Meiofauna as sentinels of beach ecosystems: A quantitative review of gaps and opportunities in beach meiofauna research

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ABSTRACT

Meiofauna are the most abundant and diverse animal group on beaches, encompassing 20 metazoan phyla and contributing to taxonomic, functional, and phylogenetic diversity of beach ecosystems. Meiofauna react fast to environmental change and disturbance, and therefore, might represent a good sentinel to efficiently anticipate human-driven perturbations and the global ecological crisis in globally threatened beach ecosystems. We review the state of meiofauna research on beach ecosystems and to what extent meiofauna are included in ecological studies and ecosystem assessments of beaches. We reviewed 14,644 studies focusing on beaches available in the Web of Science, covering 58 years, and our analysis reveals that only 312 of these references addressed meiofauna in beaches. The majority of these 312 studies are from Brazil, India and the USA, and primarily focus on taxonomy or specific meiofaunal groups, with very few addressing processes such as erosion, and impacts such as microplastics pollution, nourishment, or management—topics frequently highlighted in wider beach science research. Notably, only 70 out of 312 studies (22%) mentioning meiofauna also discuss beach ecosystem threats and services. Although molecular approaches have the potential to enhance the use of meiofauna in addressing these issues, only seven meiofaunal studies have incorporated such methods, and approximately half of the meiofaunal genera cited in our dataset have been DNA barcoded. Our findings suggest that research on the ecology of beach meiofauna is still in its early stages, and we propose a series of short- and long-term actions to address the gaps preventing the integration of meiofauna into ecological research and beach monitoring programs.

1. Introduction

Beach ecosystems are widely used for recreation and tourism and are economically significant in many coastal areas, where they provide a wide range of ecosystem services (Holzner, 2011; Pontee, 2013; Barbier, 2014; Harris and Defeo, 2022). Besides their economic importance, beaches are critical habitats for many organisms, providing key ecosystem functions such as nutrient cycling and coastal protection (McLachlan et al., 1981; Hanley et al., 2014; Harris and Defeo, 2022). However, intense human activity has led to growing threats from urbanization, habitat destruction, pollution, and climate change-induced sea level rise, commonly referred to as 'coastal squeeze' (Schlacher et al., 2007; Defeo et al., 2009; Pontee, 2013). These anthropogenic impacts negatively affect beach biodiversity (Martínez et al., 2020; Costa et al., 2022), threatening both the economic potential and biodiversity of coastal regions.

Despite their economic and ecological importance, beaches often receive less scientific attention than other coastal environments (Lercari, 2023). This lack of data hinders a deeper understanding of stressor impacts and the extent of biodiversity loss (Defeo et al., 2009). Further, research typically targets only a fraction of beach biodiversity, primarily focusing on birds, turtles, mammals, and macroinvertebrates (Schlacher et al., 2014). This overlooks significant facets of beach biodiversity, which comprises a rich, often specialized fauna, much of which isn't visible to the naked eye.

Meiofauna, microscopic animals measuring between 40 μm and 1 mm in body length and living in the interstitial environment between sand grains, represent a highly diverse community, spanning over 20 phyla (Giere, 2009). These organisms are vital to beach ecosystems, with abundances often exceeding 10,000 individuals per m^2, acting as links between microbes and macrofauna in beach food webs, and playing important roles for sediment stability and nutrient recycling (Koop and Griffiths, 1982; Albuquerque et al., 2007; McLachlan and Defeo, 2017; Schratzberger and Ingels, 2018). Meiofauna have been recognized as a

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good bioindicator due to their rapid response to disturbance (Zeppilli et al., 2015; Santos et al., 2021; Gheller and Corbisier, 2022), and understanding how meiofauna react to pollution, climate change, and urbanization can provide important insights into the broader impact of the stressors on diversity and functioning of beach ecosystems. Despite this potential, meiofauna remain understudied and poorly understood compared to other fauna, partly due to the labor-intensive nature of traditional morphology-based methods (Fonseca et al., 2018) and the dwindling number of expert taxonomists (Engel et al., 2021), which limits our understanding of meiofauna taxonomic and functional diversity. Molecular techniques, such as DNA barcoding and metabarcoding, are promising tools to overcome these limitations by enabling studies on biological communities and their dynamics (Hebert et al., 2003; Taberlet et al., 2012). These methods are effective for studying meiofauna diversity (Leray and Knowlton, 2015; Oliverio et al., 2018; Marquina et al., 2019; Miya, 2022; Macher et al., 2022, 2024a) and assessing the effect of stressors on communities (Creer et al., 2010; Fonseca and Lallias, 2016; Martínez et al., 2020; Fais et al., 2020), especially when combined with morphological methods (Macher et al., 2024a). However, the widespread application of these techniques is hindered by a lack of standardized methods (Gielings et al., 2021) and missing comprehensive DNA references (Weigand et al., 2019).

Given these challenges, a more thorough understanding of meiofauna diversity is essential for advancing the knowledge of beach ecosystems. By studying the biodiversity and ecology of beach meiofauna species and their responses to environmental changes and stressors, we can gain valuable insights into how beach ecosystems are influenced by both environmental and anthropogenic factors. In this study, we conduct a scientometric analysis of literature on beach meiofauna to assess the state of global beach meiofauna research. We emphasize the potential of meiofauna research to enhance our understanding of beaches, which in turn can inform better management and protection strategies for these globally important coastal ecosystems.

