Fundamental questions in meiofauna—how small but ubiquitous animals can help to better understand Nature

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Abstract

Meiofauna—a collective term to define microscopic animals—represent a numerically important component of biodiversity in most of Earth's ecosystems and play a crucial role in biogeochemical cycles. Meiofauna have also been used as models to understand fundamental adaptive processes, have contributed to a better understanding of the animal's Tree of Life, and are believed to be a treasure trove for future genomic studies. To celebrate the diversity of research topics brought to us by the term "meiofauna", we gathered a multidisciplinary team of 42 ecologists, taxonomists, morphologists, biogeographers, molecular biologists, and scientific disseminators to list 194 fundamental questions in meiofaunal research. Then, through an online survey, 251 scientists, administrators, students, and stakeholders assisted us in reducing this list to 50 top-priority questions. Applied topics related to anthropogenic impact and climate change received the highest scores, whereas questions related to areas in development such as genomics or adaptations, received less attention. Whereas we might not be exploiting meiofauna's full potential yet, more and more integrative approaches and technological developments will create opportunities to employ these fascinating organisms to answer broad and important questions, despite of their impediments related to their small body size. Meiofauna research agenda should balance amongst investigating general questions, addressing more specialized research topics, and generating primary data on distribution, taxonomy, traits, and DNA sequences. The geographical and taxonomic biases that have historically affected meiofaunal research can be alleviated by promoting international cooperation, open data sharing, and an increase effort in education, taxonomic training, as well as scientific communication. We hope that this will get both researchers and the general public intrigued by those small critters that constantly lurk unseen in front of us.

1. Introduction

Our knowledge on Earth's biodiversity is biased towards relatively large organisms, particularly if they are charismatic, colourful, useful, or threatening to humans (Miralles *et al.,* 2019; Mammola *et al.,* 2023). Whether this skew derives from the fact that we, humans, are relatively large mammals, which navigate the world mainly using visual stimuli, or because we respond to other biological, cultural, or socioeconomic factors remains an open question (Adamo *et al.,* 2022). Yet, the consequences of this bias permeate scientific inquiry, not only by affecting our perception of nature but also by driving the way we administer resources for research or design conservation policies (Adamo *et al.,* 2022).

As a corollary, small-sized animals and their roles in ecosystems tend to be overlooked, not only by the general public, but also by the scientific community. Consequently, small animals are typically under-represented in the conservation agenda (Adamo *et al.,* 2022; Mammola *et al.,* 2020b) and in biodiversity research at different scales (Troudet *et al.,* 2017). Among these small but functionally important creatures, those whose body size ranges between 10^{-3} and10^{-5} metres are usually referred to as "meiofauna" (Fig. 1). In fact, the term "meiofauna" is used with two different meanings depending on the context. In ecological studies, "meiofauna" refers to the fraction of the animal and protist community that is retained between sieves with a mesh size of 0.5–1 mm on the upper and 0.030–0.063 mm on the lower end of the scale (Schmidt-Rhaesa, 2020). The term was originally introduced by ecologists to describe the communities dwelling in marine sediments ("meiobenthos", Warwick & Clarke, 1984), but it soon was generalized across a broader range of habitats, such as springs (Fattorini *et al.,* 2016), aquifers (Korbel *et al.,* 2019), soils (Müller *et al.,* 2019), rivers (Schmidt-Araya *et al.,* 2020), lakes (Traunspurger *et al.,* 2020), or even the water-filled cavities of terrestrial plant (Almeida & Souza, 2020). Alternatively, evolutionary biologists and zoologists often use the term "meiofauna" to describe animals that are invisible to a naked eye, thereby establishing a correspondence between the term meiofauna and microscopic animals (Rundell et al., 2010). Although similar, these two meanings cannot be interchanged without caveats (Fontaneto, 2011). On the one hand, some of the individuals within the meiofaunal fraction of a community are not microscopic, can even reach several millimetres in length, but are still retained within the meiofaunal fraction due to their elongated and thin bodies (Ptatscheck *et al.,* 2020). Consequently, properties attributed to microscopic animals are not always applicable across all the species found in the meiofaunal fraction of a community (Cerca *et al.,* 2018). On the other hand, some organisms qualify as meiofauna during part of their life cycles, enforcing a distinction between the so-called *temporary* and *permanent* meiofauna that is not easily established across all species of a meiofaunal community, such as annelids (Worsaae et al., 2021) or platyhelminths (Curini-Galletti et al., 2023).

Notwithstanding these caveats, the term "meiofauna" has facilitated a common framework of discussion for scientists across geological and life sciences, who otherwise would hardly interact and discuss their world views. Since the pioneering studies conducted in the first half of the 20th century (Swedmark, 1964), meiofauna research has gained momentum only in recent years (Giere & Schratzberger 2023). It is now evident that meiofauna represent not only an important component of biodiversity in most of Earth's ecosystems (Fonseca *et al.,* 2010), but a crucial player in carbon and nitrogen cycling throughout aquatic trophic networks (Bonaglia *et al.,* 2014; Schratzberger & Ingels, 2018; Bonaglia & Nascimento, 2023; Maciute *et al.,* 2023). Several studies have highlighted meiofauna as sentinels for early detection of potential sources of pollution or climate change (Zeppilli *et al.,* 2018; Ridall & Ingels, 2021), as well as a fundamental service provider (Schratzberger & Ingels, 2018). Meanwhile, microscopic meiofaunal animals continue to pose fascinating research questions and provide tools to test general eco-evolutionary hypotheses (Fonseca *et al.,* 2018; Giere & Schratzberger, 2023). For example, it remains an open question whether microscopic animals respond to ecological drivers similarly to their macroscopic counterparts, challenging the generality of many ecological and evolutionary principles derived from the study of larger organisms (Fontaneto, 2011); or how universal scaling laws can apply to them due to their small body size (Hatton et al., 2019). Furthermore, many ancient metazoan lineages that are only represented today by microscopic animals exhibit an interesting combination of potentially ancestral characters and adaptations to having a small body size (Cannon *et al.,* 2016; Laumer *et al.,* 2015, 2019; Marlétaz et al 2019), thereby providing an insight into the microscopic animals that likely inhabited ancient marine ecosystems (Worsaae *et al.,* 2023). Indeed, whereas most meiofauna are too tiny and fragile to leave any recoverable trace in fossil sites (Parry *et al.,* 2017), those bearing calcareous structures, such as ostracods or foraminifera, have left extensive fossil record, valuable for palaeontological, biostratigraphical and paleoecological studies and reconstructions, both in academia and industry (Jones, 2013; Perrier et al., 2015). Meiofauna also yield potential to understand processes of ecological filtering, adaptation, and morphological change, at both lineage (Martín-Durán *et al.,* 2021) and community levels (Martínez *et al.,* 2021; Vieira et al., 2021). Some microscopic animals have dormant stages able to withstand extreme environmental conditions, even in space (Ricci *et al.,* 2005; Persson *et* *al.,* 2011), whereas others have been used as model organisms in pioneering cancer research (Kirienko et al., 2011)

In an era in which we strive to make research as diverse, multidisciplinary, and international as possible (Cardoso *et al.,* 2022), we should cherish terms such as meiofauna insofar as they provide unique opportunities to address timely and broad scientific questions from different angles across the natural sciences (Parker *et al.*, 2016). To celebrate all the research opportunities brought to us by the term "meiofauna", we gathered a multidisciplinary team of researchers to list the most fundamental questions that we can address using meiofauna. Then, we evaluated the broader interests of these questions through an online survey targeting scientists, administrators, students, and stakeholders. With this exercise, we first wanted to highlight the questions that could interest a broad audience; and secondly, we wanted to identify significant medium- and long-term goals within different scientific fields addressed by researchers using meiofauna research (Sutherland & Woodroof, 2009). We structured the discussion of our results under three overarching questions: (1) Are we exploiting the full potential that meiofauna offer as model to address questions of broad scientific and societal importance? (2) What are the critical research priorities as perceived by researchers working with meiofauna? (3) Which biases currently affect meiofauna research and how can we overcome them to move forwards in our research agenda?

2. Horizontal scanning protocol

To select fundamental questions that can be addressed using meiofauna, we followed a horizon scanning methodology (Sutherland *et al.,* 2011), as it was successfully applied in similar surveys (Patiño *et al.,* 2017; Mammola *et al.,* 2020a). Survey coordinators (Martínez and Fontaneto) defined eight panels corresponding to research areas within the published research in meiofauna: (i) Systematics and taxonomy; (ii) Macroecology and biogeography; (iii) Morphology and adaptation; (iv) Genome biology and evolution; (v) Anthropogenic impacts and global change; (vi) Population and community ecology; (vii) Biogeochemistry and applied topics; and (viii) Science communication and other topics. The goal of the latter was to identify additional questions that did not fit in the remaining seven topics and might therefore have been overlooked. For each panel, the survey coordinators invited one panel coordinator (Table 1), whose task was to establish an international panel of experts to formulate a pool of initial fundamental questions within the topic. In assembling each panel, panel coordinators invited: (i) two internationally recognized meiofaunal experts, (ii) one early career researcher (*i.e.*, a post-doc or researcher with less than 10 years of experience), and (iii) one external expert with internationally recognized expertise in the research area, but without a specialized background in meiofauna. Inviting an early career researcher provided a multigenerational view of each topic, whereas external experts were asked to emphasize the relevance of the questions outside the meiofaunal paradigms.

The panels initially assembled a list of 253 questions. The survey coordinators curated this list by removing duplicated questions, improving readability (Plavén-Sigray *et al.,* 2017), and removing unnecessary jargon (Martínez and Mammola, 2021) and acronyms (Barnett & Doubleday, 2020) (Table S1). After language editing and removal of duplicates, we kept 194 questions (hereafter List #1). List #1 was submitted to an initial scrutiny by panel members, who scored each question from 1 to 10 according to its importance. We randomized the order of the questions for each participant. Based on the bimodal distribution of total scores obtained by the questions, all the 117 questions that scored above 205 were included in the final list, referred to from now on as List #2.

We then subjected List #2 to online voting (Public Survey) by inviting a broad community of researchers, ranging from researchers with a strong background in meiofaunal studies to researchers without any knowledge of meiofauna, as well as students and stakeholders. We achieved that by promoting the survey using several channels, which included direct e-mails to peers, promotion through social media (Facebook, Twitter, and ResearchGate) and in workshops and meetings, as well as advertising the survey in different mailing lists, scientific societies, and newsletters. The latter included newsletters such as Psammonalia, and those of the Brazilian and the Japanese meiobenthologists associations; as well as different email lists such as the rotifer-family@listserv, Annelida list, the mailing lists of the members of the International Society for Subterranean Biology, the Italian Ecological Society, and the Ecological Society of India. Finally, the questionnaire was also distributed to the students in the courses that some of the panel members are teaching (see below).

Several caveats need to be considered when interpreting the results of a horizon scan survey (Sutherland *et al.,* 2011, 2013; Patiño *et al.,* 2017; Mammola *et al.,* 2020a). A summary of those as well as the countermeasures we adopted to cope with them, are included in the Supplementary methods.

3. Summary of the horizon scan

In the internal survey, involving only the 32 panel members and 2 survey coordinators (total 34 voters), the number of scores ranged from 266 (top-voted question) to 120 (least-voted question). In the public online survey, 251 voters participated including researchers with and without a primary interest in meiofauna. The highest ranked question ("*How does meiofaunal biodiversity contribute to ecosystem function, integrity, and sustainability in the context of anthropogenic activities and global change?*") scored 2257, whereas the lowest ranked question ("*Is the process of secondary miniaturization irreversible?*") scored 1640.

Voters were mostly reached by peer-to-peer messages targeting colleagues and experts (123 voters, 43%), followed by newsletters (80 voters, 28%). Other participants discovered the survey using social media (28 voters, 10%), during scientific meetings or workshops (20 voters, 7%), or were panel members (34 voters, 12%). Also including the panel members, voters' gender was slightly skewed toward males (166 identified themselves as men (58%), 116 as women (41%), and 3 (1%) participants identified otherwise). We gathered votes from all the continents, although mostly from Europe (168 voters, 57.5%), followed by South and North America (55 and 38 voters, representing 19% and 13% respectively) (Fig. 2). 93 participants (32%) identified themselves as experts in meiofauna (expertise level 5/5 or 4/5), whereas 87 (30%) declared that they have none or very little experience (expertise level 0/5 or 1/5). The remaining 105 members recognized an intermediate level of expertise (2/5 or 3/5). Participants identified primarily as interested in ecology (30%), followed by taxonomy (15%), morphology (13%), conservation science (10%), evolutionary biology (9%), molecular biology (6%), geochemistry (6%), and microbiology (4%). Most of the voters were experienced researchers (152 voters, 53%), but the voters' pool also included students (71 voters, 25%), post-docs (44 voters, 15%) and colleagues employed outside academia (18 voters, 6%). The patterns of answers were only marginally affected by the different areas of expertise of the voters, as well as the demographic parameters (gender and age), explaining less than the 11% of the total variance of the answers (Fig. 3A, 3B; see Supplementary results). In other words, voters seemingly scored the questions without prioritizing those related to their own backgrounds (Fig. 3C). The readability and number of words of each question did not significantly affect the scores that questions received (but see Supplementary Results for details).

