communications biology

A Nature Portfolio journal

Comment

https://doi.org/10.1038/s42003-025-07888-1

Fundamental questions in meiofauna research highlight how small but ubiquitous animals can improve our understanding of Nature

Alejandro Martínez, Stefano Bonaglia, Maikon Di Domenico, Gustavo Fonseca, Jeroen Ingels, Katharina M. Jörger, Christopher Laumer, Francesca Leasi, Daniela Zeppilli, Elisa Baldrighi, Holly Bik, Diego Cepeda, Marco Curini-Galletti, Asher D. Cutter, Giovanni dos Santos, Simone Fattorini, Dagmar Frisch, Sabine Gollner, Ulf Jondelius, Alexandra Kerbl, Kevin M. Kocot, Nabil Majdi, Stefano Mammola, José M. Martín-Durán, André Menegotto, Paul A. Montagna, Francisco J. A. Nascimento, Nicolas Puillandre, Anne Rognant, Nuria Sánchez, Isaac R. Santos, Andreas Schmidt-Rhaesa, Michaela Schratzberger, Federica Semprucci, Mauricio Shimabukuro, Paul J. Sommerfield, Torsten H. Struck, Martin V. Sørensen, Andreas Wallberg, Katrine Worsaae, Hiroshi Yamasaki & Diego Fontaneto

This paper identifies the top-50 priority questions for meiofaunal research, highlighting their critical roles in biogeochemical cycles and biodiversity. It calls for a balanced research agenda, international cooperation, and advances in technology to overcome current challenges and unlock meiofauna's full potential.

Our knowledge of Earth's biodiversity is biased towards relatively large organisms, particularly if they are charismatic, colourful, useful, or threatening to humans[1,2]. Whether this skew stems from the fact that we, humans, are relatively large mammals, that navigate the world mainly using visual stimuli, or because we respond to other biological, cultural, or socio-economic factors remains an open question[3]. Nevertheless, the consequences of this bias permeate scientific inquiry, not only by affecting our perception of nature but also influencing how we allocate resources for research and design environmental policies[4].

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 under-represented in the conservation agenda[4,5] and biodiversity research[3]. Among these small creatures, those whose body size ranges from 0.01 to 1 mm 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 of aquatic diversity, "meiofauna" refers to the fraction of the animal and protist community that is retained on sieves with an upper mesh size of 0.3–1 mm and a lower mesh size of 0.030–0.063 mm[6]. The term was introduced by ecologists to describe the communities dwelling interstitially in marine sediments ("meiobenthos"[7,8]) that sit in between "microbenthos" and "macrobenthos"[8]. This was soon generalised to include other non-sedimentary, aquatic, and terrestrial habitats[9–15], and even certain protists such as foraminifera[16–18]. Alternatively, organismal biologists and zoologists often use the term "meiofauna" to describe microscopic animals[19]. Although similar, these two meanings cannot be interchanged without caveats[20]. On the one hand, animals reaching several millimetres in length might still be classified as meiofaunal due to their elongated and thin bodies[21], meaning that properties attributed to microscopic animals do not always apply across an entire meiofaunal community[22]. On the other hand, some organisms qualify as meiofauna only during part of their life cycles, enforcing a distinction between the so-called *temporary* and *permanent* meiofauna that is not easily established in certain taxonomic groups[23,24]. An additional source of confusion arises when comparing meiofauna in aquatic habitats and the same organisms in soils, because soil biologists typically call them "mesofauna", indicating their size range in between soil "microfauna" and "macrofauna"[25]. Here, we will consider meiofauna in its broader meaning of minute, mostly microscopic aquatic and limno-terrestrial[26].

While many pioneering meiofauna studies were conducted in the first half of the 20th century[27], the momentum of meiofauna research has substantially increased in recent years[28]. It is now evident that meiofauna represent not only an important component of biodiversity in most of Earth's ecosystems[29], but are a crucial player in carbon and nitrogen cycling throughout aquatic trophic networks[30–33]. Meiofauna act as bioindicators for pollution or climate change[34,35], as well as providers of fundamental ecosystem services[31]. Meanwhile, microscopic animals pose fascinating research questions, provide tools to test general eco-evolutionary hypotheses[20,28,36,37] and offer insights into early animal evolution, indirectly through phylogenetics[38–41], or directly through the fossil record available for groups such as ostracods and foraminifera[42–44]. Some microscopic animals have dormant stages able to withstand extreme environmental conditions, even in space[45,46], whereas others have been used as model organisms in pioneering cancer research[47].