2. Material and methods

We conducted a standardized literature search in Web of Science on October 18, 2022, aiming to capture a wide range of references related to beach ecosystem functions and threats. We started our search using the term "beach*" in the Title, Author Keywords, and Keywords Plus fields. We refined the results by excluding topics unrelated to environmental, biological, or geological sciences, such as History, Culture, and Medicine. This search yielded a dataset of 14,674 references, which spanned topics like "Environmental Science", "Marine Freshwater Biology", "Geography Physical", "Water Resources", "Engineering Ocean", "Geosciences Multidisciplinary", "Oceanography", "Ecology", and "Zoology". Recovered references were published between 1965 and 2022. By further filtering to include only research articles, we reduced the dataset to 14,644 manuscripts, hereafter referred to as the "*beach dataset*". (Supplementary Table S1).

Our first goal was to quantify how many of the references in the "*beach dataset*" focused on fauna, comparing the number of those including meiofauna with those focusing on macrofaunal groups, such as large invertebrates, fish, birds, or turtles. We compiled a list of keywords, incorporating the word "meio", the names of all phyla with meiofaunal representatives, and other terms used to refer to specific meiofaunal groups, such as "turbellaria". We then matched each word against the abstracts, titles, and keywords of the references in our "*beach dataset*" using a loop and the function 'grepl' in the R package "base" (R Core Team, 2023; version 4.3.2). We set the option 'ignore.case' as TRUE and the option 'fixed' as FALSE to allow for partial matches (e.g. the keyword "meio" with "meiobenthos", "meiobenthic", "meiofauna" and "meiofaunal"). We then manually reviewed the resulting subset of 526 references to exclude incorrect matches and any references focusing exclusively on macrofauna, such as those dealing with macrofaunal annelids (e.g. *Arenicola*), planktonic copepods, or parasitic organisms

(Supplementary Table S2). We retained papers dealing with free-living nematodes, acoels, as well as interstitial, yet relatively large, polychaetes (e.g. Saccocirridae, Protodrilidae). We focused on beaches within the marine sandy shoreline biome (Keith et al., 2020), which includes beaches situated in seashore as well as the estuarine beaches and beaches situated within semi-open tidal lagoons. Beaches situated within inland waterbodies, such as lakes, were disregarded. This led to the final "*beach meiofauna dataset*" comprising 312 references (Supplementary Table S3). We plotted the number of references addressing meiofauna and each meiofaunal phylum using the 'barplot' function in R package "ggplot2" v. 3.4.1 (Wickham, 2016). We replicated the analyses using an alternative list of keywords that featured the word "macrofaun" and "macrobenth" along with common terms related to macrofaunal organisms often studied in connection with beaches, such as "fish", "bird", and "crab". This second search was not exhaustive and intended only for comparison, since it did not include all the possible terms linked to animals. The frequency each animal group appeared in the literature is summarized in Supplementary Table S4.

Our second goal was to characterize the diversity of topics addressed by references on meiofauna within the broader range of topics addressed in beach research. First, we extracted the keywords of each reference in the "*beach*" and "*beach meiofauna*" datasets, and then standardized the keywords by decapitalizing, removing extra spaces, and combining plural and singular forms (e.g., "beach" and "beaches"). Finally, we utilized the "wordcloud2" package v. 0.2.1 (Lang and Chien, 2018) to generate two separate word clouds, setting a keyword size of 9. Due to the extensive keyword set, we incorporated only those with a frequency above 10 into the word cloud. Because of the large number of keywords, we selected word clouds rather than other visualization techniques, such as a bar plots, which would become very long and difficult to overview. Supplementary Tables S5–S6 summarized the frequency of each keyword. We also removed the word "meiofauna", present 93 times, to allow a clear visualization of the other keywords. We acknowledge that word clouds are not formal analytical tools. Here, we use them to visually summarize the keywords employed by beach researchers, both within and beyond meiofauna studies. We also evaluated their connection with other research topics among researchers working on beaches by constructing a citation network, calculated with function 'network' and 'plot.network' in R package "network" v. 1.13.0.1 (Butts, 2015).

Since meiofauna have been proposed as a valuable bioindicator for monitoring aquatic environments, we were also interested in quantifying how many references address this topic. Therefore, we compiled a second list of keywords related to major threats and service groups, based on recent literature reviews (Brown and McLachlan, 2002; Defeo et al., 2009; Harris and Defeo, 2022) (Supplementary Tables S7–S8). These keywords were matched against titles, abstracts, and keywords in the "*beach*" and "*beach meiofauna*" datasets separately. Subsequently, we plotted the frequency of each major threat and service category using a 'barplot' using the R function "ggplot2" v. 3.4.1 (Wickham, 2016), and then connected references addressing both threats and services in using the 'chordDiagramFromMatrix' function in the R package "circlize" (v. 0.4.15) (Gu et al., 2014). The list of the papers matched with each keyword is included in Supplementary Tables S9–S10.

