed methodological approaches in ecology and conservation biology, shifting from labor-intensive sampling to a holistic and less disruptive examination of biodiversity.

The core of eDNA analysis is metabarcoding, which uses high-throughput DNA sequencing to identify multiple species from a single environmental sample. Targeting specific DNA regions allows researchers to identify a wide range of taxa – from microbes to higher organisms – and assess their abundance and diversity in ecosystems, such as using the mitochondrial cytochrome c oxidase subunit I (COI) gene of approximately 650 bp [10, 11]. eDNA fragments are usually shorter (approximately 100 bp), with sequences from other genes (often mitochondrial, chloroplast, or ribosomal RNA genes) besides COI used in analyses [12].

eDNA metabarcoding has transformed biodiversity studies and monitoring, offering valuable information for conservation, environmental impact assessments, and ecological research [13, 14]. A key advantage of eDNA metabarcoding is its ability to detect rare and elusive species, surpassing traditional survey methods in identifying hard-to-observe or -capture species [1, 15]. This non-invasive approach has been shown to be especially beneficial in aquatic ecosystems for monitoring elusive or endangered species, invasive species, and detecting pathogens or parasites [16-18].

In recent years, eDNA metabarcoding use has expanded to terrestrial ecosystems, enabling monitoring of plant communities, detection of elusive mammals, and assessment of soil biodiversity [19-21]. The growing use of eDNA metabarcoding across various ecosystems and taxonomic groups has accumulated a significant literature base, underscoring the importance of identifying trends and advancements in this field. In the last two decades, eDNA research has seen significant growth, marked by a considerable increase in publications on eDNA metabarcoding applications [22].

Previous eDNA reviews were either field-specific [23, 24] or focused on particular taxonomies [25-27]. In this study, we conducted a comprehensive bibliometric analysis of 4,524 articles published from 1992 to 2024, focusing on keywords such as "environmental DNA", "environmental DNA metabarcoding", and "eDNA metabarcoding" within the Web of Science and Scopus databases. Our goal was to offer a detailed overview of the eDNA research landscape through bibliometric analysis and structural topic modeling (STM). By analyzing the temporal trends, hot research areas, and thematic networks of eDNA research, we hope to improve our understanding of the field's evolution and identify future directions in research.

Material and Methods

Data Collection

We conducted a comprehensive literature search in the Web of Science Core Collection (WoSCC) and Scopus databases to collect relevant articles on February 18, 2024. For the search, we utilized the databases' advanced search functions, with a formula that included terms for "environmental DNA", "environmental DNA metabarcoding", and "eDNA metabarcoding" in various fields (topic, title, author keywords, and keywords plus). Notably, we excluded the term "extracellular" due to its shared abbreviation with eDNA, as publications related to this term primarily pertain to the medical field.

We retrieved a total of 4,524 articles for further analysis, comprising articles, review articles, editorial materials, early-access publications, proceedings papers, book chapters, book reviews, data papers, and letters, but excluding corrections, meeting abstracts, news items, and notes (see Table S1). Due to inadequate coverage, some Chinese publications were not included in the WoSCC and Scopus databases. To fill this coverage gap, additional databases should be incorporated, though this could introduce a bias regarding other languages [28]. A detailed workflow of literature compilation and data cleaning is provided in Fig. S1.

Bibliometric Analysis

To analyze the bibliometric characteristics of the collected articles, we utilized the R package bibliometrix [29], which allowed us to use various bibliometric indicators, such as annual publication counts, average citations per year, prominent journals, and the countries of the corresponding authors. We examined the temporal dynamics of publication output, identified the most productive journals and countries, and analyzed collaboration patterns among countries based on the literature data.

Structural topic modeling (STM)

To identify main research topics and their interrelationships in the eDNA research field, we employed the R package stm [30]. STM is a statistical method that combines topic modeling and network analysis to uncover latent thematic structures in document corpora. Before applying STM, text preprocessing included removing words with fewer than three characters and custom stopwords using the textProcessor function in the stm package [30]. The