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Fig. 1 | Examples of the diversity of meiofauna using different imaging 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 (USA), 1.2 mm. **F** *Lindrilus flavocapitatus* (Annelida), Odessa (Ukraine), 2 mm. **G** *Pontohedyle* sp. (Gastropoda), Santa Marta (Colombia), 800 µm. **H** *Pholidoskepia* sp. (Solenogastres), Friday Harbor (USA), 700 µm. **I** *Nematoplana* sp. (Proseriata), Porto Sant'Elpidio (Italy), 2 mm. **J** *Kata* sp. (Proseriata), Itaipuaçu, Rio de Janeiro, 750 µm. **K** *Notholca* sp. (Rotifera), Katwijk (The Netherlands), 250 µm. **L** *Tubiluchus lemburgi* (Priapulida), Tenerife (Canary Islands, Spain), 1 mm. **M** *Leiocanthus satanicus* (Kinorhyncha), Gulf of Mexico, 500 µm. **N** *Paradraconema* sp. (Nematoda), São Sebastião (Brasil), 200 µm. **O** *Hemicyclophora* sp. (Nematoda), Nordwijk (The Netherlands). **P** *Enoplolaimus* sp. (Nematoda), Nordwijk (The Netherlands). **Q** *Neochromadora* sp. (Nematoda), Scheveningen (The Netherlands). **R** Stilbonematinae (Nematoda), Sardegna (Italy), 750 µm. **S** *Draciculiteria* sp. (Gastrotricha), Helgoland (Germany), 200 µm. **T** *Turbanella cornuta* (Gastrotricha), Katwijk (The Netherlands), 400 µm. **U** *Halammohydra vermiformis* (Cnidaria), Helgoland (Germany), 400 µm. **V** *Callistocypris* sp. (Ostracoda) from phytothelmata Sian Ka'an (Mexico), 500 µm. **W** *Palpophria aestheta* (Copepoda) from the water column, Túnel de la Atlántida (Canary Islands, Spain), 400 µm. **X** *Eucyclops* sp. (Copepoda) from wells in Haría (Canary Islands, Spain), 750 µm. **Y** *Scaphognathus* sp. (Acarii), Arousa (Galicia, Spain), 400 µm. Measurements refer to body length. **A–E; G, I–K, N—U**, light micrographs; **F**, drawing; **H, L, M, Y**, scanning electron micrographs; **V–X**, maximal projections of confocal laser scanning stacks. Credits: **A**, **D**, **E**, Ulf Jondelius. **B**, **G** Alejandro Martínez (AM), Ana Milena Lagos and María Victoria León. **C**, **J**, **N** Maikon Di Domenico. **H** Kevin M. Kocot. **I**. Marco Curini-Galletti (MCC). **K** Diego Fontaneto. **L**, **S** Andreas Schmidt-Rhaesa (ASR). **M** Nuria Sánchez. **O–Q**, **T** Marta García-Cobo, Jan Macher and Alejandro Martínez. **R** MCC, AM. **U** ASR and Lenke Tödler. **V**, **Y** Nancy Mercado-Salas (NMC). **W** AM, NMC, Terue Kihara. **X** Guillermo García-Gómez.

To celebrate all the research opportunities afforded by "meiofauna," we gathered a multidisciplinary team of researchers to identify the most fundamental questions that we can address using meiofauna. Then, through an online survey targeting scientists, administrators, students, and stakeholders, we evaluated the appeal of these questions to a broader audience. Finally, we identified significant shortfalls and potential solutions, which we formulated as medium- and long-term goals within different fields of meiofauna research. We structured the discussion of our findings in three overarching topics: (1) exploiting the full potential that meiofauna offer as model organisms, (2) highlighting critical research priorities, and (3) overcoming biases that currently affect meiofauna research. Overall, we offer a community horizon scan of meiofauna research.

Results

Overview of the horizon scanning methods and main findings. The two survey coordinators defined eight panels corresponding to areas within the published research in meiofauna (Table 1). After an internal poll, reducing the original 194 questions to a set of 117, our public online survey reached 251 voters using different platforms (Fig. 2), including researchers with and without a primary expertise in meiofauna. The highest ranked of the 117 selected questions for public voting scored 2257 points, whereas the lowest ranked scored 1640 points (Table 2). We summarised the voters' geographical location, gender, age, level of meiofauna expertise, and career stage in Fig. 2. The scoring values in the responses were only marginally affected by the voters' areas of expertise, gender, and age: these potential biases explained less than 11% of the total variance in the model explaining voters' responses (Fig. 3; Supplementary Results). Thus, voters did not prioritise questions related to their own backgrounds. Additionally, question readability and word count did not significantly impact scores[48,49] (Supplementary Results). Further information on the methods and caveats interpreting the results along with details on the survey scores and the anonymous voters' metadata are included in the Supplementary Material[50–55]. Below, we summarise the results for each panel. We position the 5 highest-scoring questions per panel within future meiofaunal research in relation to the overall top-50 scoring questions.

Panel I: Systematics and taxonomy. The "Linnaean shortfall"[56] is particularly prominent in meiofauna research[37], attributed to the time-consuming process of describing microscopic organisms[6] and to the shortage of trained taxonomists compared to the vast undescribed meiofaunal diversity[57]. An accurate assessment of meiofaunal species diversity depends on the development of more efficient and reliable taxonomic procedures (**Q#12**). DNA metabarcoding is increasingly popular and promising for meiofauna biodiversity assessments[58–66], though challenges remain. Firstly, diversity estimates depend on target genes and workflows tailored to low population density, small-sized animals, and uncertain genetic diversity[67]. Secondly, metabarcoding accuracy depends on well-curated reference databases to ensure the correct assignment of hypothetical species to DNA sequences. Thirdly, standardised pipelines are needed for comparability of the generated data[68]. Finally, most current methods produce short sequences, which, together with the high genetic diversity and high substitution rates across meiofaunal species, complicate species identification and the design of universal primers[18,69–71].

Standardised taxonomic approaches[57] and metabarcoding[63] have boosted biodiversity estimates even in well-studied areas, highlighting the urge for community collaboration to map meiofauna species diversity at regional and global scales[57,72–74] (**Q#21**). Comparative analyses across regions and habitats might reveal areas of endemism and biodiversity hotspots supporting the overall goal of identifying patterns of diversity across different taxa (**Q#37**). This is particularly relevant for testing the "Everything is Everywhere" hypothesis[75], and the question on whether widely distributed species are robust biological entities or just an artefact of poor taxonomic resolution (**Q#31**). Several meiofaunal groups, like rotifers, nematodes, and tardigrades, have species with wide distribution ranges because their dormancy capabilities may enable long-distance passive dispersal[76,77]. However, most annelids, proseriates, rhabdocoels, and acoels lack such traits, so their reported cosmopolitan distributions depict a puzzling pattern referred to as the "meiofauna paradox"[22,78]. Recent morphological and molecular analyses have revealed that many supposed cosmopolitan species in poorly-dispersing meiofauna are actually species complexes with high molecular divergence and restricted geographical distribution ranges[79–81], although some widespread species also remain[82,83].