Molecular methods are considered pivotal for understanding meiofauna diversity and distribution (Macher et al., 2024a; b). Since the effective implementation of molecular methods relies on good molecular reference libraries, we evaluated for how many beach meiofauna genera sequences are available in NCBI GenBank, which we use as a proxy of the current molecular coverage of beach meiofaunal diversity. We quantified how many references within the datasets included the words "metabarcoding", "barcoding" or "environmental DNA" in the dataset using the same procedure as above. The list of the papers matched with each keyword is included in Supplementary Table S11. Then, in order to evaluate how many of the genera mentioned in the papers of the "*beach meiofauna dataset*" were represented in GenBank, we screened each reference within the "*beach meiofauna dataset*" and manually extracted

every mentioned taxon. All taxa names were validated against the Aphia taxonomy database to check the taxonomic rank (i.e., species, genus, family), nomenclature, and name status (i.e., accepted, invalid). Only valid genus names were retained. Then, each genus was classified as meiofauna or not, based on literature (Supplementary Table S12). Finally, we cross-referenced all genera listed as meiofauna with Gen-Bank to determine the availability of reference sequences for each genus. We considered only 18S rRNA and cytochrome oxidase I (COI) sequences as reference barcodes, as these are the most commonly used markers in meiofauna barcoding and metabarcoding (Gielings et al., 2021). We summarized the percentage of sequenced versus those unsequenced genera within every meiofaunal group using the 'barplot' function in the R package "ggplot2" v. 3.4.1 (Wickham, 2016), with bar lengths proportional to the total number of genera known within each group.

Finally, we assessed the geographical coverage of beach meiofauna studies. For this, we extracted the geographical locations in each reference within the "*beach meiofauna dataset*" and plotted a map against the shapefile of the broadest geographical division according to the Biodiversity Information Standards (https://www.tdwg.org/).

We performed data cleaning, rearrangement, and analyses using R, version 4.3.2 (R Core Team, 2023). Code used for all the analyses is available at Github (https://github.com/amartinezgarcia), along with all necessary files to run the scripts.

3. Results

We found that 312 out of the 14,644 analyzed references matched meiofauna terms (hereafter referred to as "*beach meiofauna dataset*"). A total of 169 references directly referred to the term "meiofauna", "meiobenthos" or their variations, while terms linked to "Nematoda", "Copepoda" and "Annelida" matched 128, 85, and 59 references, respectively (Fig. 1A). In contrast, mentions of macrofauna were considerably more numerous. A total of 279 references matched either with macrofauna or macrobenthos, whereas "fish" was mentioned in 1015 references, "turtle" in 509 and "birds" in 295 (Fig. 1B). We found a strong imbalance in research output on beach meiofauna between countries. Brazil emerged as a hotspot with 44 studies, followed by India (27 studies), the USA (19 studies), and Germany (16 studies). Fourteen countries, including Spain, China, and the United Kingdom, Italy, South Africa, Australia, and Belgium have 5 to 15 studies. The majority of countries have lower research output on beach meiofauna, with 26 countries contributing 1 or 2 studies each (Fig. 1C).

The word clouds of the references in the "*beach meiofauna dataset*" (Fig. 2A) show different set of keywords than that for the "*beach dataset*" (Fig. 2B). References on meiofauna used 132 unique keywords, with "sandy" being most prevalent (41 times), followed by "taxonomy" (31 times), "Nematoda" (28 times), and "meiobenthos" (20 times). Notably, taxonomy-related terms such as "new species" (9 times) and "biodiversity" (18 times), along with the names of specific meiofaunal groups like
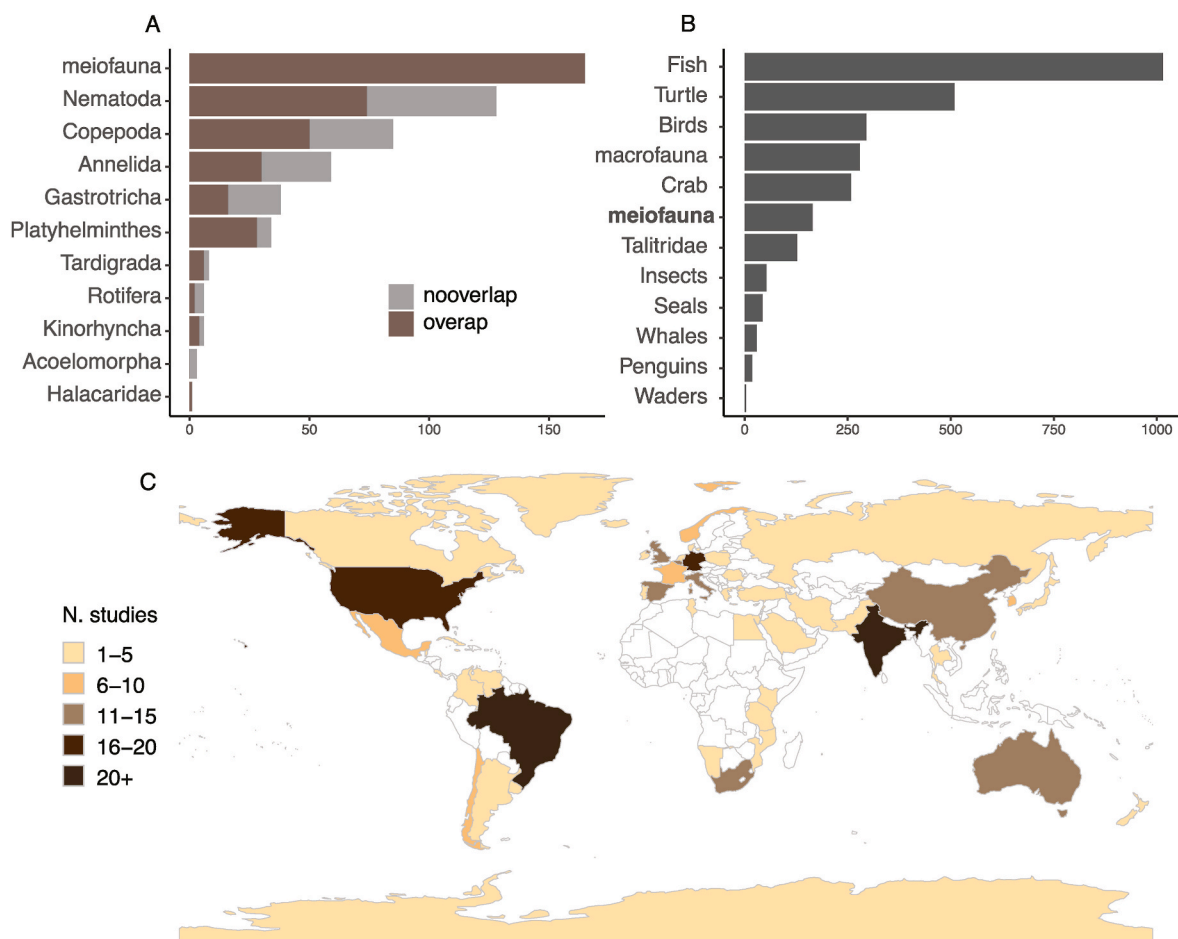