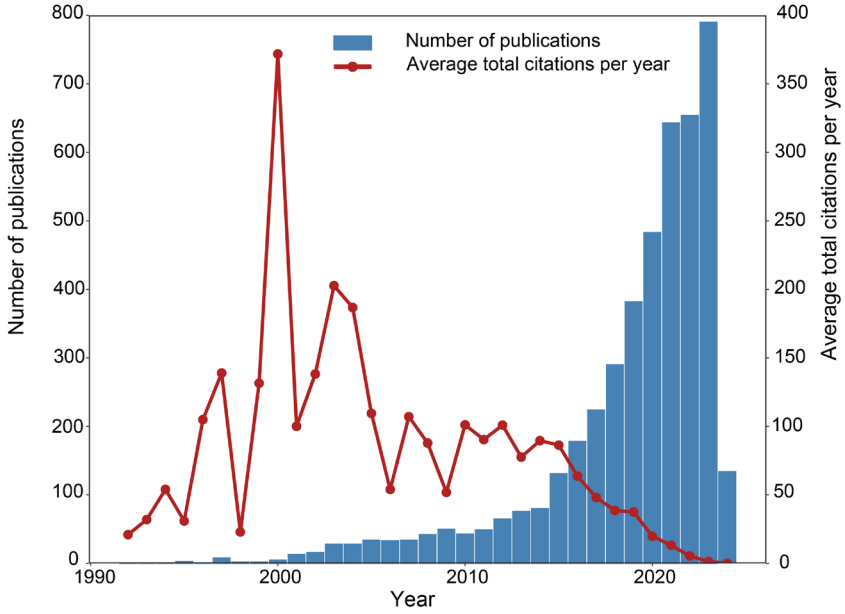

Fig. 1. Temporal evolution of outputs and citations on Environmental DNA (eDNA) research.

prepDocuments function further filtered out terms occurring fewer than 10 times to refine the corpus for analysis (Fig. S1).

We utilized STM to identify underlying themes and their evolution over time, as well as the relationships between different eDNA research topics. Words within a document are assigned to topics, allowing documents to span multiple themes. Each document is represented as a vector of topic proportions, reflecting the probabilistic distribution of words across topics. This flexibility ensures that interdisciplinary studies are not forced into rigid classifications (see Table S1 for full topic proportions). The number of topics (K = 25) was determined by evaluating model exclusivity and semantic coherence across a range of potential topic numbers (K = 8-40). For each K, models were run three times, and evaluation metrics indicated that both exclusivity and semantic coherence were jointly maximized at K = 20-30. Supplementary Fig. S2 illustrates this trade-off.

We visualized the relationships between research topics by constructing a co-occurrence network through the bibliographic coupling method. This method represents shared references between articles as nodes connected by edges [31]. We calculated the co-occurrence relationship strengths and visualized the network with appropriate visualization techniques [32]. To understand the temporal trends in the eDNA research field, relative changes in topic prevalence were analyzed by comparing studies from the rapid growth period of 2021-2024, which accounted for 49% of the analyzed studies, to those published before 2021. This metric identifies topics gaining or losing prominence relative to others. Additionally, we conducted a Mann-Kendall Trend Test (MK test) on the annual prevalence of each topic from 1992-2023 to evaluate absolute temporal trends (see Fig. S3). Additionally, we assessed the emergence and decline of specific topics to identify hot areas and potential future directions in research.

Results and Discussion

Temporal Evolution of Outputs

Fig. 1 shows the annual number of eDNA research publications from 1992 to 2024. The number of publications increased from a single one in 1992 to 790 in 2023, and reached 134 in just the first two months of 2024, with an average annual growth rate of 50%. Between 1992 and 2014, publication numbers exhibited a wavelike growth pattern, followed by a significant increase after 2015, with approximately 86.4% of outputs published from 2015 to 2024. The rising trend in eDNA research outputs aligns with the global increase in scientific output numbers [33]. Research articles constituted the majority (87.9%) of publications. Other document types included reviews (8.7%), editorial materials (1.4%), and early-access publications (23.3%).

Besides the increasing publication numbers, Fig. 1 also reveals a nearly inverse trend in average citations per publication over the past 30 years. From 1992 to 2015, average yearly citations experienced fluctuations. Four seminal articles from 2000 and 2003 [2, 11, 12, 34] received exceptionally high average total citations in their respective years. Nevertheless, average citations per publication have decreased since 2015. This trend may be due to the increased annual output of eDNA research, which has provided scientists with a broader selection of references. Consequently, the number of citations per publication might have decreased due to researchers having more options. Citation time lag