In the following sections, we discuss the results of the voting panel by panel, focusing on each panel's 5 highest-scoring questions. We decided to discussed the 5 highest-scoring questions instead of those entering the top-50, so we can still discuss the results of all panels, even when none of the questions of the panels “Genome Biology and Evolution” and “Morphology and Adaptation" entered the top-50. When the top-5 questions in each panel belonged to the 50 most-voted questions overall, their number and points were highlighted in bold. Details on the survey scores, along with the anonymous voters’ metadata are included in the Supplementary Table S2.

3.1. Panel I. Systematics and taxonomy

Systematics and taxonomy are the backbone for any scientific discipline focusing on biodiversity. Agreed-upon and stable species names are fundamental for ensuring reproducibility of biological studies, given that misidentifications or taxonomic changes may deeply affect conclusions (Vink *et al.,* 2012). Unsurprisingly, most of the 50 top-priority questions depend on a reliable taxonomic background and robust species identifications (Table 2). Unfortunately, the “Linnean shortfall,” which refers to the small fraction of species that has been described by science compared to the number of extant species (Hortal *et al.,* 2015), is particularly prominent in meiofauna research (Fonseca *et al.,* 2018). This has been attributed to the time-consuming process of describing minute and often delicate organisms, which requires specialized training and high-end microscopy for documentation (Schmidt-Rhaesa 2020), but also to the general preference of many researchers to study larger species (Mammola *et al.,* 2023). This has led to a shortage in trained taxonomists compared to the vast amount of still undiscovered or yet undescribed meiofaunal diversity (Curini-Galletti *et al.,* 2012).

Awareness of the current biodiversity crisis calls for efficient conservation approaches (Minteer *et al.,* 2012; Jefferson *et al.,* 2021), even when it has been suggested that meiofauna is less likely to go locally extinct than larger faunas (Schratzberger *et al.,* 2023 and references therein). An accurate assessment of meiofaunal species diversity is entirely dependent on the development of more efficient and reliable taxonomic procedures (Q #12). While each community of taxonomists can develop their common standards in specimen identification, species delimitation, and description (see *e.g.*, González-Casarrubios *et al.,* 2023), recent advancements in integrative taxonomy with (semi-)automated pipelines of species delineation and description using DNA have considerably accelerated the taxonomic work (*e.g.*, Fontaneto *et al.,* 2015; Jörger & Schrödl, 2013; Vences *et al.,* 2021). These advances seem particularly urgent in certain groups, such as nematodes, in which the huge diversity of species renders the species identification unpractical, restricting most ecological analyses done with the groups to the genus level (Moens *et al.,* 2013).

DNA metabarcoding is becoming increasingly popular and promising in biodiversity assessments using meiofauna (*e.g.*, Creer *et al.,* 2010; Fonseca *et al.,* 2017; de Faria *et al.,* 2018; Broman *et al.,* 2019; Atherton & Jondelius, 2020; Fais *et al.,* 2020; Martínez *et al.,* 2020, Castro *et al.,* 2021). However, methodological limitations and database biases currently still exist (see *e.g.*, Leasi *et al.,* 2018). Firstly, biodiversity estimations are sensitive to the target genes and rely on the development of *in vitro* and *in silico* workflows capable of dealing with low population density, small body mass, and uncertain genetic diversity (Gielings *et al.,* 2021). Secondly, metabarcoding should be calibrated against reference databases curated by taxonomists to ensure correspondence between barcoding molecular operational taxonomic units (MOTUs) and species hypotheses. Thirdly, a general consensus on a standardized metabarcoding pipeline is needed for comparability of the generated data in subsequent ecological studies (Gielings *et al.,* 2021). Finally, most of the currently available methods for massive DNA sequencing produce comparatively short sequences. Short sequences, together with the deep phylogenetic divergence time and the high substitution rates that are present across meiofaunal species, particularly for some loci (*e.g.* mitochondrial loci), hamper species identification and complicates the design of universal primers (*e.g.*, Fontaneto *et al.,* 2015; Bhadury & Austen, 2010; Macher *et al.,* 2021).

Standardized taxonomic approaches (*e.g.*, Curini-Galletti *et al.,* 2012) and metabarcoding (*e.g.*, Atherton & Jondelius, 2020) have boosted overall biodiversity estimates even in areas where meiofauna has been long studied. This urges for a strong community effort with joined initiatives, such as regional workshops (Wilhems *et al.,* 2009; Curini-Galletti *et al.,* 2012; Fonseca *et al.,* 2014; Martínez *et al.,* 2019; Jörger *et al.,* 2021), to reveal how many species of meiofauna are present on different regional and global scales (Q#21). Comparative analyses across different regions and habitats might reveal putative areas of endemism and biodiversity hotspots contributing towards the overall goal of identifying patterns of diversity in meiofauna across different taxa (Q#37) (see Panel II). This is particularly relevant for testing the “everything is everywhere” hypothesis (Fenchel & Finlay, 2004), and the question on whether widely distributed species truly exist or are just an artefact of poor taxonomic resolution (Q#31). Wide distribution ranges are common in several meiofaunal groups with dormancy capabilities allowing long-distance passive dispersal, such as rotifers, nematodes, and tardigrades (Frisch *et al.,* 2007; Fontaneto, 2019). However, many other meiofaunal groups lack such dispersal stages and are thus generally considered poor dispersers, making reported cosmopolitan distributions in these taxa a yet to be explained “meiofaunal paradox” (Giere, 2009). Most recent studies re-examining putative cosmopolitan species in these poor dispersing groups (*e.g.*, nemerteans, molluscs, annelids, tardigrades, or nemertodermatids) based on morphological and molecular methods have revealed complexes of species with high degree of molecular divergence with geographically restricted distributional ranges (*e.g.*, Meyer-Wachsmuth *et al.,* 2014; Leasi *et al.,* 2016; Cerca *et al.,* 2020; Morek *et al.,* 2021), although some species also exhibit broad distribution patterns regardless the approaches applied (de Oliveira *et al.,* 2017; Worsaae *et al.,* 2019) (Panel II).

Enhancing biodiversity surveys points towards a specific problem in meiofauna research, that is the re-identification of species, *i.e.*, assigning them to existing names in the classificatory system. Advances in high-end morphological and molecular approaches for species delineation have outdated older descriptions, and type material – if it exists – is often inaccessible for re-examination via modern methods. This problem prevails in “soft-bodied” meiofauna (*e.g.* Fig. 1A-F) that requires the study of living animals to retrieve diagnostic characters, or in delicate specimens, which are frequently destroyed or lost during investigation (Garraffoni *et al.,* 2019). This has led to a heated debate on type requirements in “soft-bodied” meiofauna and the role of photomicrography-based taxonomy in “type-less species descriptions” (Ceríaco *et al.,* 2016; Garraffoni *et al.,* 2019) (Q#60). In many taxa, a combination of a photomicrographic taxonomy is needed, ideally combined with subsequent deposition of a voucher suitable for molecular analyses or DNA reference sequence along with the original description. Unfortunately, thorough morphological documentation might lead to the (partial) destruction of the documented type to-be, which at least might be left as a “DNA-type” as voucher material, in agreement with the International Code of Zoological Nomenclature (Jörger & Schrödl, 2013; Félix *et al*., 2014).

3.2. Panel II. Macroecology and Biogeography

Research on meiofaunal animals might provide opportunities for testing the generality of global biodiversity patterns beyond large organisms such as plants, insects, and vertebrates (*e.g.*, Hillebrand & Azovsky 2001; Azovsky *et al.,* 2020). Being geographically widespread and ecologically ubiquitous, meiofauna present good model systems for investigating global scale biogeographical patterns and processes, gaining insights into historical events and current ecological processes that shape diversity across most of Earth’s biomes (Zeppilli *et al.,* 2018; Majdi *et al.,* 2020; García-Gómez *et al.,* 2021). Furthermore, meiofauna encompasses species across most animal phyla, allowing the formulation of general inferences through a large fraction of the animal Tree of Life (Rundell & Leander, 2010). Indeed, our survey highlights that voters appreciate the importance of performing such studies on meiofauna, given that seven questions of this panel entered the 50 top-priority list (Table 2).

Despite these premises, large-scale studies on meiofauna remain out of reach. Meiofauna research needs standardized sampling protocols to obtain comparable data worldwide (Q#8). Long implemented in larger organisms, international protocols and common data-sharing practices are lacking for most meiofaunal groups (Somerfield & Warwick 2013, De Pooter *et al.,* 2017). This might be because meiofauna remains to be recognized as a tool for assessment of environmental quality by international directives, but it is probably also inherent to the small body size of meiofauna, their morphological traits, and their ecological preferences, which demand the use of specific sampling protocols, handling procedures, and equipment (Giere 2009; Schmidt-Rhaesa 2020). Some of these impediments might be alleviated by molecular techniques (*e.g.*, metabarcoding), but those still demand a solid reference library and comprehensive global sampling campaigns to explore patterns of diversity (*e.g.*, Castro *et al.,* 2021, Leasi *et al.,* 2018, Martínez *et al.,* 2020; Panel I), not to mention that metabarcoding datasets alone do not inform on the relative abundance of different species of metazoans (Fontaneto *et al.,* 2015).

Furthermore, the ubiquity of undescribed species and the practice of working at higher taxonomic levels across meiofaunal groups hamper robust estimations of taxonomic diversity (see Panel I) (Q#13). Our overall knowledge on meiofaunal biodiversity remains poor and strongly biased towards regions with a long history in biodiversity research (*e.g.*, Europe), as a significant portion of the world remains *terra incognita* on the global meiofauna map (Garraffoni *et al.,* 2021). This uneven distribution of information is also germane to relatively well-investigated areas, such as Europe, where most species records concentrate nearby research infrastructures such as marine field stations or laboratories; and even within these areas, researchers tend to look for animals in habitats where they are more abundant, confounding ecological knowledge about species habitat breadths (Rubio-López *et al.,* 2023). The organization of workshops in different parts of the world has alleviated this problem only partially, given that they only cover limited areas within otherwise largely unexplored regions. In contrast, all we know about meiofauna in vast regions of the world is limited to punctual, nearly anecdotical, sampling efforts (Fontaneto *et al.,* 2012).

Our level of ignorance is even greater regarding functional and genetic diversity (Fonseca *et al.*, 2017). This is problematic because these alternative biodiversity metrics might enable more meaningful interpretations of biological patterns and help us better understand the biogeography of certain groups (Leasi *et al.,* 2018; Martínez *et al.,* in review). Knowledge of traits, phylogeny, or abiotic ranges might help identifying the factors determining species dispersal (Q#16), especially for complexes of morphologically similar species, which may exhibit different habitat preferences or play a different ecological role within the same area (De Meester *et al.,* 2011, 2015). Recent evidence indicates that dispersal limitation is a key driver of meiofauna distribution, which might be influenced by morphological traits—such as body size, dormancy, presence, absence or mobility of larvae, asexuality, or presence of adhesive properties (Curini-Galletti *et al.,* 2012; Fontaneto, 2019)—or ecological preferences, such as specific habitat turbulence, or adaptations to cave or deep-sea habitats (Martínez *et al.,* 2019; Azovsky *et al.,* 2020) (Q#16). Different scenarios might help to explain long-distance dispersal in these groups, such as rafting (Jokiel, 1990), phoresy (Corrêa *et al.,* 2014; Ingels *et al.,* 2020), wind and rain-mediated transport (Ptatscheck et al., 2018), or accidental transport within ballast water of ships (Radziejewska *et al.,* 2006). Understanding the dynamics of meiofauna dispersal will contribute to defining to what extent emergent ecological patterns result from the present physical barriers or ecological limitations and whether it is related to meiofaunal body size.

The need for comparable datasets (Q#8) and knowledge synthesis (Q#13) highlights a demand for information to explore large-scale drivers of meiofaunal biodiversity (Q#24, Q#38). Many such works rely on data mining from published studies, mostly based on morphological identification (*e.g*., Vanreusel *et al.,* 2010; Azovsky *et al.,* 2012; Fonseca & Netto 2015; Brustolin *et al.,* 2018; Azovsky *et al.,* 2020; Garrafoni *et al.,* 2021). Meiofaunal records are generally scarce in general distribution databases (e.g. Global Biodiversity Information Facility, GBIF), and lack taxonomic validation beyond the submitter's capability. For some lineages, such as ostracods or mites (Fig. 1W,Z), even the taxonomic backbone provided by those platforms is largely incomplete. In contrast, comprehensive global databases are available for certain groups, such as acoels (Jondelius, 2023), platyhelminths (Tyler *et al.,* 2022), tardigrades (Michalczyk & Kaczmarek, 2013; Kaczmarek *et al.,* 2015), and gastrotrichs (Hummond, 2010), geographical areas (Garlaschè *et al.,* 2020, García-Herrero *et al.,* 2021, Rubio-López *et al.,* 2022, Curini-Galletti *et al.,* 2023, Ferrari *et al.,* 2023; Fresno-López *et al.,* 2023) and habitats (Martínez *et al.,* 2018; García-Gómez *et al.,* 2022). Unfortunately, there are no global datasets available for nematodes (Fig. 1O-S), copepods (Fig. 1X-Y) and foraminifera, despite of their abundance in sediments worldwide (Giere, 2008). Future efforts should focus on interoperability (Feng *et al.,* 2022), *i.e.*, unifying those databases in terms of data format and underlying terminology, as well as combining them with other sources of information, such as genes (Weigand & Macher, 2018), or traits (Cifoni *et al.,* 2021; Chapman *et al.,* 2019), so that future research driven by big data can be streamlined.