Understanding meiofauna biodiversity faces challenges with specimen preservation for reliable re-identification (**Q#60**). Advances in technology have outdated many old descriptions, and type material – if it exists – is often inaccessible for re-examination via modern methods. This problem prevails in "soft-bodied" meiofauna that requires live study of diagnostic characters[84]. A heated debate continues over the requirements of type material and the role of photomicrography-based taxonomy in "type-less species descriptions"[85]. Ideally, photomicrographs should be combined with a voucher suitable for DNA analyses, though thorough morphological documentation risks damaging or destroying the type to-be. Still, a damaged specimen can at least serve as voucher material in the form of a "DNA-type," in agreement with the International Code of Zoological Nomenclature[86,87].

Table 1 | Subject areas, general topics addressed, panel members (* = panel coordinator; + = postdoc or early career researcher, # = external expert), *N* = number of questions included in the 50 top-priority final list out of the total retained in List #1

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 M. 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. Miniaturisation.	Francesca Leasi*, Alexandra Kerbl +, José M. 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, urbanisation, deep sea mining and other anthropogenic perturbation that could affect meiofauna.	Jeroen Ingels*, Sabine Gollner +, Paul A. 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 in describing meiofauna-bacteria interactions. Questions regarding potential applied uses of meiofauna were also considered.	Stefano Bonaglia*, Francisco J. A. Nascimento, Isaac R. Santos#, Michaela Schratzberger, Mauricio Shimabukuro+	9 of 29
VIII. Science communication and other topics	Challenges of disseminating outcomes from meiofaunal research 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

Panel members are listed alphabetically by surname.

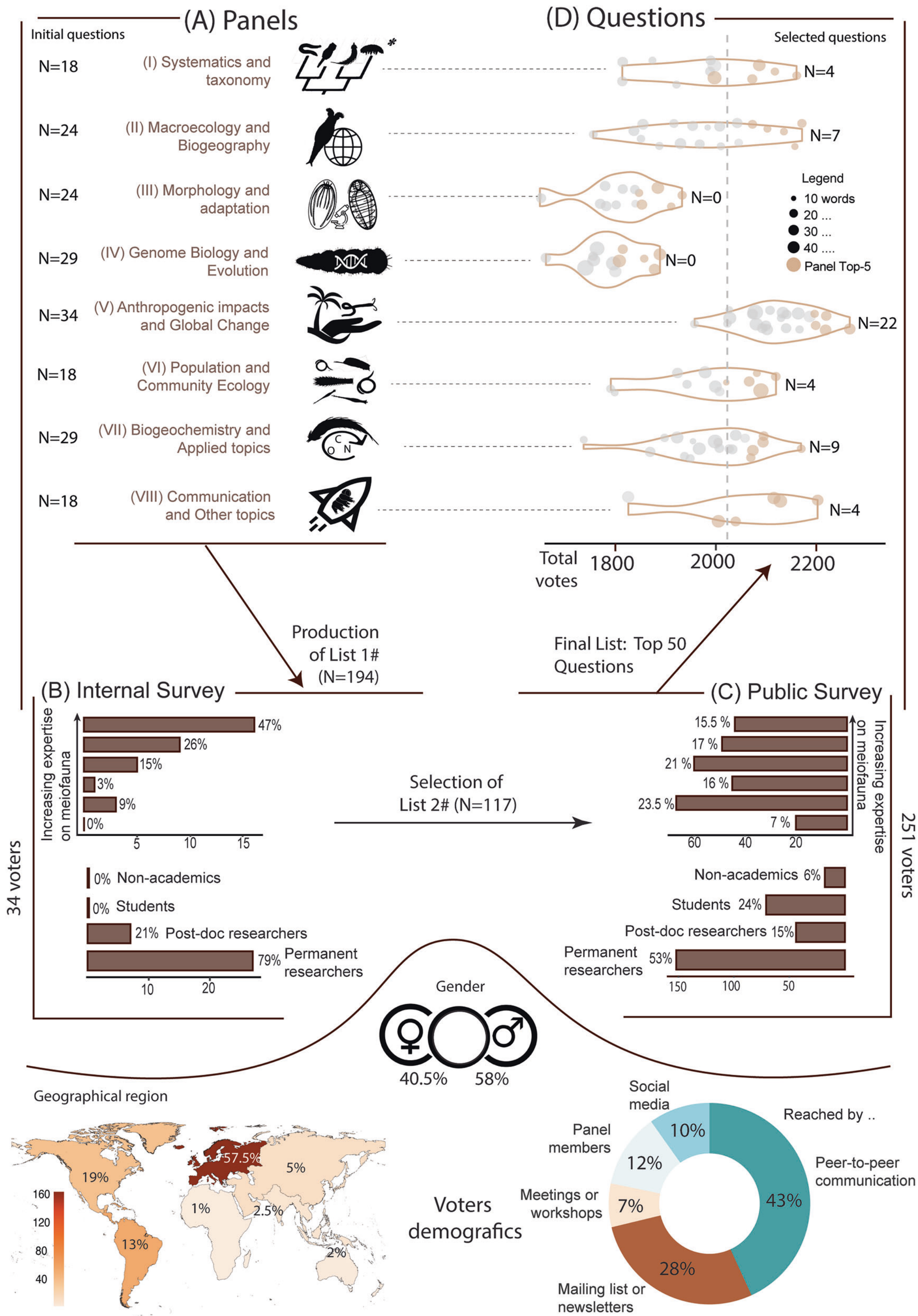
Panel II. Macroecology and biogeography. Meiofauna, being widely distributed and ecologically diverse, serve as an effective model for exploring global biogeographical patterns and processes[88]. Meiofauna encompasses species from most animal phyla[19], allowing researchers to examine the generality of global biodiversity trends beyond large organisms[89,90]. However, global meiofauna studies are limited by a lack of standardised sampling protocols, which hinders the collection of comparable data worldwide (**Q#8**). Long implemented for larger organisms, especially vertebrates, international protocols and data-sharing practices are still incipient in meiofauna research[91,92], contributing to challenges in estimating their diversity at large scales.