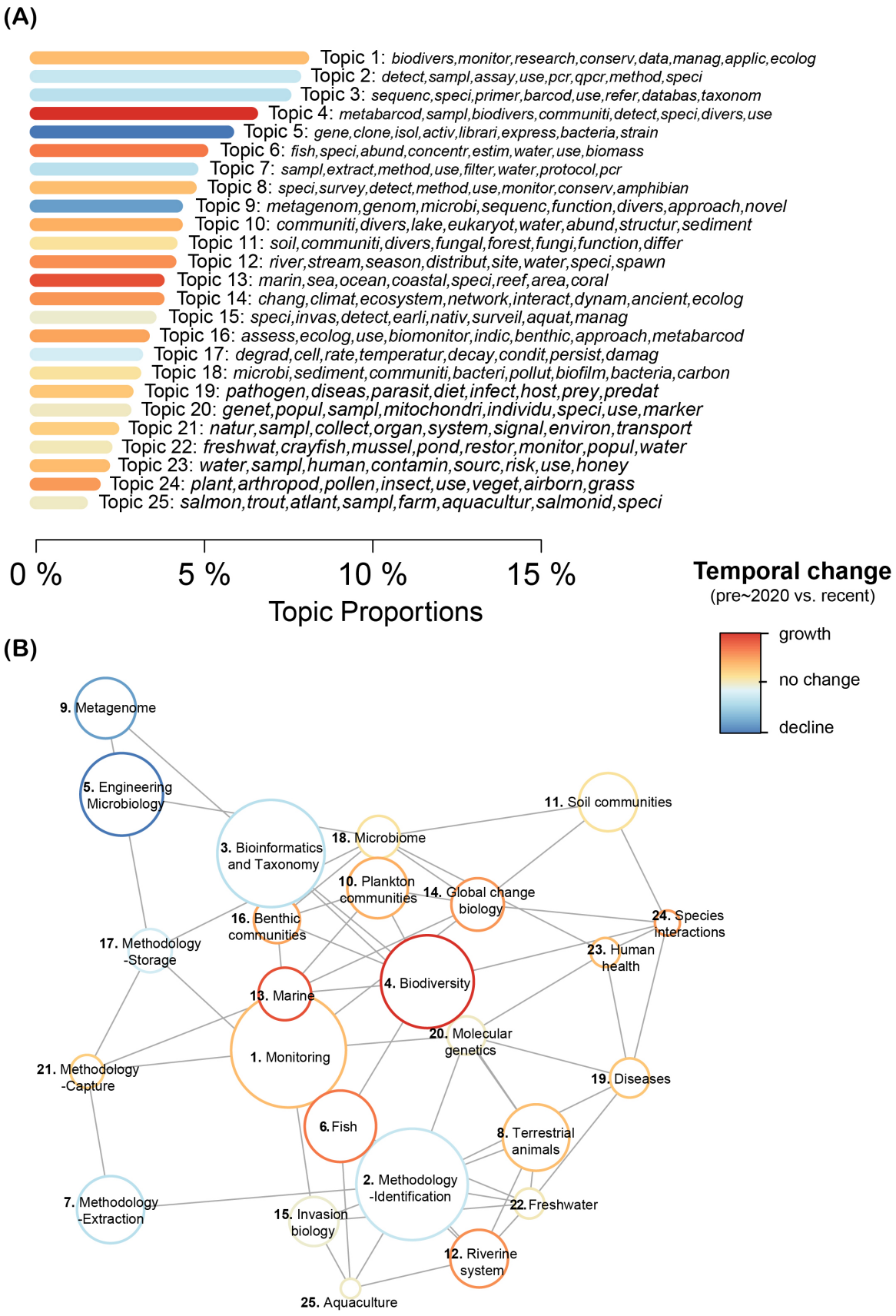

Fig. 2. Structural topic model results from 4,524 studies published from 1992 to 2024. a) Bar chart of topic proportions across all years, indicating the percentage of the total corpus that belongs to each topic, with topic numbers corresponding to topic names in the network graph. The top-eight words by probability associated with each topic are given in italics; b) Topic correlations network used to visualize quantitative associations between topics (nodes), with topics near each other and connected by a gray line more likely to appear together in a given study. Node sizes are proportional to overall topic proportions. Both bar and node color denote the relative change in prevalence over time within each topic.

could have also contributed to the decline in the number of average citations, where newer publications often receive fewer citations than earlier works, regardless of their impact. Newly published works usually take longer to reach the slow-growth citation phase.