3.3. Panel III. Morphology and adaptation

The advent of advanced microscopy and imaging technologies, coupled with the ongoing challenges posed by rapid climate change and biodiversity decline, has heightened the significance and urgency of understanding both morphology and the mechanisms and outcomes of adaptive changes (Merilä & Hendry, 2014). Yet, none of the questions proposed by the panel entered the top 50 priority list (Table 2). This can be attributed to the voters' preference for applied research or to the fact that many questions of this panel focused on specific processes that may be unknown to broader audiences.

Three of the panel's five most-voted questions emphasize the mechanisms and limitations of convergent adaptation (Q#74, Q#80, Q#84). Investigating adaptations over long phylogenetic timescales necessitates the use of comparative phylogenetic methods, which are highly sensitive to the chosen phylogenetic reconstruction method and rely on the available data—scarce for most meiofaunal lineages (Panels I, II and IV). In this context, the potential adaptive significance of small body size has been a subject of prolonged discussion (Q#80). Small body size might represent the ancestral condition in various animal lineages (Laumer *et al.,* 2015, but see Marlétaz *et al.* 2019), while in other lineages small size has more likely evolved secondarily and independently through miniaturization processes (Worsaae *et al.,* 2023).

Investigations into adaptations over shorter evolutionary timescales rely on comparing the variability of traits across populations exposed to different ecological conditions and accounting for their genetic variation (Merilä & Hendry, 2014) (Q#92). Consequently, it becomes crucial to dissect the role of gene expression plasticity in acclimation versus genetic differentiation in adaptation when evaluating the type, function, and magnitude of phenotypic traits suitable for persisting in changing environments (Hoekstra & Coyne, 2007). Studies on these topics focusing on meiofauna arecomparatively limited and lag behind compared to those on large-bodied animals (Miller et al., 2022). Despite that, recent collaborative efforts among phylogenetists, morphologists, and systematists have significantly enhanced our capacity to integrate morphological and genomic data (Fonseca *et al.,* 2017; Smythe *et al.,* 2019; Martín-Durán *et al.,* 2021; Herranz *et al.,* 2022).

The adaptive role of behaviour remains unclear in meiofauna (Giere, 2009). As in larger organisms, spatial patterns observed in meiofauna might arise from the collective behaviour of individuals within a population, resulting from their integrated responses to stimuli (Guden *et al.,* 2018, 2021) (Q#90). For example, the complex spatial patterns formed by populations of the nematode *Caenorhabditis elegans* result from their individual foraging strategies, which are optimized to maximize sensory information about the target and follow predictable trails (Ding *et al.*, 2020; Demir *et a*l., 2020). Exploring common behavioural responses across other groups might reveal how the patchy distribution patterns exhibited by meiofauna at small spatial scales might arise in relation to the distribution of resources or microvariations of the environmental parameters. Behavioural studies often demand controlled experiments, which can be difficult to conduct due to the limited ability to culture most meiofaunal organisms (Brinke *et al.,* 2011). Nonetheless, recent advancements in technologies such as 3D bio-printing, novel imaging techniques incorporating fluorescent nano-sensors, and microfluidic chambers hold promise for enabling *in situ* observations of behaviours with respect to environmental parameters at the relevant microscale (Kathol *et al.,* 2011).

Morphological investigations play a fundamental role in integrative studies aimed at comprehending an organism's behaviour, life history, functional genomics, and physiology. Advancing our understanding in these aspects is valuable from a theoretical perspective but also serves as an initial step in multidisciplinary research endeavours. As a result, we anticipate that the growth of integrative studies involving meiofauna, coupled with technological advancements such as Micro-CT and Nano-CT (Ferstil *et al.,* 2020), will reinvigorate the recognition and expand the application of morphological studies in meiofauna research**.**

3.4. Panel IV. Genome biology and evolution

Genomic tools have advanced our knowledge of the evolutionary history of many animal lineages (*e.g.*, Guijarro-Clarke *et al.,* 2020; Fernández & Gabaldón, 2020), helped link genotype to phenotype (Frisch *et al*., 2020; Evans *et al.,* 2021), and offered resources for conservation (Theissinger *et al.,* 2023). Even though the meiofaunal nematode species *Caenorhabditis elegans* is one of the most studied model organisms in biology, meiofaunal organisms still suffer from a scarcity of genomic data. This paucity of genomic resources for meiofauna limits the integration of their evolution and ecology, which has, however, become commonplace in studies of larger organisms (Paps *et al.,* 2023).

Obtaining genomic data for meiofauna has been technically challenging due to their small size. However, recent advances in complementary DNA library synthesis and amplification have facilitated the acquisition high-quality transcriptomes from meiofaunal animals (*e.g.*, Smythe *et al.*, 2019; Herranz *et al.*, 2022). Whole-genome sequencing remains a challenge, but commercially available kits to produce long-read sequencing libraries from as little as 5 nanograms of high-molecular-weight DNA have successfully been used to produce high-quality genomes from individual small animals such as mosquitos (Kingan *et al.,* 2019) and springtails (Schneider *et al.*, 2021). Furthermore, both multiple-displacement amplification-based techniques and long-range PCR library amplification techniques are in development and might be suitable for generating long-read sequencing data leading to high quality, well-annotated genome assemblies from single meiofaunal specimens or, even, their diapause eggs (O'Grady *et al.,* 2022). When such single-specimen sample preparation techniques become widely used, the sheer species and phylogenetic diversity of meiofauna will make them a fruitful source of comparative and population genomic inquiries for decades to come. The comparatively low ranking of genomic questions in this horizon scanning effort may therefore reflect only the status quo of a field that is on the cusp of dramatic changes soon to come. Anticipating this change, several international initiatives are currently working on increasing the number of high-quality genomic data available across the Tree of Life, such as the Darwin Tree of Life (darwintreeoflife.org), the European Reference Genome Atlas (erga-biodiversity.eu) and Earth BioGenome (EBP) projects, and will surely play an important role also in adding to our knowledge on meiofauna.

To date, genomic tools applied to meiofaunal systems have primarily been used to resolve the phylogenetic positions of these taxa. Microscopic animals branch off from near the root of Bilateria and various other positions within Spiralia (=Lophotrochozoa) and Ecdysozoa (Giribet & Edgecombe, 2020). Phylogenetic efforts with meiofaunal taxa are challenging due to the fast rates of molecular evolution and long branches of some of these groups (*i.e.*, highly divergent molecular sequences with extensive accumulation of substitutions) (Q#101) that can lead to artificial groupings (Telford & Copley, 2005, 2016; Struck *et al.,* 2014; Kocot, 2016; Laumer *et al.,* 2019). It remains unclear whether these long branches might be explained, at least partially, by intrinsic features of meiofaunal taxa, such as small body size, short generation times, potentially large effective population sizes (Cutter *et al.,* 2013) (Q#82), and geographical (*e.g.*, latitudinal) effects on genome evolution (Q#99) .

Genomic tools will be essential to understand the evolutionary processes and biological mechanisms responsible for biotic and abiotic adaptations in meiofauna. The analysis of genomic data will also be paramount in calculating the speed of evolutionary change and the history of morphologically cryptic species complexes (Q#88) (Bickford *et al.,* 2007; Felix *et al.,* 2014; Struck *et al.,* 2018; Cerca *et al.,* 2021) (see Panel I); but also, to understand the genetic basis for adaptation (Savolainen *et al.,* 2013; Martín-Durán *et al.,* 2021). Hand-in-hand with cryptic species inference using population genomic approaches is the interrogation of gene flow among populations and incipient species (*i.e*., hybrid introgression) and the drivers of its restrictions (Q#85). By combining genomic inferences about gene flow and genetic differentiation (Feder *et al.,* 2012; Papakostas *et al.,* 2016) with experimental measures of reproductive isolation (Coyne & Orr, 2004; Cutter, 2018), meiofauna will provide complementary test cases to assess the generality of evolutionary hypotheses beyond large-bodied organisms. Seascape genomics, the marine counterpart to landscape genomics, seeks to associate allele frequencies within and among marine populations with environmental conditions to study adaptation, connectivity, and speciation in the sea as well as to develop biodiversity conservation strategies (Riginos *et al.,* 2016; Nielsen *et al.,* 2020), and we anticipate these methods will eventually be applied to elucidate evolutionary ecology of marine meiofauna.

3.5. Panel V. Anthropogenic impacts and global chang

We are in the midst of a global climatic emergency (Ripple *et al.,* 2019) and an accelerating biodiversity crisis driven by multiple anthropogenic impacts (Cowie *et al.,* 2022). Hence, understanding how global change will impact meiofauna is perhaps an obvious, yet pressing need. Indeed, questions pertaining to meiofauna research that focus on anthropogenic impacts and global change received overwhelming attention in our survey, with twenty-two questions entering the 50 top-priority and 7 questions making it to the Top-10 (Table 2).

This result seems to be independent from the expertise held by the voters (but see Material and Methods, Fig. 2), but might be related to the fact that funding landscape increasingly favours urgent questions related to the pervasive ecological changes and disturbances caused by anthropogenic activities, such as rising sea levels, climate change, pollution events, etc., or research activities that address management, restoration, and conservation, sometimes referred to as “actionable science” (Cvitanovic *et al.,* 2021). In this context, meiofauna have long been proved to assess impacts and disturbances in aquatic environments (Moore & Bett, 1989; Kennedy & Jacoby, 1999; Ridall & Ingels, 2021). Meiobenthic organisms often entirely depend on the interstitial space they reside in, lacking the means for movement or active limnetic or pelagic dispersal beyond their immediate environment—although passive dispersal may be more common than previously assumed (Ingels *et al.,* 2020; Ptatscheck & Traunspurger, 2020). Benthic meiofauna are therefore reliant on the microscale patterns and variations in the environment and hence also subject to the pervasive changes that aquatic ecosystems are experiencing. In addition, meiofauna show high production/biomass ratios and relatively rapid reproduction compared to larger organisms, which allow for quick responses to environmental changes and pollution (Schratzberger & Ingels 2018; Baldrighi *et al.,* 2019; Vafeiadou *et al.,* 2018). Looking at the scores of the 22 most popular questions in this section, two obvious breaks on the distribution of the scores can be observed; one that separates the panel's three top-voted question, and another that separates the four questions at the lower range of score. These latter four questions focus on a specific field of study or type of disturbance, and hence may be less interesting to a broad audience than the research questions that have more general applicability. The four lowest-scoring questions of the panel focused on differences between the temporary and permanent meiofauna and the implications for impact assessments and monitoring (Q#47), and the effects of microplastics (Q#48), physical disturbance (Q#58), and deep-sea mining (Q#60), respectively.

The two highest-ranked questions (Q#1, Q#2) relate to diversity. Diversity is often linked to stability of ecosystems, and usually declines when impacted by disturbances, although exceptions have been observed in the context of adaptation to pollution and long-term recovery where a combination of persistent and opportunistic taxa co-occur (Franzo *et al.,* 2022). Taxonomic and functional diversity may respond differently to pollution or other types of disturbance (Stark *et al.,* 2017). Meiofaunal communities are diverse, exhibit high generational turnover, and usually comprise dozens of species within a very small sample size at any one point in time. This suggests that variations in community structure are easily manifested, even following very small environmental changes such as a small discrepancy in average temperature (Pontes *et al.,* 2021; Vafeiadou & Moens, 2021). In other words, in a large pool of meiofaunal species, the trade-offs between species that have adapted or have a greater ability to cope with change and those that are ill-equipped to deal with a changing environment are expressed rapidly and detected with relatively low research effort (Losi *et al.,* 2021; Franzo *et al.,* 2022). Improving our understanding of how meiofaunal biodiversity is linked to ecosystems' functioning is important to mechanistically understand its contribution to the resilience and sustainability of disturbed ecosystems. We know that meiofaunal taxonomic and functional biodiversity responds to anthropogenic impacts (including global change), but whether these are important in the assessment of anthropogenic impacts and global change is still a matter of contention (Schratzberger *et al.,* 2007).

The next two questions (Q#3, Q#5) relate to using meiofauna as bioindicators. Meiofauna have the potential to be excellent bioindicators of anthropogenic impacts because of several characteristics (Moreno *et al.,* 2011; da Silva *et al.,* 2022). Because of direct development, meiofaunal organisms have limited mobility and are continuously exposed to anthropogenic impacts throughout all or part their life cycles. Being small, meiofauna are easy to sample in large numbers using adequate techniques. Finally, being highly diverse, changes in taxonomic or functional diversity potentially produced by disturbances might be easy to detect a (e.g. disturbances typically cause declines in sensitive species, while tolerant species mantain or increase their abundances), thus making meiofaunal organisms good bioindicators to detect environmental change (Kennedy & Jacoby, 1999; Zeppilli *et al.,* 2015). However, whether meiofaunal organisms are useful indicators of ecosystem quality and function is relatively unknown, mainly hampered by the lack of information on how community composition relates to other ecosystem metrics.

The last top-voted question (Q#6) is about resilience, which has become an important avenue of research with respect to global change. We need to know how to promote the ability of communities and ecosystems to recover disturbance events, whether those are "pulsed events", such as large storm or a catastrophic pollution event, or slow "press events", such as the drain of pollutants in the environment. Since they reproduce and grow rapidly and may tolerate disturbances, meiofauna should include good candidates for measure ecosystem resilience, at least to a certain extent (Bonaglia *et al.,* 2019). Furthermore, meiofauna pioneer successional events in disturbed ecosystems (often in close relationship with microbial communities), facilitating ecosystem's recovery before larger organisms arrive and grow (Gaudes *et al.,* 2010; Fleeger *et al.,* 2015).