Amongst the issues hindering robust estimations of meiofaunal taxonomic diversity (**Q#13**), the most pervasive factors include the prevalence of undescribed species, reliance on higher taxonomic levels, and biases towards regions such as Europe[93]. Many geographical areas remain unexplored for meiofauna, and even within well-investigated regions, species records are often concentrated near research facilities or specific habitats, distorting our understanding of species distribution and ecology[94]. While workshops around the world have facilitated some progress, they only cover limited areas within largely uncharted regions[95].

Our understanding is even more restricted when it comes to functional and genetic patterns of diversity[37], which is concerning since these aspects are crucial for inferring processes behind observed macroecological patterns[57,67,94,96]. Traits, phylogeny, and abiotic ranges might help to identify the factors determining species dispersal (**Q#16**), especially for morphologically similar populations that may differ in habitat requirements or fulfil various ecological roles[97,98]. Morphological traits[57,77] or ecological preferences[90,99] can facilitate long-distance dispersal through mechanisms such as rafting[100], animal phoresy[95,101], wind and rain-mediated transport[102], or accidental transport via ship ballast water[103]. Understanding meiofaunal dispersal dynamics will clarify how ecological patterns are shaped by physical barriers and limitations - or advantages - related to their body size[16].

Comparable datasets are also essential to explore large-scale drivers of meiofaunal biodiversity (**Q#24, Q#38**). However, existing datasets primarily rely on data mining from published studies, most of which are based on morphological identification[90,104–107]. Meiofaunal records are scarce in general open-source databases, such as the Global Biodiversity Information Facility (GBIF), and often lack taxonomic validation or even an updated taxonomic backbone. Comprehensive databases do exist for certain groups (e.g., acoels[108], platyhelminths[109], tardigrades[110,111], gastrotrichs[112]), geographical areas[23,113–118] and habitats[13,110]. Unfortunately, global datasets have few available records for nematodes, copepods, and foraminifera, despite their abundance in sediments worldwide[78]. Future research efforts should prioritise interoperability by unifying database formats and terminology[119], as well as integrating genetic[120] and trait information[121,122], to enhance big data-driven research.

Panel III. Morphology and adaptation. The advent of advanced microscopy and imaging technologies[123], along with the challenges imposed by climate change and biodiversity loss emphasise the urgent need to understand morphology and adaptive mechanisms across animal groups[124]. Because the entire meiofaunal organism and its internal contents can be studied simultaneously with high-resolution microscopy, meiofauna are particularly well-suited models to spearhead morphological research. However, none of the panel's proposed questions entered the top-50 priority list (Table 2). We attribute this to the voters' preference for applied research and the specificity of the questions proposed by this panel, which may have addressed unfamiliar topics to broader audiences.


(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
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10 words
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Panel Top-5
Total votes
1800
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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
34 voters
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 %
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Increasing expertise on meiofauna
251 voters
Non-academics 6%
Students 24%
Post-doc researchers 15%
Permanent researchers 53%
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2.5%
13%
2%
Voters demografics
Social media
10%
Panel members
12%
Meetings or workshops
7%
Mailing list or newsletters
28%
Reached by ..
Peer-to-peer communication
43%

Fig. 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** The initial 194 non-redundant questions were reduced to 117 after voting by panel members and survey coordinators, and then (**C**) further to 50 after a public survey. **D** Results of the public survey by panel. Brown circles represent each panel's 5 most-voted questions, size is proportional to the number of words. Numbers on the right show the number of the top-50 questions per panel (N). Lower panel shows the gender composition of respondents, geographical origin, and how they heard of our survey. Silhouettes drawn by Alejandro Martínez.

Three of the five highest-voted questions focused on convergent adaptation (**Q#74, Q#84**), and particularly, on the adaptive significance of small body size (**Q#80**). Small body size might be ancestral in some animal lineages[39,41], while in others it likely evolved secondarily through miniaturisation processes[125]. Unfortunately, investigating adaptations over long phylogenetic timescales requires robust phylogenies, whereas currently available trees remain sensitive to the chosen phylogenetic reconstruction approach insofar as they rely on limited data for most meiofaunal lineages.

Research on adaptations over shorter evolutionary timescales relies on comparing the variability of traits and genetic variation across populations exposed to different ecological conditions[124] (**Q#92**). This variability emphasises the importance of understanding gene expression plasticity in acclimation versus genetic differentiation when assessing phenotypic traits suited for changing environments[126]. Studies on meiofauna in this context remain rare compared to those on large-bodied animals[127], despite recent collaborations among phylogeneticists, morphologists, and systematists having improved the integration of morphological and genomic data[59,128–130].