Temporal Evolution of Research Areas

A computational text analysis of the 4524 studies from 1992-2024 identified 25 major topics. Each topic is characterized by high-probability words in titles, abstracts, and author keywords, as shown in Fig. 2. The unsupervised structural topic model uncovered a wide range of topics without prior classifications, including application-based (e.g., topic 1, Monitoring), conceptually based (e.g., topic 8, Metagenome), methods-based (e.g., topic 2, Methodology-Identification), and system-focused (e.g., topic 13, Marine) topics. No single topic overwhelmingly dominated as a proportion of the overall corpus. Biodiversity/species monitoring was the most common topic (topic 1; 7.9% of all text analyzed), whereas aquaculture survey was the least common topic (topic 25; 1.3% of all text analyzed).

We used correlation network analysis to visualize clusters of related research topics, as illustrated in Fig. 2. Related topics share common word sets within and across studies. Topics related to biodiversity and community ecology, global change biology, and species interactions clustered together (i.e., upper-right portion of Fig. 2), as did those related to eDNA methodology (i.e., left portion of Fig. 2). Biodiversity (topic 4) served as a key node, playing a pivotal role in linking different elements of the network.

Based on our results, eDNA research topics have evolved over time: some have significantly declined in prevalence, while others have increased (see Fig. 2). Despite their overall prevalence, methodology-based topics related to extraction, identification, and storage have decreased by 29.9%, 24.1%, and 18.1%, respectively. Studies applying eDNA to biodiversity (topic 4) and community ecology (topics 10, 11, 16) have increased by 86.4% and 9.6%-40.9%, respectively. Topics related to global change biology (topic 14), such as climate change and human activities, and species interactions (topic 24) have increased by 46.2% and 44.7%, respectively. Topics related to engineering microbiology (topic 5) and metagenome (topic 9) saw the largest decline in prevalence, decreasing by 85.1% and 68.1%, respectively (see Fig. 2).

Our findings suggest a shift in eDNA-based research focus from methodology and theory towards practical applications. In other words, researchers are now interested in understanding not just the basic principles and theory of eDNA but are also starting to apply this method to specific ecological and biodiversity issues. For instance, foundational studies such as Jerde et al. [35] and Thomsen et al. [1] employed species-specific PCR primers to validate the feasibility and sensitivity of eDNA for detecting rare or invasive species, focusing primarily on technical validation and single-species detection. In contrast, recent research has shifted toward multi-taxa metabarcoding using universal primers (e.g., mitochondrial 12S rRNA for fish, COI for invertebrates) to address broader ecological questions. For example, Blackman et al. [36] and Li et al. [37] applied eDNA metabarcoding to assess spatio-temporal patterns of multi-trophic biodiversity across river catchments, explicitly investigating how human activities like dam construction alter multitrophic community structures and food-web dynamics.

The review by Ruppert et al. [38] and Schenekar's [39] study on freshwater ecosystems support this perspective. Since 2014, a broad spectrum of research has explored the use of eDNA metabarcoding in areas such as biodiversity conservation, community identification, fisheries management, targeting invasive species, and estimating fish biomass [40, 41]. This methodological shift has enabled researchers to analyze entire communities, quantify biodiversity responses to global change, and provide actionable insights for ecosystem assessments and environmental decision-making. Moreover, eDNA has demonstrated significant potential in human and animal health research, particularly for pathogen microorganisms detection, monitoring, and assessing environmental disease-related risks [42, 43]. This indicates that eDNA is a valuable tool not only for ecological research but also for tackling human health issues related to environmental exposures and pathogens [44, 45].

While relative changes highlight shifts in topic dominance (e.g., methodological topics declining relative to applied ecology), absolute trends confirm that all topics grew in publication volume over time (see Fig. S3). For instance, engineering microbiology (topic 5) decreased by 85.1% in relative prevalence but still showed a significant upward trend ($Z = 3.23$, $p<0.01$) in the MK test, despite having the lowest Z-value among topics. This dual perspective ensures readers do not misinterpret relative declines as reductions in research activity, but rather as a rebalancing of focus within an expanding field.