In the past few decades, research focused on meiofauna responses to anthropogenic disturbance and global change and their use as indicators has increased substantially. However, most of these studies were limited to the interpretation of patterns and evoking knowledge from, for instance, autecological, physiological, or behavioural response studies to explain the observed patterns (Giere and Schratzberger, 2023). As our efforts increase to laern how and why meiofauna fulfil their roles in ecosystems, answers to the questions above will gradually become clearer.

3.6. Panel VI. Population and community ecology

The study of population and community ecology using meiofauna is a challenging endeavour. First, there are biological impediments connected to the small size of the organisms under study, the fact that many of these possess soft bodies and cannot be identified after traditional fixation methods (Balsamo *et al.,* 2020; Leasi & Cline, 2022), and that a few, ubiquitous species might dominate in the community showing limited environmental specialization (Gansfort *et al.,* 2020), although with notable exceptions in certain oligotrophic environments (Michiels & Traunspurger, 2005; Traunspurger *et al.,* 2020; Martínez, 2023). Second, understanding population and community ecology in meiofauna is dwarfed by technical impediments, mirroring some of those that ecologists face when documenting and understanding biodiversity patterns in other systems. One of such impediments is to assemble meaningful data required to bring out the characteristic features of biodiversity patterns at such small spatial scales, while ensuring these patterns are not biased by sampling effort and by how the human observer perceives this microscopic environment. Another of such impediments is to combine multiple sampling techniques, species identification methods, and biodiversity metrics in a meaningful way. Given all these difficulties, it is no surprising that the study of community ecology in meiofauna is still in its infancy, and that only four rather general questions entered the 50 top-priority list (Table 2). These questions highlighted the need to advance understanding of meiofaunal species interactions and connections across multiple scales, identifying the importance of feedback from individual functioning and interactions to ecosystem dynamics (Baldrighi & Manini, 2015; Corte *et al.,* 2017).

Understanding the influence of connectivity on meiofaunal diversity patterns was scored as the most important deficit in population/community ecology (Q#20). Studying connectivity is essential to predict the effectiveness of dispersion through ecological corridors and steppingstone habitats (Baum *et al.,* 2004), as well as to infer the extent to which meta-population dynamics affect meiofauna (Gansfort *et al.,* 2020). Importantly, the connectivity among habitats at different spatial and temporal scales is essential to develop effective conservation strategies for different ecosystems, particularly in partially isolated habitats such as hydrothermal vents (Gollner *et al.,* 2020) or aquifers (Korbel *et al.,* 2019), which might be predominantly reached via migration from local refuge areas by those meiofauna taxa that lack dispersal stages.

Another question that entered the 50 top-priority questions revolved around the possibility to transfer ecological theories developed for macroscopic organisms (especially vertebrates) to a microscopic context (Q#30). This topic highly connects with the need of understanding how these microscopic organisms sense the environment (Q#32) and interact with one another within a selective abiotic setting (Q#40) (Cronin-O'Reilly *et al.,* 2018). At the individual level, meiofaunal organisms show complex behaviours in response to environmental stimuli, as is the case for their macrofaunal counterparts (Panel III) (Demir *et al.,* 2020; Ding *et al.,* 2021). However, since they live in a microscopic world, meiofaunal organisms experience their environments differently than larger animals, mainly using chemo- and mechanoreceptors to orient and find food (Parry *et al.,* 2017). As the well-studied "quorum-sensing" in microbial biofilms, chemical cues could be an important communication pathway for meiofauna. For example, there is strong evidence that volatile organic compounds can trigger attraction towards food patches (Höckelmann *et al.,* 2004), and food quality and quantity seem to be critical triggers for feeding behaviours (Ingels *et al.,* 2011), overruling other triggers such as competition or predation risk (Kreuzinger-Janik *et al.,* 2022). But meiofauna can also respond to other types of stimuli. For example, the free-living nematode *Chromadorina bioculata* has been found to show a positive photo-response (Croll & Zullini 1972), probably due to its search for algae. Finally, at the scale of meiofauna, water has a higher apparent viscosity than at macroscopic scale, thus changes in osmotic concentration, shear-stress or hydrostatic pressure could also be fairly well sensed by meiofauna (Yeates Steyaert *et al.,* 2007). Some meiofauna are highly effective predators, particularly amongst acoels and platyhelminths, and are provided with pharyngeal structures specialized to capture certain preys (Curini-Galletti *et al.,* 2023).

Many animals modify their surroundings to increase their chances of survival (Moens *et al.,* 2005; Meysman *et al.,* 2006). These changes sometimes imply nurturing their potential preys to ensure a continuous food supply—a process called "gardening" in an analogy to human strategies. Evidence shows that meiofaunal organisms "garden" their favourite food (Q#51) as well. For example, bacterial-grazing nematodes promote the mobility of microbial colonies, while their burrows, pellets, or other mucus-driven micro-structures maintain microbial populations near exponential growth (Jensen, 1987). Laboratory experiments show that increasing numbers of bacterial-feeding nematodes stimulate rather than limit bacterial activity (Traunspurger *et al.,* 1997), and that increasing numbers of algal-feeding nematodes stimulate rather than limit photosynthesis as well (Mathieu *et al.,* 2007, d'Hondt *et al.,* 2018). Kinorhynchs might also secrete mucus to "garden" and trap bacteria, diatoms, microalgae that they would then use as potential food (Adrianov, 1991); whereas Stilbonematinae nematodes (Fig. 1S), gutless clitellates *Olavius* and nerillid polychaete *Meganerilla bactericola* entirely depend on symbiotic bacteria to survive in reduced anoxic sediments (Ott *et al.,* 2004; Dubilier *et al.,* 2001) or dysoxic deep sea basins (Müller *et al.,* 2001). The manipulation of microbial assemblages by meiofauna might even have large-scale implications that remain to be understood, given the tight relationships between microbes, their meiofaunal predators (or gardeners), and ecosystem processes such as denitrification in marine sediments or demineralization of organic matter (Nascimento *et al.,* 2012; Bonaglia *et al.,* 2014).

Finally, it is interesting to draw a parallel with a classic paper by Sutherland *et al.,* (2013) on the 100 fundamental questions in ecology, primarily developed by researchers working on birds and mammals and largely revolving around the importance of advancing our understanding of dynamics of environmental change and complex ecosystem interactions, as well as the interactions between ecology and evolution. Both historically and today, some of the most discussed paradigms in meiofauna are “Meiofauna paradox” (Giere, 1993), “Meiofauna ubiquity” (Fenchel & Finlay, 2004), and “Is everything small everywhere?” (Fontaneto, 2011), which may actually reflect either the absence of general patterns or the lack of a feasible meiofauna definition. For example, the processes that determine community assembly developed for plants (HilleRisLambers *et al.,* 2012) show that abiotic and biotic components of the environment, trait-phylogeny-environment relationships, and frequency-dependent population growth strongly influence species fitness and the outcome of community assembly. Simulations that combine niche and dispersion measures of species have demonstrated that the same model that explains plant community assembly also explains marine nematodes assemblages (Vieira & Fonseca, 2019). Likewise, using species traits in community ecology showed to be a promising way to move forward from the “Everything small is everywhere” paradigm (Martínez *et al.,* 2021). Furthermore, the individual phenotype, behaviour, and how meiofauna sense and react to the contemporary environment are essential to understand the functional diversity of meiofauna (Takola & Schielzeth, 2022). Combining current approaches derived from the terrestrial community and population ecology may represent our best chance of achieving several of these goals while developing unified conceptual ecological theories.

3.7. Panel VII. Biogeochemistry and applied topics ***[1006 words]***

Meiofaunal organisms distinctly shape soils and sediments worldwide, including their role as catalyst of globally important benthic ecosystem processes (Schratzberger & Ingels, 2018, Schratzberger *et al.,* 2019). Therefore, it is not surprising that the topic received a high score, with nine of the proposed questions entering the 50 top-priority list. However, our knowledge of how meiofauna directly and indirectly affect biogeochemical cycles is scant, making this scientific area underexplored compared to topics other panels were charged with. Thus, these high scores may also imply that we urgently need more studies in this emerging field, particularly regarding multidisciplinary studies to understand and quantify how microbes-meiofauna interactions affect carbon cycling and, in particular, carbon sequestration under climate change.

Organisms living in soils and sediments alter their habitat by constructing and maintaining burrows, by ingestion and egestion, and by burrow flushing with overlying water for respiratory and feeding purposes (Giere and Schratzberger, 2023). Bioturbation includes all these three processes and may directly or indirectly affect biogeochemical cycles (Kristensen *et al.,* 2012). Meiofauna bioturbation was first recognized to play a significant role in shaping sediment several decades ago (Cullen, 1973). Due to high abundance and widespread distribution, bioturbation by meiofauna is potentially important in every aquatic benthic environment, from lake shores to intertidal mudflats and the deep-sea floor. However, scientific literature on how meiofauna directly and indirectly influence sediment biogeochemistry remains sparse (Schratzberger & Ingels 2018). One question addressed the influence of meiofauna on global carbon cycling and sequestration (Q#27). The direct contribution of meiofauna biomass to total sediment carbon stocks may be small (Krishnapriya *et al.,* 2021). However, meiofauna activity indirectly modifies carbon exchange at the sediment water-interface, where it can increase the rate of bacterial carbon mineralization by up to 50% (Nascimento *et al.,* 2012). By contributing between 3 and 33% of total oxygen uptake in coastal sediments (Maciute *et al.,* 2023), meiofauna activity responds to, and influences, the overlying seawater carbon chemistry. As a result, meiofauna might alter the ultimate sequestration of carbon in sediments over large spatial scales (Ravaglioli *et al.,* 2020), although their net effect on carbon sequestration remains to be quantified.

The critical roles of meiofauna on nutrient cycling and on biogeochemistry were the subject of two questions (Q#9, Q#28). Meiofauna primarily influences oxygen, sulphur, and nutrient cycles through direct solute uptake and bioturbation (Aller & Aller 1992; Berg *et al.,* 2001; Maciute *et al.,* 2021), by stimulating nitrogen cycling microbes (Bonaglia *et al.,* 2014), and via interactions with millimeter-long cable bacteria (Bonaglia *et al.,* 2020) in coastal sulphide-rich sediments. Thus, meiofauna can influence ecosystem functions also in anoxic and sulfidic sediments (Q#46). Several factors determine how the roles of meiofauna differ between ecosystems. Most meiofauna need relatively high levels of oxygen and organic matter, which makes the upper millimetres or centimetres of soils and sediments more populated and more affected by meiofauna bioturbation than the deeper ones (Bonaglia & Nascimento 2023). Respiration rates of meiofauna significantly decrease in response to decreasing ambient oxygen levels (Braeckman *et al*., 2013, Maciute *et al.,* 2023). Muddy, fine-particle sediments dominate most of the seafloor and can be rich in organic matter promoting active meiofauna bioturbation, which, in turn, affects solute advection and microbial community structure (Bonaglia *et al.,* 2014; Nascimento *et al.,* 2012; Bonaglia *et al.,* 2020; Maciute *et al.,* 2023). In contrast, foraminifera can promote sediment reworking in sandy sediments, rich in granulated materials and more common in intertidal and shelf (Bouchet & Seuront 2020; Deldicq *et al.,* 2023). In general, we still lack understanding of the role of meiofauna in other ecosystems, such as the deep sea, where the relative importance of macrofauna lessens (Rex *et al.,* 2006). Also, it remains unclear whether meiobenthos influence cycling of other macro nutrients, such as phosphorus.

Two questions focused on the ecological interactions between meiofauna and prokaryotes (Q#35) and on whether meiofauna can drive organic contaminant degradation by microbes and heavy metal distribution (Q#111). Past research has uncovered the largely unanticipated influence that meiofaunal-prokaryotes interactions have on benthic ecosystem processes, including the remineralization of organic matter (Nascimento *et al.,*2012) and degradation of organic pollutants (Näslund *et al.,* 2010; Louati *et al.,* 2013). However, there is virtually no empirical data on the effects of meiofauna on the fate and distribution of heavy metals. Outcomes from future experimental and modelling studies are needed to better understand how meiofauna-prokaryote interactions will evolve under anthropogenic stress, and whether meiofauna could be harnessed in biodegradation processes, water treatments and other biotechnologies. Another ecological interaction that received attention in our survey is that of fish predating on meiofauna (Q#49). Some fishes predate exclusively on meiofauna. In estuarine environments, juvenile fishes primarily feed only on harpacticoid copepod species (Carpentier *et al.,* 2014). In the southern North Sea, solenettes and gobies preferably prey on harpacticoids as well, but their predation rates decrease with increasing fish size, attesting to the important role of meiofauna in juvenile fish diets (Schückel *et al.,* 2013). In coral reefs, sifting gobies efficiently separate meiobenthic prey from heavier inorganic particles (Brodnicke *et al.,* 2022).

The potential effects of meiofaunal activity on microplastics (Q#41) have received little attention to date. Annelids (Gusmão *et al.,* 2016; Lagos *et al.,* 2023) and nematodes (Kang et al., 2021; Fueser *et al.,* 2019; 2020) might accidentally ingest microplastics, but it remains unknown how meiofaunal bioturbation affects microplastic transport and fate in the sediment. Finally, we known that meiofauna community can mediate ecosystem processes in sediments with little or no macrofauna, such as the deep sea (Danovaro *et al.,* 2008) or certain areas in the Baltic Sea (Bradshaw *et al.,* 2006; Nascimento *et al.,* 2012) (Q#45). Nascimento *et al.,* (2012), for example, found that organic matter mineralization in sediments with high meiofauna abundance did not increase further when macrofauna were present. It follows that meiofauna communities can drive organic matter mineralization in sediments with reduced macrofauna abundance. This increases the resilience of those benthic biogeochemical processes that are essential for the continued delivery of ecosystem services desired by society.