Fig. 1. Macrofaunal groups were mentioned considerably more often than meiofaunal ones in the literature on sandy beaches. **A:** Number of references mentioning groups with meiofaunal taxa in the title, abstract or keywords. In brown, the subset of references in which also the word "meiofauna" is mentioned. **B:** Number of beach references mentioning macrofaunal taxa. References mentioning the word "meiofauna" are included in the grab for comparison. Note the differences in the scales of the x axis between A and B. **C.** Global distribution of the references included in the "*beach meiofauna dataset*". (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)
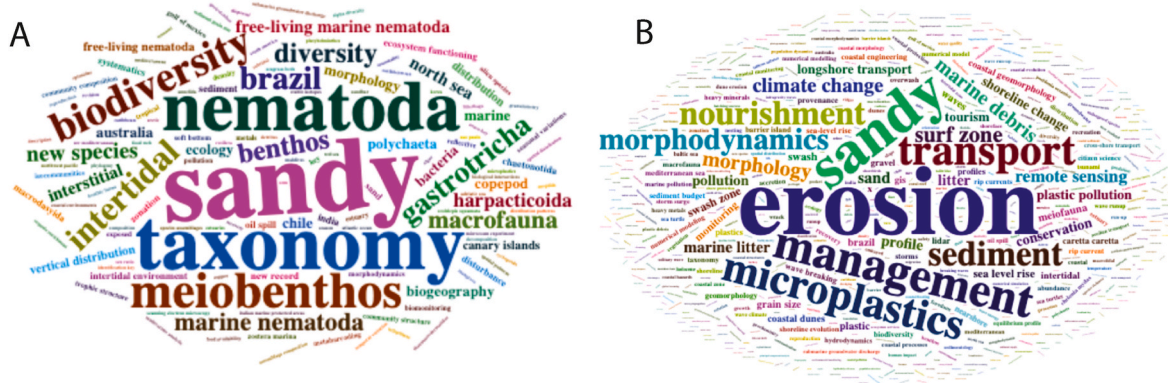
Fig. 2. Word clouds. **A:** References mentioning meiofauna in the abstract or title ("*beach meiofauna dataset*"), the five most frequent keywords were sandy (frequency = 41), taxonomy (31), Nematoda (28), meiobenthos (20) and biodiversity (17); **B:** References not mentioning meiofauna ("*beach dataset*"), the five most frequent keywords were erosion (frequency = 820), sandy (511), management (405), transport (369), and microplastic (368). The frequency of each keyword is included in Supplementary Tables S5–S6.

"Nematoda" and its derivation (e.g., free-living Nematoda, marine Nematoda, 50 times), "Harpacticoida" and "Copepoda" (14 times), "Gastrotricha" (12 times), or "Polychaeta" (6 times) were amongst the most frequently used keywords. In contrast, the "*beach dataset*" included 23,691 different keywords. The most common were "erosion" (820 times), "sandy" (511 times), "management" (405 times), "transport" (369 times), and "microplastics" (368 times), followed by "sediment" (296 times). Keywords related to impacts, such as "nourishment" (288 times), "marine debris" (174 times), "climate change" (173 times), and "marine litter" (135 times), or geological terms like "morphodynamics" (260 times), "surf zone" (189 times), and "swash zone" (102 times), were among the most common.

The analyses of the citation network showed that references in the "*beach meiofauna dataset*" discussing meiofauna do not tend to cite each other and thereby do not form a cluster, but instead are dispersed throughout the entire network, which suggests that they cited or are cited by references with various other focuses connected to beach ecosystems (Supplementary Fig. S1).