Despite current uncertainties in the biology and ecology of marine eDNA, its potential for monitoring marine environments is significant. A decade after Ficetola et al.'s [13] pioneering study, we are likely only witnessing the tip of the iceberg in terms of potential applications. Numerous new and unexplored areas hold interest for fisheries management and monitoring, including ecosystem monitoring, migration pattern assessment, stock structure, and diet and processed fish product analysis [46]. Our findings confirm Hansen et al.'s predictions about the dynamic and rapid development of marine eDNA research. eDNA-based monitoring is anticipated to evolve further, significantly benefiting the research and management of future fisheries and aquaculture [47, 48].

A significant challenge in eDNA research is the variability in extracts obtained from environmental

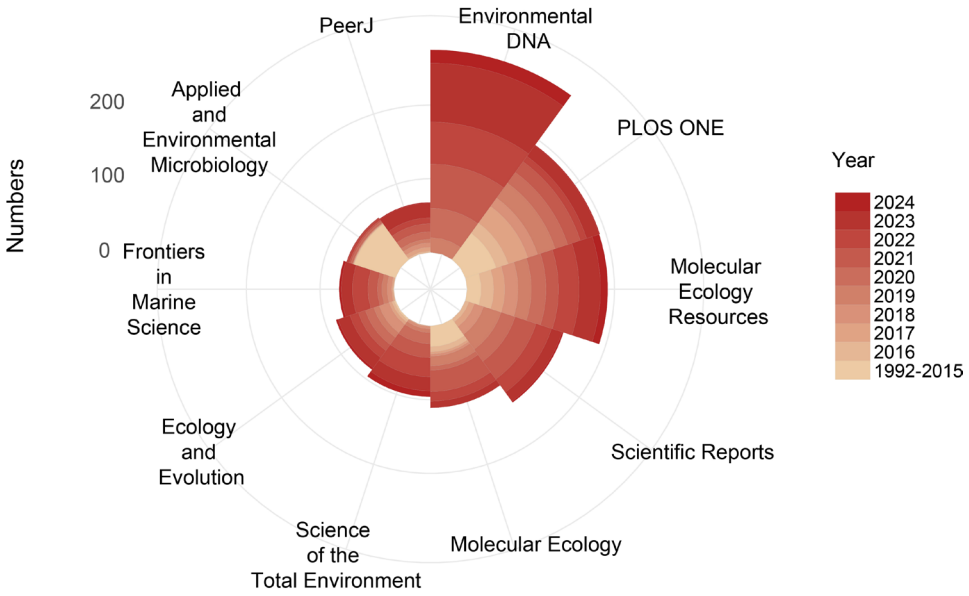

Fig. 3. Temporal trends of the top-ten most productive journals on eDNA research.

samples [15]. The quality of eDNA extracts varies widely, from high-quality concentrated DNA without enzyme inhibitors (akin to tissue-extracted DNA) to highly diluted and degraded DNA (comparable to ancient DNA research). This problem explains the recent surge in research on DNA collection (Topic 21). Although many studies have provided suggested operational methods [49-51], the spatial and temporal relevance of eDNA highly depends on environmental conditions [52, 53]. Therefore, understanding the environmental processes affecting the fate of eDNA in aquatic systems is crucial for linking collected eDNA to its organismal origins more accurately [54, 55].

While fish (topic 6) have been the primary focus of eDNA research, there is a notable gap in studies targeting some ecologically important taxa playing critical roles in aquatic ecosystems, such as corals and algae [56-58]. This underrepresentation may be attributed to challenges such as the lack of robust primers and efficient detection methods for low DNA concentrations [59-62]. To address this, it is essential to improve primer specificity, enhance reference databases, and optimize techniques for detecting low-concentration DNA.

The future development of eDNA applications can be anticipated to progress through three strategic phases. First, standardization of qualitative monitoring through technological refinement and database unification will establish eDNA as a routine tool for species detection, enabling large-scale biodiversity surveys. Second, centered on species quantification and abundance estimation, represents the current exploratory stage. Advancements in this phase will be invaluable for future research on community-level dynamics and ecosystem health assessments using eDNA [63-66]. Finally, the ultimate phase will focus on leveraging eDNA data to assess ecosystem functionality, thereby providing critical support for aquatic biodiversity conservation, ecosystem management, and evidence-based environmental policymaking [67].