3.8. Panel VIII. Science communication and other topics

It is challenging to promote awareness about organisms that are hardly visible to the naked eye. Indeed, humans tend to choose their favourite species based on criteria rarely fit by meiofauna, such as prettiness, size, and familiarity (Miralles *et al.,* 2019; Mammola *et al.,* 2023).

However, there are still venues to promote the interest for meiofauna among students and young researchers (Q#4). Meiofauna stands out by their astonishing number of species and variety of forms (Fig. 1), even in places where more conspicuous forms of life are scarce, such as sandy beaches, temporal ponds, glaciers (Zawierucha *et al.,* 2022), and extreme environments such as anoxic deep-sea trenches (Danovaro *et al.,* 2012), sulphide-rich sediments (Fenchel & Riedl, 1970; Ott *et al.,* 2004), or anchialine caves (Martínez *et al.,* 2017; Worsaae *et al.* 2019) (Fig. 1X). The rather high probability of finding new species might attract students with more taxonomic aspirations; whereas the description of unexpected life forms, morphologies, and anatomies might appeal those who want to make their ways into general zoological textbooks (Kristensen, 1983; Kristensen & Funch, 2000). Students and researchers interested in applied sciences might be drawn into working with meiofauna due to their practical role in ecosystem conservation and management, for example, as sentinels in marine and freshwater ecosystems (Zeppilli *et al.,* 2015; Hägerbäumer *et al.,* 2017) (Q#19) even at low level of anthropogenic impact (Michelet *et al.,* 2021); or in habitats hardly reachable by humans (e.g. deep sea, Ingels *et al.,* 2020) (Q#57). Finally, from a theoretical perspective, microscopic animals help us understanding broader eco-evolutionary questions, once sufficient data regarding their biology, distribution, and genetics are available (Panels I-IV). This diversity of topics allows to train students and young researchers in complementary disciplines and stimulate a new generation of meiobiologists.

Students and young academics might more likely be engaged in meiofauna research if they are introduced to the topic during their study programs (Q#44). Very few high-level programs include courses related to meiofauna, but several summer schools and PhD courses have been organized in recent years in which meiofauna has been a central element (Zeppilli & Sarrazin, 2013; Jörger *et al.,* 2021) (Fig. 4D). Those courses can also be combined with workshops, in which internationally renowned researchers not only teachl,, but also collect and describe the local biodiversity. This strategy often brings knowledge and resources to areas where biodiversity research is lagging behind and might even lead to joint publications (Fonseca *et al.,* 2014; Jörger *et al.,* 2021). Notably, this survey was used to introduce meiofauna to the students of the master and bachelor Zoology courses of the University of Paraná (Brazil) and University Complutense of Madrid (Spain), and some of them even took an active part in the voting process.

The interest exhibited by some early career researchers in the description of biodiversity can also be channelled into building baseline data sets and catalogues of aquatic life, including meiofauna (Q#22). Taxonomic impediment might be sped up by DNA-based taxonomy and metabarcoding (Taberlet *et al.,* 2012; Fontaneto *et al.,* 2015), revitalizing taxonomy (Puillandre *et al.,* 2012) and initiating the development of fast fingerprinting techniques (Fonseca *et al.,* 2010, Cowart *et al.,* 2015). Automated high-resolution imaging together with automated classification through machine learning and artificial intelligence might to overcome the limitations of these techniques (Panel I). These new approaches can process meiofaunal samples with convolutional neural networks at a pace that exceeds manual human interrogation. A massive effort including the combination of these newly developed technologies might allow, in a relatively short term, the dispelling of the taxonomic impediment and finally to assess meiofauna diversity reliably. Nevertheless, meiofauna can help increase general awareness about Earth's ecosystems, thereby spotlighting the current biodiversity crisis., e.g. by organizing interactive talks and hands-on activities targeting the general public (Fig. 4A-C). This can be organized in combination with scientific workshops, so the public can interact and see scientists in action (Pardos *et al.,* 2021) (Fig. 4J) or conveyed through the exhibitions of natural history museum (Fig. 4L). The diversity of meiofauna has been brilliantly illustrated by few books and fairytales written for the general public, and particularly children (*e.g.*, Rajcak & Laverdunt, 2016; Zeppilli, 2022) (Fig. 4A-C). Infrastructures provided by national parks and UNESCO Geoparks might support dissemination, while integrating research projects in which scientific outreach is central (Martínez *et al.,* 2019; 2020; Brodnicke *et al.,* 2022) (Fig. 4E).

Remarkably, few microscopic animals have become part of Internet pop-culture through memes and videos (Fig. 4F-I). For example, tardigrades are popular due to their resistance to extreme temperature or space radiation (Persson *et al.,* 2018) (Fig. 4K, N), whereas bdelloid rotifers are famous by their lack of males (Fontaneto & Barraclough, 2015), and mud dragons and penis worms don't cease surprise by their evocative body shapes and catchy vernacular names (Herranz *et al.,* 2019) (Fig. 4M). Indeed, naming new species in reference to peculiar features (Cepeda *et al.,* 2020) (Fig. 1M) or to famous artists, sportspeople, and the like (*e.g.*, Worsaae *et al.,* 2009; Di Domenico *et al.,* 2019), might also bring them to the spotlight (but see Guedes *et al.,* 2023). Some meiofaunal organisms, particularly *Caenorhabditis elegans,* have been used with the goal of better understanding and eventually curing human diseases (Kato *et al.,* 2008; Kirienko *et al.,* 2010; Kyriakakis *et al.,* 2015), whereas soil nematodes are fundamentally important in agriculture (Puissant *et al.,* 2021). Yet, they are rarely mentioned in relationship to the practical importance of meiofauna, perhaps because many researchers emphasize meiofaunal organisms associated with marine sediments.

4. Concluding remarks: the next generation of meiofauna research

4.1. Are we exploiting the full potential that meiofauna offer as a model to address questions of broad scientific and societal importance?

Not yet, but integrative approaches and technological developments have been creating opportunities to employ these fascinating organisms to answer broad and important questions (Giere and Schratzberger, 2023). Meiofauna have been used as models to understand fundamental adaptive processes, have contributed to unravel the animal Tree of Life (Laumer *et al.,* 2015), are believed to be a treasure trove for future genomic studies (Martín-Durán *et al.,* 2021), play a key role in ecosystem functioning and integrity (Bonaglia *et al.,* 2014; Schratzberger & Ingels, 2018), and have been used as models delve deeper into human diseases (Kirienko *et al.,* 2010). Meiofauna also represents a valuable biomonitoring tool for freshwater and marine environments alike, even where larger-sized fauna has become depleted or absent (Zeppilli *et al.,* 2015; Ridall & Ingels, 2021; Schratzberger et al., 2023). This very broad spectrum of topics is likely just the tip of the iceberg, with new ideas and research avenues continuing to emerge as technological developments and accumulation of information sheds light on the strange life of the small, ubiquitous animals around us.

4.2. What are the critical research priorities as perceived by the meiofauna community?

Our research agenda should balance between investigating general questions—sparking the interest of a broad audience—and addressing specialized research topics focusing on theoretical aspects concerning the meiofauna itself. The latter aspects, which often involve generating primary data on distribution, taxonomy, traits, and DNA sequences, are not only crucial to address some of the knowledge shortfalls that pervasively affect the development of the field (Fonseca *et al.,* 2017), but also are foundational for supporting applied science.

The results of our survey, largely favouring questions with a more applied scope, contrast with the diverse research topics initially proposed by our panels and traditionally tackled by meiofauna researchers. These results were not influenced by the background of the voters (Fig. 2A, B; Supplementary Methods), nor by the linguistic features of the questions (readability, length, use of jargon and acronyms). Whether those preferences might be influenced by other factors not controlled for in our analysis, such as the current funding landscape or the growing eco-anxiety driven by widespread environmental problems, rests in the mind of each voter. Regardless, these results should not be accepted uncritically as a roadmap guiding our research priorities; rather, they should be considered as a diagnosis of how broad international audiences perceive the importance of the different topics addressed traditionally within meiofauna.

4.3. Which biases currently affect meiofauna research and how can we overcome them to move forwards in our research agenda?

Geographical and taxonomic biases, as well as biases inherent to the small size of meiofauna, have affected the development of the meiofauna research (Fonseca *et al.,* 2018). Therefore, it is unsurprising that they were the focus of many top priority questions of every panel.

Technological innovation might alleviate some of those biases. New imaging and microscopical techniques, for example, have provided unprecedented insight to meiofauna, whereas artificial intelligence and molecular methods might soon expedite sample processing and analyses. Implementing these methods, though, requires urgent training of taxonomists to create essential reference databases of images and DNA, as well as optimizing sequencing technologies for small meiofaunal organisms. While reduced genome representation methods like transcriptomics can offer interim solutions (Wang et al., 2009; Dodsworth, 2015), the full potential lies in generating complete reference genomes. To achieve this, greater collaborative and development efforts are essential, as demonstrated by initiatives like the Darwin Tree of Life, Earth BioGenome Project, and European Genome Reference Atlas projects.

Geographical gaps will only be overcome through the establishment and reinforcement of international collaborations (Menegotto & Rangel, 2018). This role has been already played by the International Association of Meiobenthologists, as well as the periodically organized conferences and thematic sessions of international meetings. Summer schools and regional workshops has proven useful as well, especially in engaging local students and researchers from areas with limited resources available to study meiofaunal organisms. For all these activities, improving our communication skills is crucial in reaching diverse audiences and making our research community even more international and diverse.

In conclusion, meiofauna have many desirable properties to answer a broad range of research questions, but those are often overrun by multiple shortfalls and impediments. It is our task as a research community to turn these impediments into exciting challenges, which potentially get both researchers and the general public intrigued by those small critters that constantly lurk unseen in front of us.

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Table 1. Subject areas, general topics addressed, panel member composition (* = panel coordinator; + = postdoc or early career researcher, # = external expert), and number of questions included in the 50 top-priority final list out of the total retained in List #1. Panel members are listed alphabetically by surname

Subject area	**Topics**	**Members**	**N**
I. Systematics and Taxonomy	Challenges in identifying new species of microscopic animals and main open questions in relation to new integrative taxonomic techniques and species concepts.	Katharina Jörger*, Ulf Jondelius, Nicolas Puillandre#, Martin V. Sørensen, Hiroshi Yamasaki+	4 of 18
II. Macroecology and Biogeography	Global diversity patterns, biogeography theory, and diversity drivers. Problems and discussion on meiofauna distribution and biogeography, including the “Everything is Everywhere” hypothesis, meiofaunal paradox, cryptic diversity, etc.	Gustavo Fonseca*, Marco Curini-Galletti, Simone Fattorini#, André Menegotto+, Torsten H. Struck	7 of 24
III. Morphology and adaptation	Morphological, physiological and behavioural evolution and adaptation to different environments. Miniaturization.	Francesca Leasi*, Alexandra Kerbl+, José Martín-Durán#, Andreas Schmidt-Rhaesa, Katrine Worsaae	0 of 24
IV. Genome biology and evolution	Genome evolution in meiofauna and the role of meiofauna in the development of genomic tools	Christopher Laumer*+, Asher D. Cutter, Dagmar Frisch, Kevin M. Kocot, Andreas Wallberg#	0 of 29
V. Anthropogenic impacts and Global Change	Climate change, pollution, microplastics, urbanization, deep sea mining and other anthropogenic perturbation that could affect meiofauna	Jeroen Ingels*, Sabine Gollner+, Paul Montagna#, Giovanni dos Santos, Federica Semprucci	22 of 34
VI. Population and community ecology	Abiotic and biotic interaction, functional traits, ecological niche occupation, spatial and temporal dynamics at the local scale, and ecological successions in meiofaunal communities	Maikon Di Domenico*, Nabil Majdi, Stefano Mammola#, Nuria Sánchez+, Paul J. Sommerfield	4 of 18

VII. Biogeochemistry and applied topics	The role of meiofauna in biogeochemical cycles, as well as on describing meiofauna-bacteria interactions. Questions regarding potential applied uses of meiofauna might also be considered.	Stefano Bonaglia*, Francisco Nascimento, Isaac Santos#, Michaela Schratzberger, Mauricio Shimabukuro+	9 of 29
VIII. Science Communication and Other Topics	Problems link to dissemination of meiofaunal to the general public, stakeholders and decision makers; other topics affecting the community of meiofaunal researchers	Daniela Zeppilli*, Elisa Baldrighi, Holly Bik#, Diego Cepeda+, Anne Rognant	4 of 18

Table 2. Fundamental questions in meiofaunal research, including the Top-50 most voted questions (in bold), as well as the 5 highest ranked questions arranged by panel. Five highest ranked questions are also discussed so we do not dismiss panels without questions in the Top-50. Abbreviations: Q#, ranking position.