The adaptive role of behaviour in meiofauna also remains unclear[78] (**Q#90**). Understanding behaviour is not trivial because spatial patterns observed in meiofauna may result from the collective behaviour within populations responding to stimuli[131,132]. Pioneering studies on the soil nematode *Caenorhabditis elegans* Maupas, 1900[133,134] pose the question of how behavioural responses across different meiofaunal groups may explain the relationship between the patchy distribution patterns exhibited by meiofauna and resource availability, as well as environmental variations at small spatial scales. However, behavioural studies are challenging, not only because of meiofauna's small size, but also due to the difficulties in culturing most meiofaunal organisms[135]. Recent advancements in novel imaging techniques incorporating fluorescent nano-sensors, 3D bioprinting, microfluidic chambers, and geometric morphometrics offer potential for in situ observations of behaviours concerning environmental parameters at the relevant microscale[136,137].

Panel IV. Genome biology and evolution. Genomic tools have advanced our knowledge of the evolutionary history of many animal lineages[138,139], linking genotype to phenotype[140,141], and aiding conservation efforts[142]. While the soil nematode *Caenorhabditis elegans* remains one of the quintessential biological model organisms, the lack of genomic data for most meiofaunal species hinders the integration of their evolution and ecology—a practice that has become commonplace in studies of larger organisms[143].

Small body size presents technical challenges to acquiring genomic data for meiofauna but advances in complementary DNA (cDNA) library synthesis and amplification now enable high-quality transcriptome collection from meiofaunal animals with relative ease[128,130]. Whole-genome sequencing remains difficult; however, new kits can produce long-read sequencing libraries from minimal DNA concentrations, yielding high-quality genomes from (relatively) small animals such as mosquitos[144] and springtails[145]. Emerging techniques such as multiple-displacement amplification[146] and long-range PCR[147] may facilitate high-quality genome assemblies from individual meiofaunal specimens or even their diapause eggs[148]. As these techniques become widely adopted, meiofauna will provide rich opportunities for comparative and population genomic studies. The low ranking of genomic questions in current research reflects the field's *status quo*, which is poised for significant advancements not only from specific research groups but also due to the interests of several international initiatives, such as the Darwin Tree of Life[149,150], European Reference Genome Atlas, and Earth BioGenome[151] projects, which include meiofauna to increase high-quality genomic data across the Tree of Life.

Genomic tools applied to meiofauna have primarily been used to resolve their phylogenetic placement. Many microscopic animals occupy deep branches near the root of Bilateria, Spiralia, and Ecdysozoa and, therefore, are crucial in understanding character evolution across Metazoa[152]. This task is complicated by the rapid molecular evolution and long branches exhibited by some lineages, leading to artefactual groupings due to highly divergent sequences (**Q#101**)[40,153–156]. It remains unclear whether rapid genome evolution and other genomic traits observed in meiofauna can be attributed to intrinsic features such as small body size, short generation times, potentially large effective population sizes[157] (**Q#82**) or whether these traits exhibit any geographical patterns, such as latitudinal gradients[158] (**Q#99**).

Genomic tools are essential to understanding the adaptation of meiofauna to biotic and abiotic factors[129,159], determining the tempo of morphological evolutionary change, and exploring cryptic species complexes (**Q#88**)[87,160–162]. As with cryptic species delimitation, population genomics enables insights into gene flow and reproductive isolation, providing powerful tests for evolutionary hypotheses (**Q#85**). By combining genomic inferences about gene flow and genetic differentiation[163,164] with experimental measures of reproductive isolation[165,166], meiofauna will provide complementary test cases to assess the generality of evolutionary hypotheses beyond large-bodied organisms. We anticipate that applying methods such as landscape genomics, which studies adaptation, connectivity, and speciation by associating allele frequencies and environmental conditions[167,168] and macrogenetics, which searches for common trends in intraspecific genetic variation across many species[169], will help elucidate the evolutionary ecology of meiofauna.

Panel V. Anthropogenic impacts and global change. Amid a global climatic emergency[170] and accelerating biodiversity crisis[171], it is not surprising that questions addressing anthropogenic impacts and global change overwhelmingly lead the scores, with 22 questions in the top-50 and seven in the top-10 (Table 2).

Meiofaunal diversity, an established indicator of aquatic ecosystem health[35,172,173], typically declines with disturbance, though exceptions exist[174]. Meiofaunal communities, with rapid generational turnover and numerous species even in small samples, show rapid, detectable shifts in structure even following very small environmental changes such as minor differences in average temperature[175,176]. This sensitivity reflects trade-offs between resilient and vulnerable species (e.g., disturbance cause declines in sensitive species, while tolerant species maintain or increase their abundance),

Table 2 | Top-50 most voted questions in our survey (in bold in the main text when mentioned)