The transition from qualitative detection to robust quantitative and functional analysis hinges on resolving two core challenges. The first concerns the standardization of eDNA quantification, which remains a critical bottleneck in the field. Advancing quantitative methodologies for aquatic organisms requires systematic calibration to address biological (e.g., species-specific shedding rates) and environmental variables (e.g., UV exposure, hydrological dynamics). While novel methodological advancements continue to emerge [68], their widespread validation across diverse taxa and ecosystem types remains an urgent priority. The second challenge involves extending eDNA applications to non-aquatic systems, including air, soil, and organic substrates (e.g., honey), each of which requires matrix-specific standardization protocols [69-71]. Only through such harmonization efforts can eDNA realize its full potential as a universally applicable tool for biodiversity monitoring across terrestrial, aquatic, and aerial ecosystems.

Marked Journals and Most Locally Cited Papers

Most eDNA research is concentrated in major journals, with the top ten most productive journals publishing 1302 articles, accounting for 28.78% of the total 4524 outputs, and each contributing more than 1.5%. These findings suggest that, despite the wide dispersion of eDNA research across journals, a few select ones remain the primary focus. Fig. 3 shows the top ten journals in eDNA research and their annual publication counts, which showed varied trends over

Table 1. Top ten most-cited papers in environmental DNA research.

Ranking	Title	Paper type	Year	Citations		LC/GC[1] Ratio (%)
				Local	Global	
1st	Environmental DNA – An emerging tool in conservation for monitoring past and present biodiversity [76]	Review	2015	759	1223	62.06
2nd	"Sight-unseen" detection of rare aquatic species using environmental DNA [35]	Article	2011	560	752	74.47
3rd	Monitoring endangered freshwater biodiversity using environmental DNA [1]	Article	2012	539	699	77.11
4th	Environmental DNA metabarcoding: Transforming how we survey animal and plant communities [16]	Review	2017	500	965	51.81
5th	Environmental DNA for wildlife biology and biodiversity monitoring [77]	Review	2014	482	694	69.45
6th	The detection of aquatic animal species using environmental DNA – a review of eDNA as a survey tool in ecology [24]	Review	2014	465	582	79.9
7th	Critical considerations for the application of environmental DNA methods to detect aquatic species [15]	Review	2016	435	625	69.6
8th	Next-generation monitoring of aquatic biodiversity using environmental DNA metabarcoding [4]	Article	2016	433	594	72.9
9th	Detection of a Diverse Marine Fish Fauna Using Environmental DNA from Seawater Samples [78]	Article	2012	427	556	76.8
10th	Estimation of Fish Biomass Using Environmental DNA [79]	Article	2012	410	481	85.24

Note: [1] LC: local citations; GC: global citations.

time. Recently, journals such as Environmental DNA, Scientific Reports, Science of the Total Environment, Frontiers in Marine Science, and Peerj have experienced significant growth. Environmental DNA's ranking among the top journals stems from its role as a dedicated platform for eDNA research, enabling researchers to publish and share findings in this rapidly evolving field.

Conversely, in recent years, there has been a decrease in total outputs from Applied and Environmental Microbiology and PLOS ONE. In the 2000s, Applied and Environmental Microbiology published many articles on microbial metagenomics [8, 72-74], laying a solid foundation for subsequent eDNA metabarcoding research. That is why, perceived as a modern-day technique, eDNA did not truly emerge until the early 2000s, when microbiologists started recognizing the potential of using genetic material to analyze biological communities [8, 75].

The document "Environmental DNA–An emerging tool in conservation for monitoring past and present biodiversity" by Thomsen and Willerslev [76] received the highest citation count of 759. Among the top ten most locally cited documents, there were five articles and five reviews. Full details are shown in Table 1. We found that six of these papers focus on monitoring and protecting aquatic biodiversity, and three complement field biodiversity surveys.

Corresponding Authors and Collaborations by Country

Fig. 4 lists the top twenty countries by number of eDNA publications according to the corresponding authors. The publication output of the top ten countries was more than four times higher than the combined total of the next ten countries. The United States had the highest number of single-country publications (892 articles) and the most multiple-country publications (176 articles). China and Japan also contributed significantly to the number of single-country publications. Although Portugal ranked last in overall publications, it had the highest rate of international collaborations (MCP ratio: 0.639). Lack of international collaboration has notably hindered eDNA research, particularly in Asian regions, underscoring the need to address this issue in the future [80].