Only 70 references in the "*beach meiofaunal dataset*" addressed beach ecosystem threats, ecosystem services, or both (<0.01% of the total 14,644 analyzed references, and 22% of the "*beach meiofauna dataset*"), whereas 7087 (48%) of references in the "*beach dataset*" addressed ecosystem threats, ecosystem services or both (Fig. 3). Specifically, 65 references in the "*beach meiofauna dataset*" addressed threats and 14 addressed ecosystem services; in contrast to 5125 and 3794 respectively for the full "*beach dataset*". The proportion of references discussing each threat category was similar between those focusing on meiofauna and the rest of the dataset, with the majority addressing "pollution", followed by "erosion", "recreation", and "coastal development and protection" (Table 1). When considering services, both meiofauna and non-
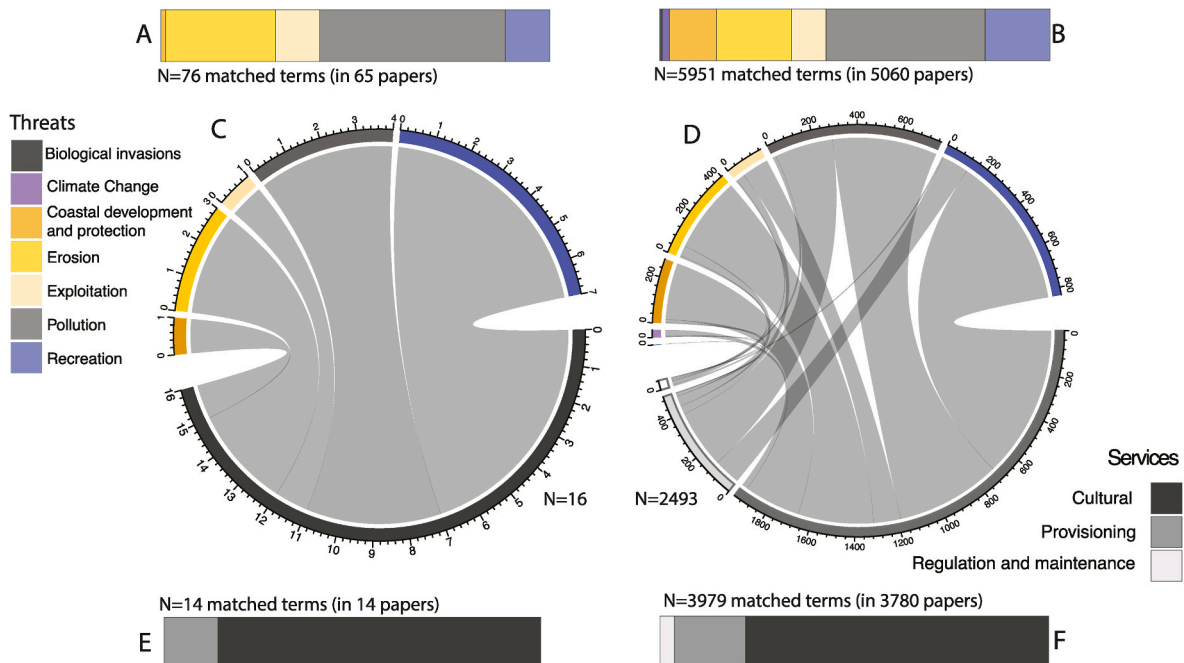

Fig. 3. Summary of references including keywords related to threats and ecosystem services in the abstract, title, or keywords of the sandy beach dataset. **A.** Number of matches for threat-related keywords in the "beach meiofauna dataset". **B.** Number of matches for threats-related keywords in the "beach dataset". **C.** Chord diagram connecting references including pairs of threat- and service-related keywords, as well as meiofauna. **D.** Chord diagram connecting references including pairs of threat- and service-related keywords, but not meiofauna. **E.** Number of matches for ecosystem service-related keywords as well in the "beach meiofauna dataset". **F.** Number of matches for ecosystem service-related keywords in the "beach dataset". Notice that a given reference might be counted more than once if it contained more than a keyword. Number in size the bar charts reflect the percentage of references for each category (see material and methods).

Table 1

Frequency of the different categories of threats and services mentioned in the "*beach meiofauna*" and the "*beach*" datasets. The exact lists of keywords used to match the references are in Supplementary Tables S9–10. Abbreviations: N, number of times that a keyword under each category has been matched; %, frequency of the category in each dataset.

Services	Meiofauna		Total	
	N	%	N	fraction
Cultural	12	0.04	3102	0.21
Provisioning	2	0.01	729	0.04
Regulation and maintenance	0	0	148	0.01
Threats				
Biological invasions	0	0	43	<0.01
Climate Change	0	0	111	0.01
Coastal development and protection	1	<0.01	710	0.05
Erosion	18	0.06	1145	0.08
Exploitation	8	0.03	522	0.04
Pollution	39	0.12	2418	0.17
Recreation	10	0.03	989	0.07

meiofauna references most frequently addressed "cultural" services, followed by "provisioning" and "regulation and maintenance". A larger percentage of non-meiofauna references focused on cultural services (21%) compared to those focusing on meiofauna (0.04%). References overlapping in discussions on threats and services numbered 42 for meiofauna and 2493 for non-meiofauna (see Table 1).