Q#	Points	Panel	Question
1	2257	V	*How does meiofaunal biodiversity contribute to ecosystem function, integrity, and sustainability in the context of anthropogenic activities and global change?*
2	2210	V	*Is meiofauna taxonomical and functional diversity important in assessing anthropogenic impacts and global change on ecosystems?*
3	2209	V	*Are meiofauna good indicators of ecosystem quality status and functioning or do they need support from additional sources of evidence?*
4	2193	VIII	*How can we promote the interest for meiofauna amongst students and young researchers thereby ensuring the future of the field?*
5	2189	V	*Can meiofauna be used to understand better how pollution impacts ecosystems as a whole?*
6	2187	V	*How do meiofauna contribute to ecosystem resilience, particularly after a disturbance?*
7	2177	V	*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.)?*
8	2162	II	*Can sampling protocols be standardised to gather comparable distribution and ecological data worldwide?*
9	2160	VII	*How and how much do meiofauna influence nutrient cycling in different ecosystems?*
10	2157	V	*What are the main effects on meiofauna caused by anthropogenic pollution?*
11	2154	V	*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?*
12	2151	I	*How can we efficiently and reliably estimate and measure meiofaunal species diversity?*
13	2148	II	*What are the main knowledge gaps in meiofaunal diversity?*
14	2131	V	*What are the roles of meiofauna in the natural restoration process that follow anthropogenic impacts?*
15	2130	V	*Are meiofaunal species effective indicators for conventional pollutants and emerging contaminants (pharmaceuticals, pesticides, personal care products)?*
16	2126	II	*Which are the main barriers for meiofaunal species dispersal/colonisation?*
17	2124	V	*Are meiofauna more or less resilient compared to other benthic components in an ecosystem when under pressure of anthropogenic impacts and global change?*
18	2120	V	*What are the main effects on meiofauna caused by climate change?*
19	2119	VIII	*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?*
20	2110	VI	*How does connectivity among different habitats affect meiofaunal diversity patterns across different spatial scales?*
21	2108	I	*How species-rich are meiofauna on a regional and global scale?*
22	2106	VIII	*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?*
23	2098	V	*Do meiofauna in different habitats respond differently to similar anthropogenic impacts or global change?*
24	2093	II	*What drives patterns of meiofaunal diversity over large-scale gradients?*
25	2092	V	*Are there suitable early warning meiofaunal organisms, i.e. organisms useful to detect early stages of anthropogenic activities and global change?*
26	2090	V	*What functional traits or adaptations make meiofauna resistant against the impacts of anthropogenic activities and global change?*
27	2086	VII	*What do we know about the contribution of meiofauna to global carbon cycling and sequestration?*
28	2084	VII	*What are the most critical roles of meiofauna in biogeochemical cycling and how do they differ between different ecosystems?*
29	2083	V	*How will global change affect meiofauna distribution ranges and biogeography; for example, through contraction, expansion or shifts?*
30	2080	VI	*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?*
31	2077	I	*Do cosmopolitan meiofaunal species exist, do they represent complexes of cryptic species with narrower distributions, or are they just an artefact of poor taxonomy?*
32	2072	VI	*How do meiofaunal animals sense and react to their environment?*
33	2071	V	*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?*
34	2069	V	*How do anthropogenic activities and global change affect the different levels of biological organisation (for example genes, proteins and other compounds, cells, organs, organisms, life stages, populations, communities) in meiofaunal communities, and how could they be used as indicators?*
35	2064	VII	*What is the relative importance of ecological interactions between meiofauna and prokaryotes, such as facilitation and predation, in ecosystem processes?*
36	2063	V	*What is the best way to measure meiofauna diversity when assessing impacts from anthropogenic activities and global change?*
37	2063	I	*What patterns of diversity exist and how do they vary among different groups of meiofauna?*
38	2063	II	*What drives patterns of meiofaunal phylogenetic and functional diversity up to global scales?*
39	2060	VII	*Do meiofauna drive organic contaminant biodegradation and heavy metal distribution in different ecosystems?*
40	2057	VI	*What is the relative contribution of abiotic features versus biotic interactions in determining community assembly in meiofauna?*
41	2048	VII	*How and how much do meiofauna bioturbation affect transport, transformation, and burial of marine litter and microplastics?*
42	2036	II	*What are the environmental and biological mechanisms that drive dispersal distance in meiofaunal species?*
43	2033	II	*What is the relative contribution of local versus regional ecological factors on the distribution of meiofaunal organisms?*
44	2030	VIII	*Which community efforts are needed to dispel the taxonomic impediment and train new generations of meiobenthologists?*
45	2030	VII	*How would aquatic ecosystems function without meiofauna and to what extent can meiofauna sustain rates of key biogeochemical processes alone?*
46	2023	VII	*How and how much do meiofauna living in anoxic and sulfidic sediment layers influence ecosystem functions?*
47	2018	V	*Do permanent and temporary meiofauna respond differently to anthropogenic impacts and global change and what are the implications of these differences in impact assessments and monitoring?*
48	2017	V	*What are the main effects on meiofauna caused by microplastics?*
49	2017	VII	*Are the meiofauna a quantitatively important food source for fish and other vertebrates?*
50	2013	V	*What are the main effects on meiofauna caused by physical disturbance?*

Q#, ranking position.