These gaps stem partly from methodological limitations: our reliance on English-language databases

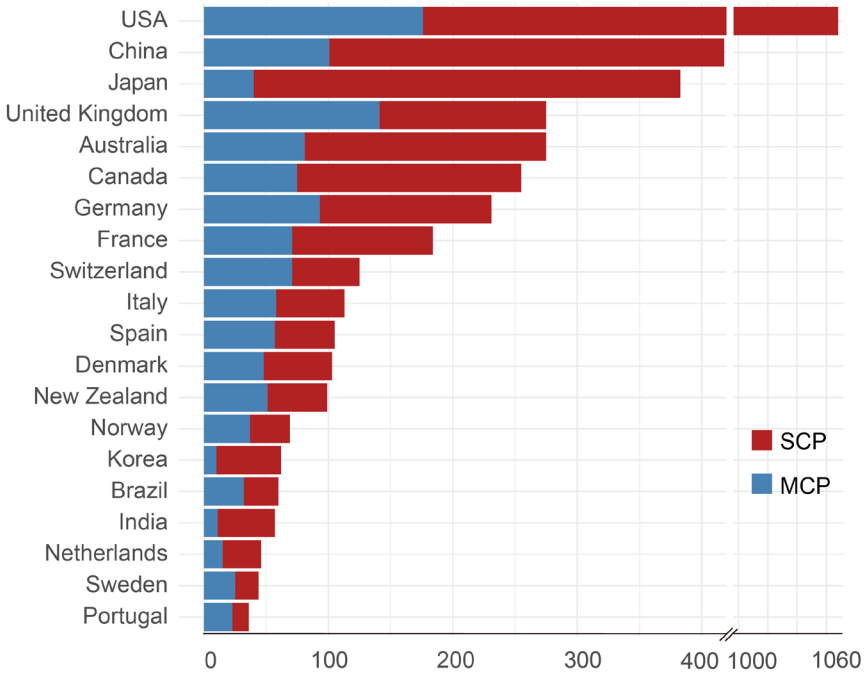

Fig. 4. Top-twenty countries for eDNA research based on corresponding authors. MCP: multiple-country publications; SCP: single-country publications.

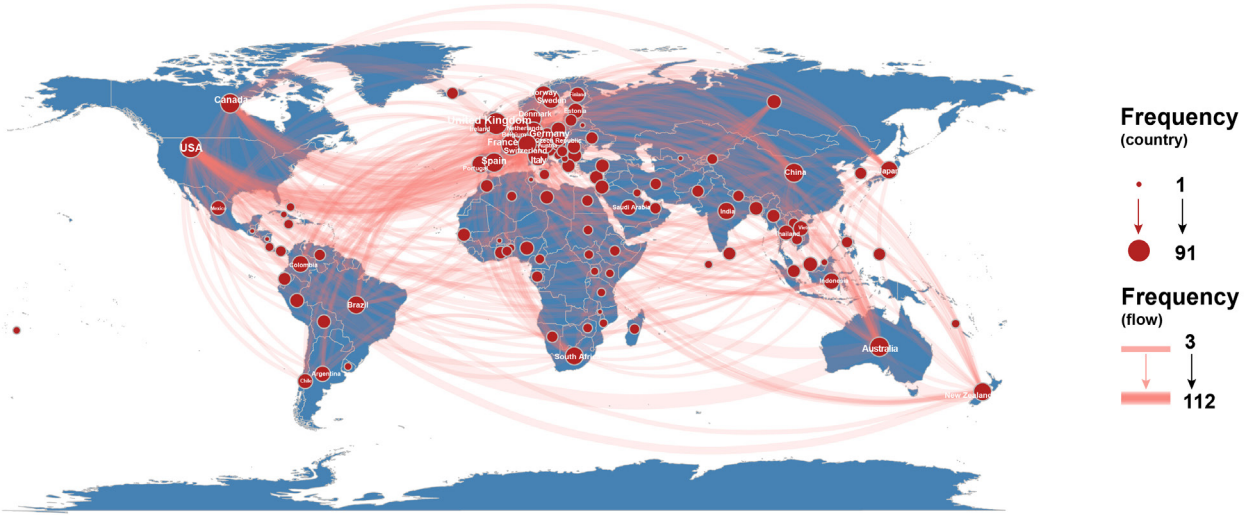

Fig. 5. World Map of Country Collaborations. Each circle represents a country, with its size representing the frequency of cooperation in eDNA research with other countries. A larger circle signifies more collaborations. The width of a chord between two circles represents the frequency of their research cooperation, with a thicker line denoting more frequent collaboration. Frequencies below three are not drawn on the map.

inherently overlooks non-English publications. For instance, biodiversity studies in the Caribbean or Southeast Asia are often published in regional journals or government reports in Spanish, French, or local languages, which are rarely indexed in global databases. This aligns with broader findings that monolingual systematic reviews disproportionately exclude non-English contributions, exacerbating visibility gaps for biodiverse regions [81, 82].