In total 18 papers mentioned molecular methods in their abstract, title or keywords, 5 of them part of the "*beach meiofauna dataset*". Our manual screening of all the beach meiofauna papers showed that out of 312 references, 101 did not name any genera, but only higher taxonomic ranks (Table 2). The remaining 211 references mentioned a total of 1014 valid genera, 920 of which were considered meiofauna. Nematoda had the highest number of mentioned genera (333), and our comparison of genus names with available 18SrRNA and COI sequences in NCBI Gen-Bank showed that 226 (69%) of these have available reference sequences. The second most commonly reported group were the Copepoda (176 genera), for 90 (52%) of which a reference sequence is available in NCBI GenBank (Fig. 4). Notably, for some commonly mentioned groups the DNA reference database seems almost complete, e.g., reference sequences are available for 77 (96%) out of 81 mentioned Annelida genera. However, other groups are less well represented, e.g., only 75 (47%) out of 161 Platyhelminthes genera are represented in the DNA

Table 2

Summary of the number of meiofaunal genera cited in the meiofaunal dataset. Total includes the total number of different genera mentioned in the meiofauna dataset; sequenced, non-sequenced, and % sequenced include the number of genera for which 18s or COI sequences are available in GenBank, as well as the proportion. Finally, 18s and COI represent the number of different sequences for each marker available for that genus.

Taxa	Genera	Sequenced	Frequency	18SrRNA	COI
Acari	1	1	1.00	2	1
Annelida	81	71	0.88	1969	3364
Branchiopoda	3	3	1.00	73	790
Cnidaria	1	1	1.00	94	48
Copepoda	176	99	0.56	369	1805
Entoprocta	1	1	1.00	17	14
Gastrotricha	68	49	0.72	685	536
Kinorhyncha	6	5	0.83	61	374
Malacostraca	5	4	0.80	21	42
Mystacocarida	2	2	1.00	3	1
Nematoda	333	240	0.72	5209	2887
Nemertea	1	1	1.00	308	731
Ostracoda	4	4	1.00	5	67
Platyhelminthes	161	82	0.51	889	503
Priapulida	1	1	1.00	6	3
Rotifera	18	16	0.89	568	2547
Tardigrada	27	9	0.33	68	450
Xenacoelomorpha	31	30	0.97	351	131

reference database.

4. Discussion

Our research shows that studies on meiofauna in beach ecosystems are still in their infancy. Despite being abundant and diverse, meiofauna are often neglected in the scientific literature when discussing biodiversity and understanding the impacts on beach ecosystems. This result is not surprising given that meiofauna have been historically neglected in many other aquatic ecosystems, such as seagrass meadows, lakes, or subterranean environments (García-Gómez et al., 2022; Martínez, 2023; Majdi et al., 2020). We address the main challenges in the study of beach meiofauna following the framework of the seven biodiversity shortfalls, proposing short- and long-term solutions on how to improve these issues (Table 3) (Hortal et al., 2015). Our results are limited to studies indexed in Web of Science until 2022, excluding technical reports, non-English papers, and non-peer-reviewed articles. While these omissions may exclude some references, they are unlikely to alter the general trends presented here.

Our findings show several key points: a strong contrast in research focus between manuscripts on meiofauna and macrofauna, a lack of use of meiofauna as bioindicators, and technical hurdles in meiofauna research.

While research on beach meiofauna mostly focuses on taxonomy and biodiversity, beach macrofauna studies more commonly focus on environmental processes such as erosion (Harris et al., 2011; Walker et al., 2008), pollutants such as microplastics (Costa et al., 2023; Carrasco et al., 2019), or management of beaches (Laurino et al., 2022; Augusto et al., 2023). These differences suggest that research on beach meiofauna is more often explorative and descriptive, focusing on describing species and understanding their distribution. While this is highly valuable, the lack of ecological knowledge may limit the use of meiofauna in broader studies on ecosystem functioning, but also for measuring and monitoring biodiversity and ecosystems (Martínez et al., 2023). This is further limited by the lack of studies on basic aspects such as the limits of tolerance of beach meiofauna towards fundamental environmental parameters. Examples include temperature (e.g. Wieser et al., 1974; Ape et al., 2018), salinity (e.g. Ingole and Parulekar, 1998; Baia et al., 2021), or hydrodynamics (e.g. Di Domenico et al., 2014; Martínez et al., 2024), to mention a few.

The potential of meiofauna as indicators of natural and anthropogenic impacts on beach ecosystems appears to be underexplored. As our results show, only 22% of manuscripts focusing on meiofauna also study ecosystem services or threats (e.g. Brannock et al., 2017; Corinaldesi et al., 2022, Mitwally, 2022), whereas 48% of manuscripts in the "*beach dataset*" also focus on ecosystem services and threats (Gül, 2023; Ludka et al., 2023). This discrepancy could be explained by the methodological challenges inherent to meiofauna studies, such as difficulties with taxonomic identification, the lack of DNA reference sequences making identification of species difficult for researchers without morphological expertise and preventing the use of (meta)barcoding techniques for taxonomic identification, and the lack of ecological knowledge on many species (Fonseca et al., 2018; Zeppilli et al., 2018; Vanreusel et al., 2023). It also seems possible that the comparatively rich and more accessible data and knowledge on macrofauna leads to a 'Matthew Effect' (Perc, 2014; Bol et al., 2018); that is, the focus on and the better data availability on beach macrofauna might further amplify research on macrofauna, whereas meiofauna receive less attention due to the difficulties of answering ecological questions when limited data is available. Indeed, previous research pointed out that while meiofauna could be an excellent group for ecological work and monitoring of beach ecosystems, the need for expert knowledge and costs due to labor-intensive sorting and identification limit its usefulness for this task (Schlacher et al., 2014).