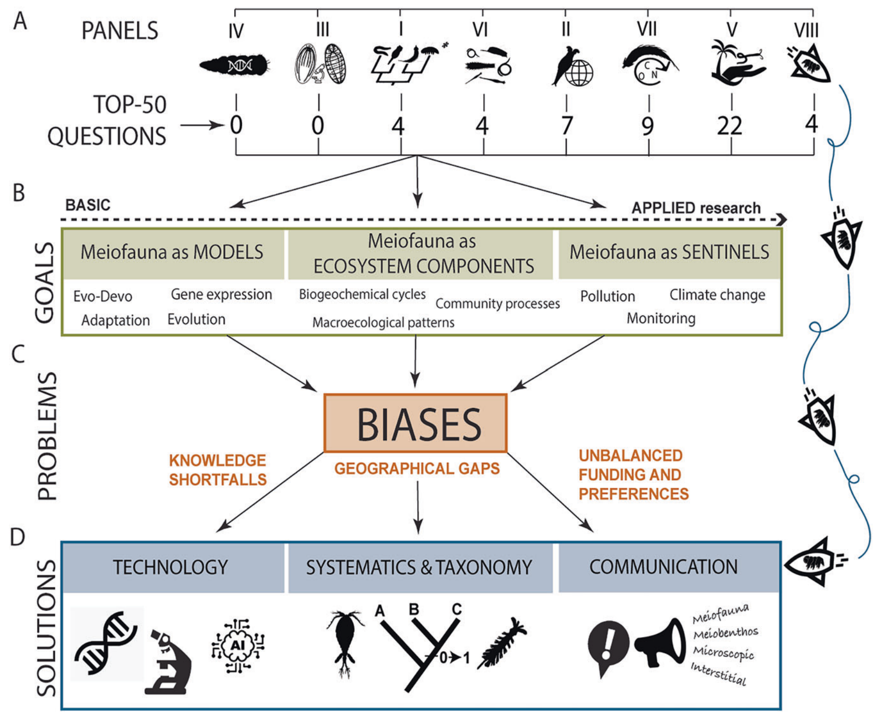

Fig. 3 | Conclusions. Panels are organized according to their focus, from basic to more applied research. **A** Applied questions received higher scores. **B** Questions have emphasised the role of meiofauna as eco-evolutionary models, their importance in ecosystem functioning and diversity across spatial scales, as well as their properties as sentinels for biomonitoring. **C** Knowledge shortfalls, gaps in geographic coverage, and the unbalanced preferences exhibited by researchers are major impediments affecting meiofauna research agenda. **D** Technological advancements, as well as improving and generalising taxonomic and communication skills as a research community will alleviate those issues. Attracting more students and researchers with diverse backgrounds will increase the utility of meiofauna to help us better understand Nature. Silhouettes drawn by Alejandro Martínez.

making meiofauna a valuable tool for monitoring ecosystem health[172,177]. Studying how taxonomic and functional meiofaunal diversity is linked to ecosystem functioning is important to mechanistically understand its contribution to the resilience and sustainability of ecosystems[35,173] (**Q#1, Q#2**). However, to what degree those biodiversity metrics respond to anthropogenic impacts, including global change[174,178], remains debated[167].

Meiofauna have strong potential as bioindicators of anthropogenic impacts[179,180] (**Q#3, Q#5**). Meiofauna's limited mobility likely expose organisms to ongoing anthropogenic impacts throughout their entire life cycle. Their small size facilitates large-scale sampling with appropriate techniques, and their high diversity makes shifts in taxonomic or functional composition readily detectable[34] over relatively short time scales. However, the effectiveness of meiofaunal organisms as indicators of ecosystem quality and function remains uncertain, primarily due to insufficient information on how community composition correlates with other ecosystem metrics.

Resilience has become an important research focus in the context of global change (**Q#6**). Understanding how to promote the ability of communities and ecosystems to recover from disturbance—whether sudden "pulsed events" like storms or gradual "press events" such as pollutant accumulation in the environment—is essential. Given their rapid reproduction and growth, meiofauna are promising indicators of ecosystem resilience[181]. Furthermore, meiofauna pioneer successional processes in disturbed ecosystems, often in close interaction with microbes, facilitating ecosystem recovery before larger organisms arrive and establish themselves[182,183].

Panel VI. Population and community ecology. The study of population and community ecology using meiofauna faces biological and technical challenges that connect to: small size, identification problems—particularly of fixed specimens[184,185]—, and dominance of few species in many communities[12,14,186–188]. Furthermore, the assemblage of meaningful data at such a small spatial scale is biased by our perception of the microscopic world. All in all, the study of meiofauna community ecology remains in its infancy and, consequently, only four rather general questions of this panel entered the top-50 list (Table 2).

Understanding how connectivity influences meiofaunal diversity is essential to predict dispersal effectiveness through ecological corridors and stepping stone habitats[189] in a meta-population dynamics context[186] (**Q#20**). The spatial and temporal connectivity among habitats informs effective conservation strategies, especially in partially isolated habitats[9,190], which meiofauna might predominantly reach via migration from local refugia.

Integrating approaches from terrestrial ecology may increase our chances to develop unified conceptual ecological theories[52]. However, the applicability of such theories to meiofauna remains uncertain (**Q#30**), because establishing unified theories requires improved knowledge on how microscopic organisms experience the environment (**Q#32**). The higher relative water viscosity at microscopic scales crucially affects how meiofauna sense their environment compared to larger organisms. Meiofauna show complex responses to stimuli[133,134], mainly using mechano- and chemoreceptors for orientation and food detection[42]. Volatile organic compounds can trigger attraction towards food patches[191], and food quality and quantity might critically activate feeding behaviours[192], overruling competition or predation risk[193]. Light might also be an important stimulus in illuminated habitats shown for free-living nematodes[194]. Finally, at their microscopic scale, shear-stress and changes in osmotic and hydrostatic pressure could also be sensed by meiofauna[195].

As performed by some macroscopic animals[196,197], meiofauna can manage their favourite food to enhance survival (**Q#51**). Bacterial-grazing nematodes promote microbial mobility, while their burrows, pellets, or mucus structures sustain the growth of microbial populations[198]. Laboratory experiments show that increasing abundance of nematode populations can promote bacterial activity[199] and photosynthesis[200,201]. Kinorhynchs secrete mucus to grow and trap microorganisms[202]; gutless nematodes and annelids rely on symbiotic bacteria to survive in low-oxygen environments[203–205]. Although it remains to be quantified, the gardening behaviour of meiofauna may have significant implications for ecosystem processes such as denitrification in marine sediments and organic matter decomposition[30,206].