Panel I

How can we efficiently and reliably estimate and measure meiofaunal species diversity? **[Q#12, 2151 points]**

How species-rich are meiofauna on a regional and global scale? **[Q#21, 2108 points]**

Do cosmopolitan meiofaunal species exist, do they represent complexes of cryptic species with narrower distributions, or are they just an artefact of poor taxonomy? **[Q#31, 2077 points]**

What patterns of diversity exist and how do they vary among different groups of meiofauna? **[Q#37, 2063 points]**

How can we preserve the different groups of meiofauna for long-term storage to keep the reference material of a species available and valuable for future generations of meiofauna researchers? [Q#60, 1988 points]

Panel II

Can sampling protocols be standardized to gather comparable distribution and ecological data worldwide? **[Q#8, 2162 points]**

What are the main knowledge gaps in meiofaunal diversity? **[Q#13, 2148 points]**

Which are the main barriers for meiofaunal species dispersion/colonization? **[Q#16, 2126 points]**

What drives patterns of meiofaunal diversity over large-scale gradients? **[Q#24, 2093 points]**

What drives patterns of meiofaunal phylogenetic and functional diversity up to global scales? **[Q#38, 2063 points]**

What are the environmental and biological mechanisms that drive dispersal distance in meiofaunal species? [Q#42, 2036 points]

What is the relative contribution of local versus regional ecological factors on the distribution of meiofaunal organisms? [Q#43, 2033 points]

Panel III

Do distant lineages evolve convergent morphological adaptations to similar habitat and ecological conditions? [Q#74, 1923 points]

What are the adaptive limits and potentials of small body size? [Q#80, 1901 points]

To what degree are common traits in meiofauna the product of convergent evolution due to a shared ecology or constrained by the ancestral condition? [Q#84, 1875 points]

Are there any behavioural adaptations (aggregation, patchiness, negative phototaxis) that all/most meiofaunal animals have in common? [Q#90, 1843 points]

What is the role of intra-specific variability in adaptive change? [Q#92, 1837 points]

Panel IV

How much fluctuation in effective population size do meiofaunal species experience as a function of life-history traits, abiotic perturbations, and ecological community interactions? [Q#82, 1879 points]

How restricted is gene flow among populations of meiofaunal species and what are the principal sources of gene flow restriction? [Q#85, 1868 points]

What kind and magnitude of genomic differences distinguish cryptic meiofaunal species? [Q#88, 1848 points]

Are there consistent geographical (for example, latitudinal) patterns in genome evolution across different meiofaunal taxa? [Q#99, 1805 points]

What biological factors (for example generation time, mutation rate, population size), if any, explain the observed long branch lengths seen for meiofaunal taxa in many molecular phylogenies? [Q#101, 1798 points]

Panel V

How does meiofaunal biodiversity contribute to ecosystem function, integrity, and sustainability in the context of anthropogenic activities and global change? **[Q#1, 2257 points]**

Is meiofauna taxonomical and functional diversity important in assessing anthropogenic impacts and global change on ecosystems? **[Q#2, 2210 points]**

Are meiofauna good indicators of ecosystem quality status and functioning or do they need support from additional sources of evidence? **[Q#3, 2209 points]**

Can meiofauna be used to understand better how pollution impacts ecosystems as a whole? **[Q#5, 2189 points]**

How do meiofauna contribute to ecosystem resilience, particularly after a disturbance? **[Q#6, 2187 points]**

What are the most damaging impacts for meiofauna (for example extraction of resources, modification of habitat, creation of man-made structures, pollution, warming, ocean acidification, deoxygenation, etc.)? [Q#7, 2177 points]

What are the main effects on meiofauna caused by anthropogenic pollution? [Q#10, 2157 points]

Are meiofaunal organisms a good tool in evaluating the success of habitat restoration projects in different ecosystems, for example, by assessing ecosystem function and health? [Q#11, 2154 points]

What are the roles of meiofauna in the natural restoration process that follow anthropogenic impacts? [Q#14, 2131 points]

Are meiofaunal species effective indicators for conventional pollutants and emerging contaminants (pharmaceuticals, pesticides, personal care products)? [Q#15, 2130 points]

Are meiofauna more or less resilient compared to other benthic components in an ecosystem when under pressure of anthropogenic impacts and global change? [Q#17, 2124 points]

What are the main effects on meiofauna caused by climate change? [Q#18, 2120 points]

Do meiofauna in different habitats respond differently to similar anthropogenic impacts or global change? [Q#23, 2098 points]

Are there suitable early warning meiofaunal organisms, i.e. organisms useful to detect early stages of anthropogenic activities and global change? [Q#25, 2092 points]

What functional traits or adaptations make meiofauna resistant against the impacts of anthropogenic activities and global change? [Q#26, 2090 points]

How will global change affect meiofauna distribution ranges and biogeography; for example, through contraction, expansion or shifts? [Q#29, 2083 points]

Which are the most accurate monitoring protocols and tools, including meiofauna-based metrics and indices, to quantify meiofaunal changes in response to anthropogenic impacts and global change? [Q#33, 2071 points]

How do anthropogenic activities and global change affect the different levels of biological organization (for example genes, proteins and other compounds, cells, organs, organisms, life *stages, populations, communities) in meiofaunal communities, and how could they be use as indicators?* [Q#34, 2069 points]

What is the best way to measure meiofauna diversity when assessing impacts from anthropogenic activities and global change? [Q#36, 2063 points]

Do permanent and temporary meiofauna respond differently to anthropogenic impact and global change and what are the implications of these differences in impact assessments and monitoring? [Q#47, 2018 points]

What are the main effects on meiofauna caused by microplastics? [Q#48, 2017 points]

What are the main effects on meiofauna caused by physical disturbance? [Q#50, 2013 points]

Panel VI

How does connectivity among different habitats affect meiofaunal diversity patterns across different spatial scales? **[Q#20, 2110 points]**

Are the ecological paradigms that we have developed for macroscopic organisms (for example, vertebrates, plants) transferable to a microscopic context, or do we need new theories and approaches to understand the population and community ecology of meiofauna? **[Q#30, 2080 points]**

How do meiofaunal animals sense and react to their environment? **[Q#32, 2072 points]**

What is the relative contribution of abiotic features versus biotic interactions in determining community assembly in meiofauna? **[Q#40, 2057 points]**

Are meiofauna predators or gardeners of microbial resources? [Q#51, 2011 points]

Panel VII

How and how much do meiofauna influence nutrient cycling in different ecosystems? **[Q#9, 2160 points]**

What do we know about the contribution of meiofauna to global carbon cycling and sequestration? **[Q#27, 2086 points]**

What are the most critical roles of meiofauna in biogeochemical cycling and how do they differ between different ecosystems? **[Q#28, 2084 points]**

What is the relative importance of ecological interactions between meiofauna and prokaryotes, such as facilitation and predation, in ecosystem processes? **[Q#35, 2064 points]**

Do meiofauna drive organic contaminant biodegradation and heavy metal distribution in different ecosystems? **[Q#39, 2060 points]**

How and how much do meiofauna bioturbation affect transport, transformation, and burial of marine litter and microplastics? [Q#41, 2048 points]

How would aquatic ecosystems function without meiofauna and to what extent can meiofauna sustain rates of key biogeochemical processes alone? [Q#45, 2030 points]

How and how much do meiofauna living in anoxic and sulfidic sediment layers influence ecosystem functions? [Q#46, 2023 points]

Are the meiofauna a quantitively important food source for fish and other vertebrates? [Q#49, 2017 points]

Panel VIII

How can we promote the interest for meiofauna amongst students and young researchers thereby ensuring the future of the field? **[Q#4, 2193 points]**

How can we further promote and/or sustain the use of meiofauna as a tool or requirement in standard protocols for assessing and monitoring the quality status of ecosystems? **[Q#19, 2119 points]**

How can we strengthen collaboration to speed up the production of a joined global inventory of meiofaunal species in times of biodiversity crisis and global change? **[Q#22, 2106 points]**

Which community efforts are needed to dispel the taxonomic impediment and train new generations of meiobenthologists? **[Q#44, 2030 points]**

What types of messages related to the health of our aquatic ecosystems and, more generally, of our planet can we convey with the scientific topic of meiofauna? [Q#57, 1995 points]

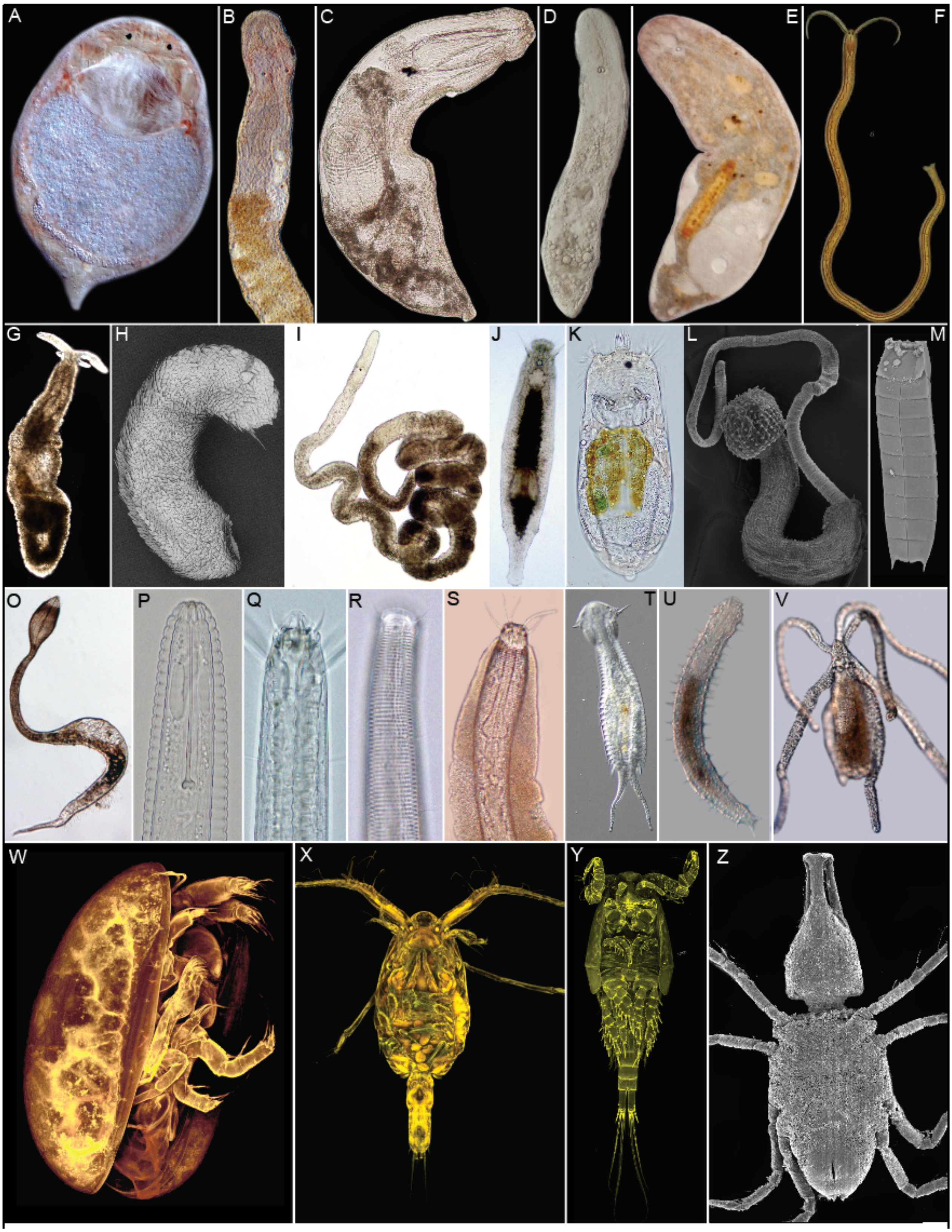
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Figure 1. Examples of the diversity of meiofauna using different imagining techniques. **A**. *Dalyella* sp. (Platyhelminthes) from a cave in Toscana (Italy), 250 µm. **B.** *Ototyphlonemertea* aff. *elenae* (Nemertea), Santa Marta (Colombia), 1 mm. **C.** Schizorhynchia (Platyhelminthes), São Sebastião (Brasil), 500 µm. **D.** *Flagellophora apelti* (Nemertodermatida) Helgoland (Germany), 700 µm. **E.** *Paraproporus* sp. (Acoela) Fort Pierce, 1.2 mm. **F.** *Lindrilus flavocapitatus* (Annelida)*,* Odessa (Ukraine), 2 mm. **G.** *Pontohedyle* sp. (Gastropoda), Santa Marta (Colombia), 800 µm. **H.** Pholidoskepia n. gen. n. sp. (Solenogastres) Friday Harbor (USA), 700 µm. **I.** *Nematoplana* sp. (Proseriata), Porto Sant'Elpidio (Italy), 2 mm. **J.** *Otoplana* sp. (Proseriata), São Sebastião (Brasil), 750 µm. **K.** *Notholca* sp. (Rotifera) Katwijk (The Netherlands), 250 µm. **L.** *Tubiluchus lemburgi* (Priapulida)*,* Tenerife (Spain), 1 mm. **M**. *Leiocanthus satanicus* (Kinorhyncha) Gulf of Mexico, 500 µm. **O.** *Paradraconema* sp. (Nematoda) São Sebastião (Brasil), 200 µm. **P.** *Hemicyclophora* sp. (Nematoda), Nordwijk (The Netherlands). **Q.** *Enoplolaimus* sp. (Nematoda) Nordwijk (The Netherlands). **R.** *Neochromadora* sp. (Nematoda) Scheveningen (The Netherlands). **S.** Stilbonematinae (Nematoda), Sardegna (Italy), 750 µm. **T.** *Draciculiteria* sp. (Gastrotricha) Helgoland (Germany), 200 µm. **U.** *Turbanella cornuta* (Gastrotricha), Katwijk (The Netherlands), 400 µm. **V.** *Halammohydra vermiformis* (Cnidaria)*,* Helgoland (Germany), 400 µm. **W.** *Callistocypris* sp. phytothelmata Siam Khan (Mexico), 500 µm. **X.** *Palpophria aestheta,* water column, Tunel de la Atlántida (Canary Islands), 400 µm. **Y.** *Eucyclops* n. sp. wells in Haria (Canary Islands), 750 µm. **Z.** *Scaphognathus* sp. (Acarii) Arousa (Galicia), 400 µm. **A-E; G, I-K, O—V,** light micrographs; **F**, drawing; **H, L-M, Z**, scanning electron micrographs; W-Y, maximal projections of confocal laser scanning stacks. Credits: **A, D, E**, Ulf Jondelius. **B, G** Alejandro Martínez (AM), Ana Milena Lagos and Maria Victoria León. **C, J, O.** Maikon Di Domenico. **H.** Kevin M. Kocot. **I.** Marco Curini-Galletti (MCC). **K**. Diego Fontaneto. **L, T**. Andreas Schmidt-Rhaesa (ASR). **M**. Nuria Sánchez. **P-R, U**. Marta García-Cobo, Jan Macher and Alejandro Martínez. **S.** MCC, AM. V. ASR and Lenke Tödler. **W, Y.** Nancy Mercado-Salas (NMC). **X**. AM, NMC, Terue Kihara. **Z.** Guillermo García-Gómez