As pressures on beach ecosystems intensify due to urbanization and climate change, there is a need to integrate the highly diverse meiofauna
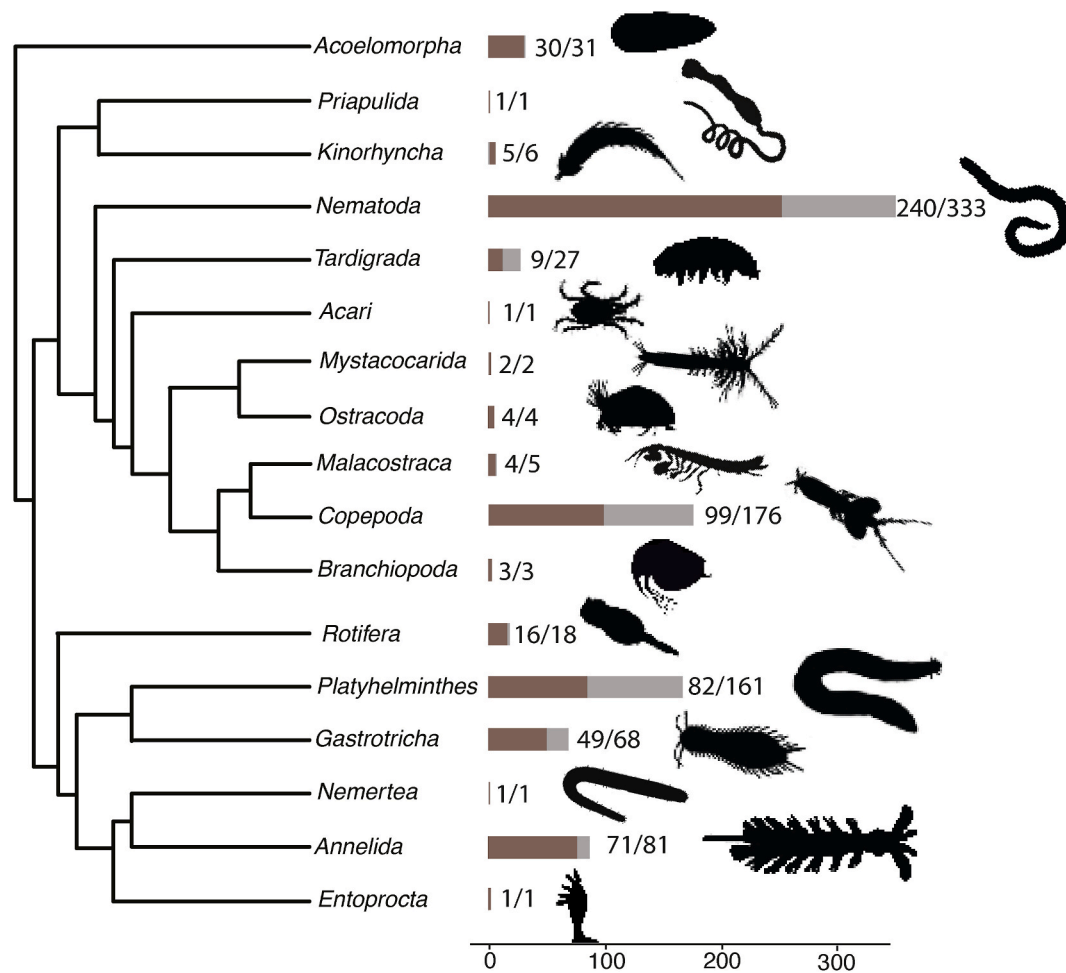
Fig. 4. Meiofauna genera cited in the papers of the "*beach meiofauna dataset*". The bar plots show the total number of genera with meiofaunal representatives (s.l.) mentioned in the dataset. The subset of genera with available COI and/or 18SrRNA sequences in GenBank is shown in brown. The tree topology is based on Fernández and Gabaldón (2020); branch lengths are for illustrative purposes only. The details on the sequences per each group are provided in Supplementary Table S13. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