Beyond database biases, systemic inequities in the global scientific ecosystem also play a role. High-income countries dominate applied ecological research, while biodiverse regions in the Global South – despite facing urgent environmental challenges – are constrained by economic limitations, scarce funding, and language barriers [83]. Addressing these disparities requires multifaceted strategies: 1) Funding agencies should prioritize capacity-building initiatives in under-

resourced regions, such as establishing regional eDNA hubs with affordable sequencing technologies and bioinformatics training; 2) Collaborative frameworks must emphasize local leadership to align research agendas with regional conservation priorities; 3) Journals and databases should actively promote multilingual science by accepting non-English abstracts, subsidizing translation costs, and indexing regional repositories. Additionally, we recommend practical steps to address skill gaps: standardization of methodologies tailored to diverse environments (e.g., simplified sampling procedures and low-maintenance field equipment) can reduce technical barriers [84]. Citizen science initiatives – such as Nanjing University's "Thousand Rivers Project" – demonstrate how non-experts can contribute via user-friendly sampling kits and digital data platforms [85]. Coupled with collaborative networks, these approaches empower researchers in under-resourced regions and promote equitable global adoption of eDNA technologies for biodiversity conservation.

We also created a world map to illustrate international collaborations in eDNA research, as shown in Fig. 5. Summary statistics show that the United Kingdom is at the forefront of initiating collaborations in eDNA research, partnering with 91 countries, followed by USA, Italy, France, Germany, Australia, Canada, Spain, and China. European countries are central to the global network of international collaboration, closely engaging with the USA, Canada, Australia, and other European nations. USA, as the second-most-active participant, collaborates extensively with the UK and Canada. These collaborations advance research on biodiversity and traditional knowledge, and enhance the scientific capabilities of each participating country [86].

Notably, historical patterns of scientific cooperation reveal that shared competencies and institutional co-authorships across borders enhance research efficiency and innovation [87]. For instance, China's Global Trench Exploration and Diving Program (Global TREnD), launched in 2020, unites scientists from over 15 countries to explore hadal zones, combining advanced technologies with multinational expertise [88]. Such joint efforts could inspire eDNA research programs to pool resources for sampling in understudied transboundary ecosystems (e.g., coral reefs or river basins), ensuring equitable participation from biodiversity-rich nations.

Furthermore, geopolitical frameworks like the Belt and Road Initiative (BRI) demonstrate how regional hubs can catalyze scientific cooperation [89]. BRI has established a science-driven infrastructure to address sustainability challenges across 64 participating countries, fostering collaborative eDNA research through shared facilities and training programs [90]. Such models could inspire eDNA programs to integrate regional databases and harmonize protocols in biodiversity hotspots (e.g., Southeast Asia's Mekong Basin), where fragmented efforts currently limit scalability. A global analysis highlights that 53.8% of terrestrial species ranges span international borders, yet fewer than 10% of conservation initiatives address these overlaps, underscoring the urgency of transboundary collaboration [91].

Conclusions

Our research offers a new starting point for understanding the evolution of eDNA research. We categorized 4524 studies from 1992-2024 into 25 themes, analyzing the relationship between changes in eDNA research topics and their evolution over time. Our results showed that the application of eDNA research has shifted from methodological research to biodiversity and community research since 1992. Furthermore, we observed a significant increase in interest towards community-themed topics, indicating a pivot from monitoring specific species to examining interactions among multiple species in eDNA research.

Despite its promise, eDNA research remains far from reaching its full potential. Although there has been a significant increase in publications recently, our study highlights ongoing spatial gaps, such as under-researched regions or countries. Countries with greater economic power have historically produced more publications. Although some biodiversity hotspots (e.g., the Caribbean and Indo-Burma) are located in multi-national regions, collaboration among these areas remains limited. Therefore, overcoming financial constraints and addressing the lack of professional training are crucial for this emerging technology.

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Conflict of Interest

The authors declare no conflict of interest.

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Supplementary Material

Supplementary Information (pdf):

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