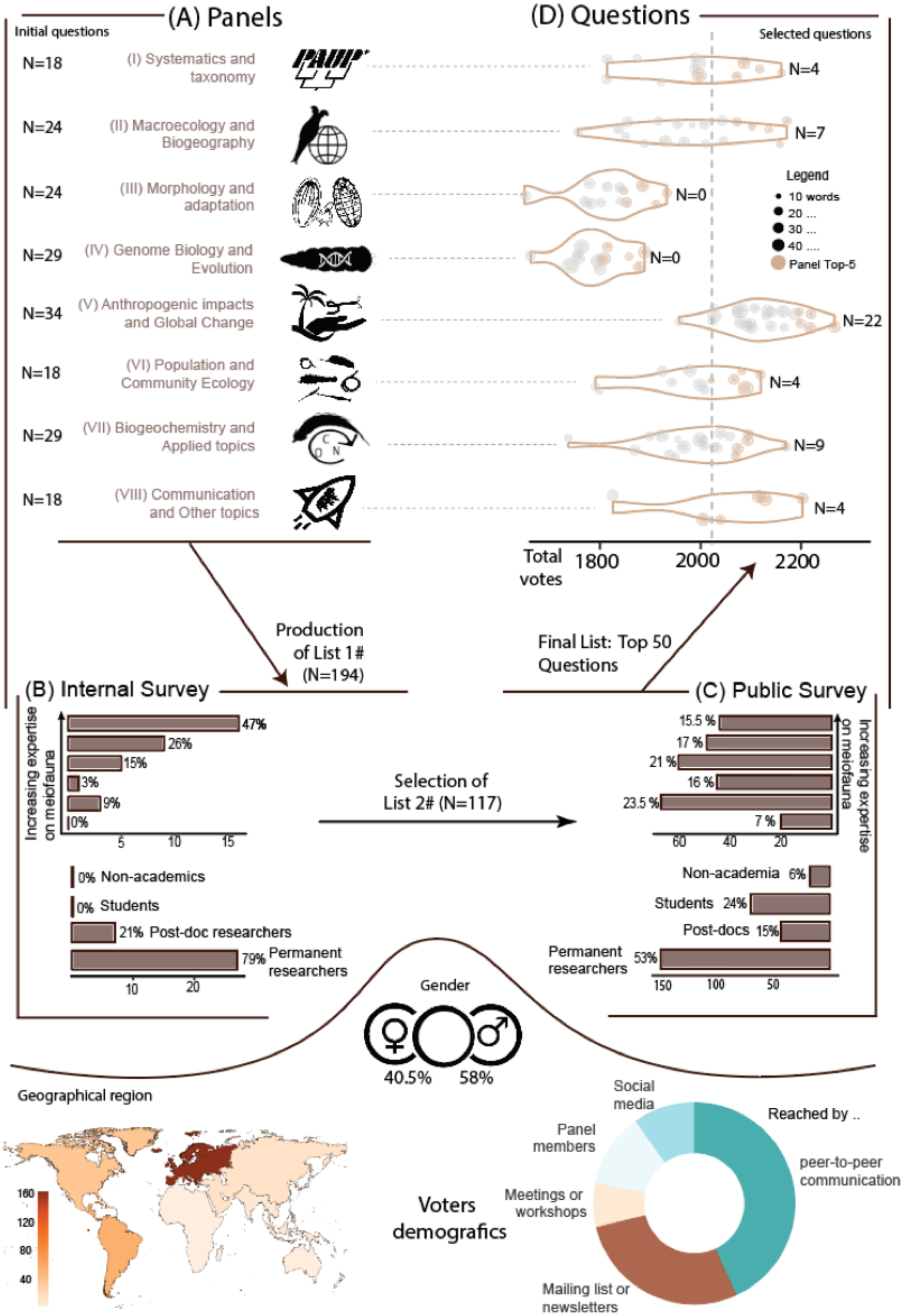
(A) Panels
Initial questions
N=18
(I) Systematics and taxonomy
N=24
(II) Macroecology and Biogeography
N=24
(III) Morphology and adaptation
N=29
(IV) Genome Biology and Evolution
N=34
(V) Anthropogenic impacts and Global Change
N=18
(VI) Population and Community Ecology
N=29
(VII) Biogeochemistry and Applied topics
N=18
(VIII) Communication and Other topics
(D) Questions
Selected questions
N=4
N=7
N=0
N=0
N=22
N=4
N=9
N=4
Legend
10 words
20 ...
30 ...
40 ....
Panel Top-5
Total votes
1800
2000
2200
Production of List 1# (N=194)
Final List: Top 50 Questions
(B) Internal Survey
Increasing expertise on meiofauna
47%
26%
15%
3%
9%
0%
5
10
15
0% Non-academics
0% Students
21% Post-doc researchers
79% Permanent researchers
10
20
Selection of List 2# (N=117)
(C) Public Survey
15.5 %
17 %
21 %
16 %
23.5 %
7 %
60
40
20
Increasing expertise on meiofauna
Non-academia 6%
Students 24%
Post-docs 15%
Permanent researchers 53%
150
100
50
Gender
40.5%
58%
Geographical region
160
120
80
40
Voters demografics
Social media
Panel members
Meetings or workshops
Mailing list or newsletters
Reached by ..
peer-to-peer communication

Figure 2. Summary of the survey to identify the top-50 questions in meiofaunal research. **(A)** List of panels and number of questions (N) proposed by the panel members, after editing and removing duplicated questions. **(B)** Those 194 questions were reduced to 117 after the votation by the panel members and survey coordinators, and then **(C)** to 50 after a public survey. **(D).** Rresults of the public survey by panels. Brown circles represent the panel 5 most-voted questions, size is proportional the number of words. Numbers on the right show number of top-50 questions per panel (N). Lower panel shows the gender composition, geographical precedence, and how they declared they heard of our survey.

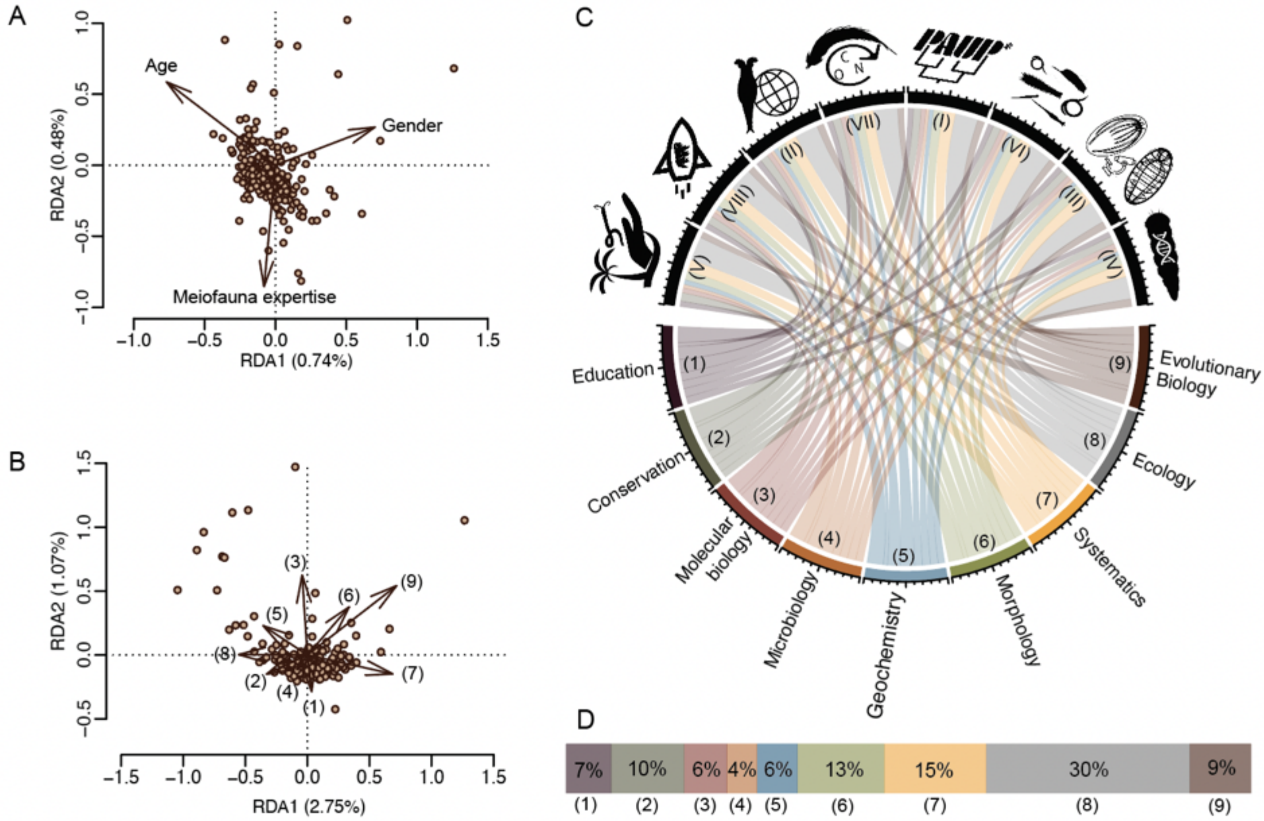

Figure 3. Redundancy analyses, showing the relationships between the voters demographic parameters and their expertise **(A)**, and between their scientific background **(B)**: numbers between parentheses refer to the numbers of the nine categories in **C** and **D**. **(C)**. Percentage of the votes received by each panel according to the scientific background of the voters. **(D)**. Scientific background of the voters.


A
HÉLÈNE RAJCAK · DAMIEN LAVERDUNT
Les mondes invisibles des
ANIMAUX
MICROSCOPIQUES
ACTES SUD junior
B
C
Dans mon château de sable
À la découverte
d'une vie insoupçonnée
D
E
Cabildo de Lanzarote
F
G
LIVE TINY, DIE NEVER
5-TIME APOCALYPSE CHAMPION
H
Tardigrade
Inferno
I
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KALAALLIT NUNAAT
GRØNLAND
10,00
N
Life Interstitial
What does it take to live between the grains of sand?
Text by Adrienne Mason
Art by Mark Garrison and Amorina Kingdon
O

Figure 4. Dissemination and public engagement activities and items related to meiofauna. **A.** Book cover of "The invisible worlds of microscopic animals" by Laverdunt and Rajcak (lestigresgauchers.fr/category/livre/). **B.** Hélène Rajcak presenting her book to young public. **C.** Book cover of the fairy tale "In my sand castle", produced and donated to French primary school. (Zeppilli, et al. 2015). **D**. Students and mentors from the Biodiversity and Integrative Taxonomy of Invertebrates (BITI) at Friday Harbor Labs, WA, USA on the RV Kittiwake. The course brought together 12 world-expert taxonomists and 18 students who learned marine invertebrate diversity with an emphasis on meiofauna and both morphological and molecular techniques. **E.** Architect Patricia Betancort presents the permanent exhibition on cave meiofauna at Los Jameos del Agua (Lanzarote, Spain) (cactlanzarote.com/museo-casa-de-los-volcanes/). **F.** Tardigrate key holder (www.GIANTmicrobes.com). **G.** Tardigrate t-shirt (www.facebook.com/aTardigrade). **H.** Cover of the single "A Grain of Sand" by the dark cabaret metal band "Tardigrate inferno" (www.tardigradeinferno.com/). **I.** A kinorhynch represented as American Northwest Coast indigenous artwork, by Rob Higgins. **J.** Meiobenthologist A. Todaro interacts with young public during a workshop organized at Naturalis Biodiversity Center (Photo by Jan Macher). **K**. Sand castle at the exposition "Cyclops, explorateur de l'océan", organized by Océanopolis for kids. **L.** Reconstruction of a loriciferan at the Natural History of Denmark. **M.** Greenlandic stamp showing *Limnognathia maerski,* a micrognatozoan endemic from the Isunngua thermal spring in Qeqertasuaq. **N.** Dissemination article by A. Mason (adriennemason.com), M. Garrison and A. Kingdom on Hakai Magazine (https://hakaimagazine.com/videos-visuals/life-interstitial/). **O.** Astronaut Luca Parmitano working with the Kubik 6 Incubator in the Columbus European Laboratory during Experiment Container installation for the Rotifer -B1 investigation. The Rotifer B-1 investigation examines the possible effects of spaceflight on gene expression using bdelloid rotifers (Photo credit: Nasa).