into the ecological study of beaches, and molecular tools like DNA barcoding and metabarcoding are promising for understanding their taxonomy (Jörger et al., 2012; Fontaneto et al., 2015), biogeography (Leasi and Norenburg, 2014; Czechowski et al., 2012; Vanreusel et al., 2023), and ecology (Schratzberger and Ingels, 2018; Fais et al., 2020; Broman et al., 2019). Yet, only 7 papers within our "*beach meiofauna dataset*" address molecular methods, and only 5 include metabarcoding (Brannock et al., 2017; Martínez et al., 2020; Castro et al., 2021; Macher et al., 2022; Okamoto et al., 2022). The broader application of molecular methods in meiofauna research is currently limited by the lack of DNA reference sequences for many meiofaunal groups, and a pronounced geographical bias (Macher et al., 2024a), making the build-up of local reference databases necessary. Our analyses show that while DNA references are available for almost all genera of Annelida, less than half of the genera of Platyhelminthes, which frequently dominate meiofauna populations (Delgado et al., 2009) and are highly diverse (Curini-Galletti et al., 2023), have reference sequences. Similarly, for two other highly abundant and diverse beach meiofaunal taxa, Nematoda and Copepoda, sequences are available for just half of the genera mentioned in literature. This limitation is similar to findings in other taxonomic groups and environments (Weigand et al., 2019; Salmaso et al., 2022; Csabai et al., 2023) and makes identification and ecological profiling of meiofauna from molecular datasets challenging.

Furthermore, we show a strong geographic bias in beach meiofauna research towards a few countries. This approach will inadvertently overlook taxa from highly biodiverse yet understudied marine regions, such as the coral triangle in the eastern Pacific (Briggs, 2009). Additionally, studies from commonly researched areas still reveal a high number of undescribed species (Curini-Galletti et al., 2020; Rossel and Martínez-Arbizu, 2019; Armonies, 2017), and regional-scale meiofauna diversity patterns are mostly explained by uneven sampling effort (Rubio-López et al., 2023). Thereby, the actual beach meiofauna diversity is likely higher and not represented in the current literature and databases. Combining technological innovation such as high-throughput imaging with Artificial Intelligence (Kitahashi et al., 2018, Brito de Jesus et al., 2023), molecular studies, and morphological taxonomic techniques will be needed to allow for a rapid identification of species and enabling ecological studies on beach meiofauna and ecosystems (Hita-Garcia et al., 2019; Rogers et al., 2022; Macher et al., 2024b).

Looking ahead, as beaches are global hotspots for recreation, easily accessible, and widely popular, we see opportunities for forging synergies among researchers, citizen scientists, and local communities. By building networks of engaged citizens, stakeholders and scientists, the data collection, methodological innovations and knowledge dissemination in beach meiofauna research can be greatly amplified. In conclusion, we advocate for recognizing the potential of meiofauna as vital components of beach ecosystems and as bioindicators, which will be crucial in improving understanding of beach ecosystem processes and facilitating beach conservation and management strategies.

Table 3
Biodiversity shortfall affecting beach meiofauna research, according to Hortal et al. (2015), along with short- and long-term proposed solutions to improve them.

Shortfall	Short term solutions	Long term solutions
Linnean (Species identity)	* Sequencing and improvement of reference libraries (Macher et al., 2024) * Revitalize taxonomy (Karbstein et al., 2023)	* Training of taxonomists (Engel et al., 2021) * Increase scientific impact of taxonomy (Pinto et al., 2021) * Programs and founding devoted to taxonomic descriptions (https://oceancensus.org/taxonomy-and-science-awards-2024/)
Wallacean (Species distribution)	* Organization of regional workshops (Curini-Galletti et al. 2012; Fonseca et al., 2014; Martínez et al., 2019) * Global sampling surveys and metabarcoding (Datry et al., 2018).	* Training of experts in meiofauna in poorly known regions (Zeppilli and Sarrazin, 2015) * Promote international cooperation in funding programs
Prestonian (Species abundance)	* Promote ecological studies including abundances * Theoretical research devoted to understand species abundance distributions within beaches (Chave, 2004)	* Development of automatized methods for sampling processing (Martínez et al., 2024; Anthonin et al., 2023)
Darwinian (Evolutionary history)	* Sequencing and improvement of reference libraries (Macher et al., 2022, 2024) * Acquisition of high-quality -omic data from meiofaunal animals (Smythe et al., 2019; Herranz et al., 2022)	* Promote the inclusion of meiofaunal species in European genomic programs (erga-biodiversity.eu) * Improve molecular protocols and bioinformatic pipelines to maximize extraction efficiency from small quantities of tissue (Kingan et al., 2019)
Raunkiaeran (Biological traits)	* Inclusion of biological traits in ecological papers (Martínez et al., 2021, 2024a) * Promote ecological traits collection in workshops * Literature mining and data sharing in open access repositories (Cifoni et al., 2021)	* Automated and artificial intelligences systems to extract morphological traits
Eltonian (Biological interactions)	* Experimental lab work * Recollection and sharing of observations, such as predation or symbiosis (Hernández et al., 2024) * Joined species distribution models (Pollock et al., 2014; Macher et al., 2024b)	* Development of high-resolution video recording systems and artificial intelligence systems to automate the recollection of species interactions *in vivo* (Ballentine and Dorgan, 2024)
Hutchinsonian (Environmental requirements)	* Experimental lab work (Maciute et al., 2023) * Literature mining and data sharing in open access repositories (Curini-Galletti et al., 2023) * Encourage the measurement and publication of environmental variables along with species records or ecological studies	* Promote collaboration with experts in different fields, such as morphodynamics, hydrogeology or biogeochemistry into beach meiofauna research (Lercari, 2023)

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2024.109092.

Data availability

All data and code is available in https://github.com/amartinezgarcia.

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