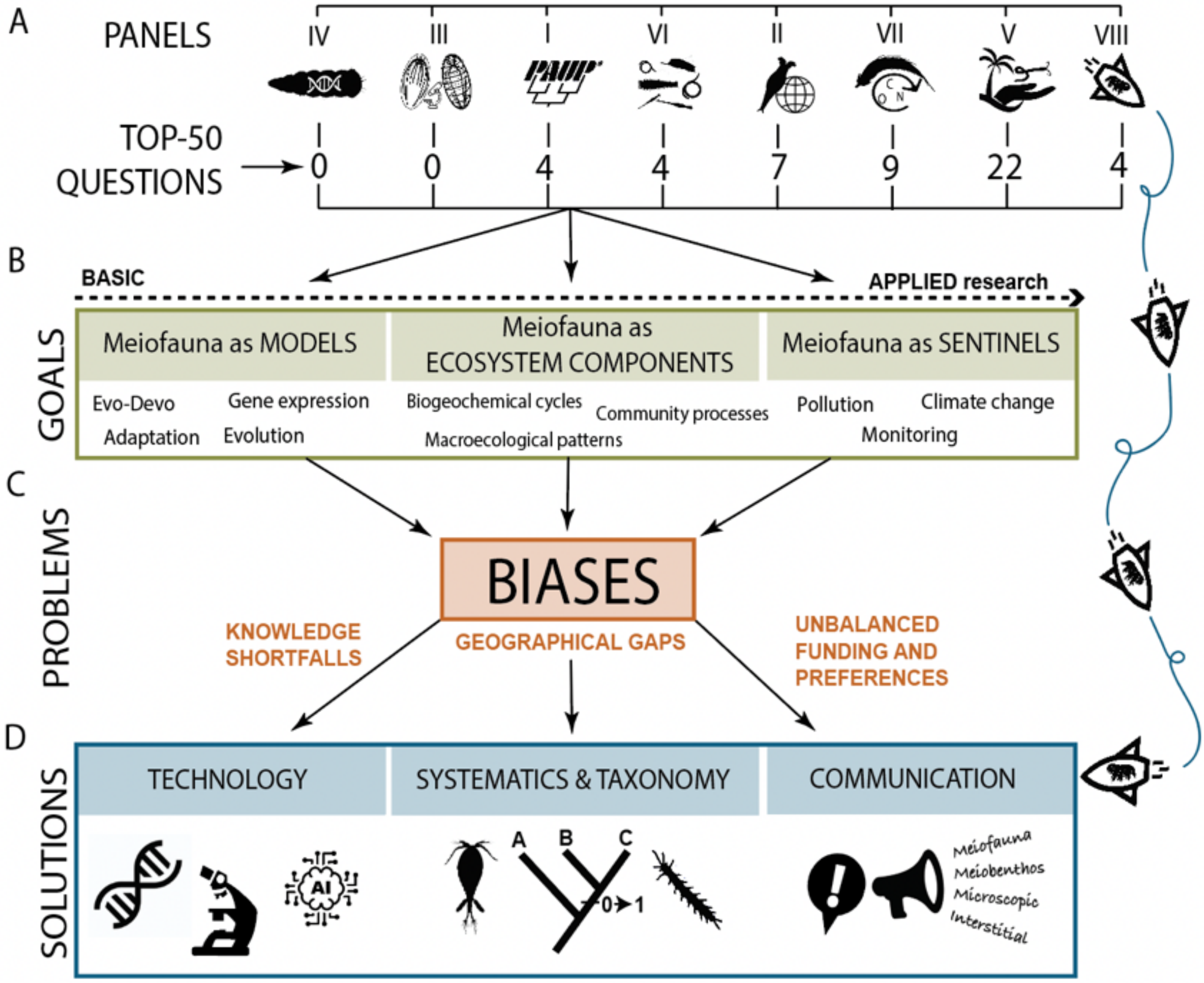

Figure 5. Conclusions. **A.** Applied questions received higher scores. **B.** Questions have emphasized the role of meiofauna as eco-evolutionary models, their importance in ecosystem functioning and diversity across spatial scales, as well as their properties as sentinels for biomonitoring. **C.** Knowledge shortfalls, geographical gaps, and the unbalanced preferences exhibited by researchers are major impediments putting forward meiofauna research agenda. **D.** Yet, we hope that technological advancements, as well as improving and generalising our taxonomic and communication skills as a community will alleviate those issues. Attracting more students and researchers with diverse backgrounds will greatly help us to overcome the challenges upon us.

Table S1. Full list of questions, including the results of the surveys. The column “List” specifies whether the questions made it to the List#1 or List#2 after the internal or the public survey; “Panel” indicates the panel; “Question ID” includes the question’s unique identificator; and “Question” includes the question as it was presented in the surveys.

Table S2. Scores of the surveys, including the scores received by each question (columns “Q001 to Q230) as well as the voter’s anonymous metadata. Column explanations: “Timestamp”, date and time of the submission of the questionnaire, “Reached.by”, how did the voters got to know about the questionnaire; “Reached.by(sorted)”, previous column categorized to facilitated the analyses; “Birth”, year of birth of the voter; “Country”, voter’s country of work; “Gender”, gender of the voter; “Career”, career status of the voter; “Field.Evolution”, voter’s declared expertise in evolutionary biology; “Field.Ecology”, voter’s expertise in ecology biology; “Field.Morphology”, voter’s expertise in morphology; “Field.Geochemistry” voter’s expertise in biogeochemistry; “Field.Microbiology”, voter’s expertise in microbiology; “Field.Molecular” voter’s expertise in molecular biology and genomics; “Field.Conservation”, voter’s expertise in conservation biology; “Field.Education”, voter’s expertise in education; “Expertise”, voter’s declared level of expertise in meiofauna, from 0-5.

Supplementary methods and results

1. Data visualization

We visually displayed the distribution of voters in terms of expertise and career stage of the voters using bar plots generated with the function “geom_bar”. To illustrate the proportion of voters reached through different communication channels, we used the function “geom_rect”. Additionally, we plotted the number of voters per region using the function “geom_sf” on the shapefile TDWG.level1, provided by the Biodiversity Information Standards (www.tdwg.org/). All three functions are included in the package ggplot2 version 3.4.1 (Wickham, 2016) in R 4.1.2 (R Core Team, 2023). The impact of the voters’ demographics, their declared expertise on meiofauna, and scientific background on the voting results was graphically represented using redundancy analyses (RDA) with the function “rda” included in the package vegan 2.6-2 (Oksanen *et al.,* 2022).

2. Caveats on interpretation and counter measures

Several caveats need to be considered when interpreting the results of a horizon scan survey (Sutherland *et al.,* 2011, 2013; Patiño *et al.,* 2017; Mammola *et al.,* 2020a). Firstly, the background knowledge and preferences of the panel members and the voters might introduce subjectivity both in the formulation of the questions and throughout the voting process. This implies that lower scores do not necessarily reflect the importance or timeliness of a given question, but rather that experts in those topics may have been underrepresented amongst the voters. Indeed, meiofauna research has traditionally been dominated by ecologists and a large percentage of the researchers within the overall community are interested in the use of meiofauna for monitoring and as indicators of anthropogenic impacts. This imbalanced expertise may also explain the differences in how the votes were parsed across the panels. To control for these biases, we asked voters to indicate their scientific background in the survey form, so that we could incorporate this as a confounding factor in the analyses. Details on the panel composition are available in Table 1; whereas information on the methods followed in data visualization and the elaboration of the figures are included in the Supplementary methods.

Given the multidisciplinary character of meiofauna research, we were particularly mindful of maximizing the readability during the formulation of the questions (see above). Despite our efforts, some questions might have remained less readable than others, largely because of their intrinsic complexity. We therefore included the Flesch readability of the questions (Flesch, 1948), and the number of words as confounding factors in the analyses of the survey results.

Finally, we implemented an additional countermeasure to further reduce bias, in addition to targeting a broad audience and using a diverse panel composition, by allowing voters to suggest additional questions when voting in the survey. We thereby empowered voters to expand the range of priority topics.

2.1 Impact of voter's demographics and scientific backgrounds on the voting patterns.

We evaluated the impact of voters' traits in the response matrix, using permanova. We used a Jaccard distance matrix calculated from the response of the surveys as a response variable, and demographic (*i.e.*, year of birth, gender, continent, and meiofauna background) and the background (*i.e*., declared expertise in research areas of Evolution, Ecology, Systematics, Morphology, Geochemistry, Microbiology, Molecular, Conservation, and Education) traits of the voters as predictors. Career stage was omitted as it provides the same information as year of birth. Jaccard matrix was calculated using the function "vegdist" and the permanova was calculated with the function "adonis" by setting 999 permutations, both implemented in the R package "vegan" v. 2.6-2 (Oksanen et al. 2022).

The demographic predictors "year of birth" ($R^2 = 0.01$; $p = 0.008$), "gender" ($R^2 = 0.01$; $p = 0.001$), "continent" ($R^2 = 0.03$, $p = 0.029$) and expertise ($R^2 = 0.01$; $p = 0.003$), and the expertise predictors "evolution" (R2 = 0.02; $p = 0.001$), "systematics" ($R^2 = 0.02$; $p = 0.001$), and "ecology" ($R^2 = 0.01$; $p = 0.003$) were significant, but the total amount of the variance explained by these predictors was very low ($R^2 = 0.11$) (Table S3).

2.2. Impact of question's properties on the voting scores

We evaluated the impact of the length and readability of the questions using generalized linear models. The total score for each question was selected as the response variable, whereas the number of words, Flesch readability index, the panel, and the interactions between these variables were selected as predictors. We adjusted our model using a binomial distribution because scores are positive integers and exhibit overdispersion. Models were adjusted using the function "glm.nb" in the R package "MASS" version 7.3-57 (Venables & Ripley, 2002). Overdispersion and the model's performance were evaluated using the functions "check_overdispersion" and "check_model" included in the R package "performance" version 0.10.0 (Lüdecke et al. 2021). For the models that included a set of predictors with both categorical and continuous variables, we used Type II ANOVA tables using the function "Anova" in the R package car v. 3.0.10 (Fox & Weisberg, 2019) to produce output tables.

Panel exhibited a significant effect on the question's score (LR χ^2 = 151.938, p < 0.0001), but not the number of words (estimate = 0.000, p = 0.811) nor the Flesch readability (estimate = 0.000, p = 0.822). Interestingly, the interaction between readability and panel was also significant (LR χ^2 = 22.032; p = 0.002), suggesting that within a given topic, questions with different readability receive different scores (Table S4).

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Table S3. Effect of voters' traits on the voting patterns across questions. Abbreviations: Df = degrees of freedom, SS = sum of squares; R2, and p values are reported. P values for significant predictors are marked in bold. Notice that the analysis is sensitive to the order of the predictors.

	Df	SS	R^2	F	p-value
Birth	**1**	**0.1585**	**0.00838**	**2.4125**	**0.008**
Gender	**1**	**0.2072**	**0.01095**	**3.1541**	**0.001**
Continent	**6**	**0.6467**	**0.03419**	**1.6407**	**0.029**
Expertise	**1**	**0.1766**	**0.00933**	**2.6879**	**0.003**
Evolution	**1**	**0.3419**	**0.01807**	**5.2045**	**0.001**
Systematics	**1**	**0.3526**	**0.01864**	**5.3673**	**0.001**
Ecology	**1**	**0.1924**	**0.01017**	**2.9289**	**0.003**
Morphology	1	0.0943	0.00499	1.436	0.096
Geochemistry	1	0.0725	0.00383	1.1039	0.294
Microbiology	1	0.0526	0.00278	0.8005	0.646
Molecular	1	0.1052	0.00556	1.6014	0.055
Conservation	1	0.0734	0.00388	1.1179	0.289
Education	1	0.0858	0.00454	1.3068	0.171
Residual	249	16.3566	0.86469		
Total	267	18.9162	1		

Table S4 voter's declared expertise in evolutionary biology;**.** Output of the generalized linear model to test the effects of the question length (in number of words), readability, and panel in the scores. The output of a type II ANOVA table is reported for the model to include both categorical and continuous predictors. Abbreviations: χ^2 = chi-square values, Df = degrees of freedom, Std.Error = standard error; P-values and estimates for significant predictors are marked in bold

	LR χ^2	Df	estimate	Std.Error	z value	p-values
intercept	**-**	**-**	**7.5560**	**0.0843**	**89.6650**	**< 0.0001**
words	0.1320	1	-0.0011	0.0044	-0.2580	0.7167
flesch	0.2800	1	-0.0001	0.0023	-0.0580	0.5967
panel	**200.4860**	**7**	**-**	**-**	**-**	**< 0.0001**
words:Flesch	0.0100	1	-	-	-	0.9198
words:panel	10.0270	7	-	-	-	0.1870
Flesch:panel	**22.0320**	**7**	**-**	**-**	**-**	**0.0025**
words:Flesch:panel	6.8430	7	-	-	-	0.4454