Overall, community ecology questions revealed the need for understanding meiofaunal interactions and connections across multiple scales, emphasising feedback from individual functioning and interactions to ecosystem dynamics within a selective abiotic setting (**Q#40**)[207–212]. Simulations integrating niche and dispersion measures have demonstrated that trait-phylogeny-environment relationships, and frequency-dependent population growth explain community assembly in marine nematodes[213], similar to patterns observed in plants[214]. Likewise, including species traits in community ecology offers a promising avenue for moving beyond the "Everything is everywhere" paradigm for microscopic animals[96,215]. Furthermore, determining the individual phenotypes, behaviours, and mechanisms for how meiofauna sense and react to the contemporary environment is essential to understand the functional diversity of meiofauna[216].

Panel VII. Biogeochemistry and applied topics. Meiofauna probably shape ecosystems worldwide, although it is in soils and sediments where we know that meiofauna catalyse globally important processes through burrow construction, ingestion and egestion, and the flushing of overlying water for respiration and feeding[28,31,217]. Therefore, questions of this panel received high scores highlighting the need for further research in this relatively underexplored, yet relevant field[28].

Meiofauna primarily influence oxygen, sulphur, carbon, and nutrient cycles through direct solute uptake and bioturbation[218–220], stimulating nitrogen cycling microbes[30], and interacting with cable bacteria in anoxic sulphide-rich coastal sediments[221] (**Q#9, Q#28**). Most meiofauna require relatively high levels of oxygen and organic matter, which leads them to primarily inhabit and bioturbate the upper layers of soil and sediment[32]. The role of meiofauna from deeper sediment layers in ecosystem processes remains poorly understood. Respiration rates of meiofauna significantly decrease in response to decreasing ambient oxygen levels[33,222]. Muddy sediments dominate most of the seafloor and promote active meiofauna bioturbation that affects solute transport and microbial community structure[30,33,206,221]. Conversely, foraminifera promote sediment reworking in sandy environments common in intertidal and shelf areas[16,17]. However, the role of meiofauna in other ecosystems, such as the deep sea[223] as well as their influence on the cycling of other macronutrients, such as phosphorus, remain poorly understood.

The direct contribution of meiofauna biomass to total sediment carbon stocks is small[224] (**Q#27**). However, meiofauna activity significantly modifies carbon exchange at the sediment-water interface, potentially increasing bacterial carbon mineralisation by up to 50%[206]. Meiofauna contribute 3–33% of total oxygen uptake in coastal sediments[33], influencing the carbon chemistry of overlying seawater and possibly altering carbon sequestration in sediments across large spatial scales, although their net effect remains unquantified[225]. Interestingly, meiofauna can mediate ecosystem processes in sediments with minimal or no macrofauna as observed in the deep sea[226] and hypoxic Baltic Sea areas[227].

Past research has revealed the significant yet largely unexpected role of meiofaunal-prokaryote interactions in benthic ecosystem processes, including organic matter remineralisation[206] and organic pollutant degradation[228,229] (**Q#35**). However, empirical data on the effect that meiofauna have on the fate and distribution of heavy metals is lacking (**Q#39**). Effects of meiofaunal activity on microplastics have also received little attention. Annelids[230,231] and nematodes[232–234] might accidentally ingest microplastics, but it remains unknown how meiofaunal bioturbation affects microplastic transport and fate in the sediment. Future experimental and modelling studies are necessary to understand how meiofauna-prokaryote interactions evolve under anthropogenic stress and their potential in biodegradation and water treatment technologies.

Panel VIII. Science communication and other topics. Despite being hardly visible to the naked eye, meiofauna stand out by the astonishing number of species and variety of forms (Fig. 1), even in places where more conspicuous life forms are scarce[14,188,235]. Indeed, meiofauna includes representatives from at least 23 out of 35 animal phyla. However, the total number of species remains uncertain, with estimates ranging from 10 to 10^7, the vast majority of which are yet to be described[236]. The high probability of describing new species may attract taxonomists to study meiofauna, and the description of unexpected life forms and morphologies could appeal to researchers focused on animal evolution[237,238] (**Q#4**). Microscopic animals might also help us address broad eco-evolutionary questions, once data on their biology, distribution, and genetics are available (see discussion above). This diversity of topics offers training in complementary disciplines, fostering a new generation of meiobiologists.

Researchers interested in applied sciences may value meiofauna for their practical role in ecosystem conservation and management[34,188,239–241] (**Q#19**). Certain microscopic species, particularly the soil nematode *Caenorhabditis elegans*, have helped us understand human disease to eventually lead to cures or treatments[47,242,243]. Soil nematodes and other soil microscopic animals—more commonly referred to as mesofauna—are fundamentally important in agriculture[244]. Despite their importance, meiofauna are often underrepresented in discussions of practical applications.

Students are likely to engage in meiofauna studies if first introduced to the topic during their early academic programmes (**Q#44**). Although not many university courses focus on meiofauna, several summer schools and extracurricular courses have made them a central element[72,74,245]. Those courses often include workshops led by renowned researchers, who teach but also collect and describe the local biodiversity[246–248]. This approach brings knowledge and resources to areas where biodiversity research is limited, often leading to joint publications[72,74].

Early career researchers interested in biodiversity can contribute to building baseline datasets and catalogues of aquatic life, including meiofauna[113,114,118]. New technologies, such as DNA-based taxonomy[71,249], rapid DNA fingerprinting techniques[29,250], and automated high-resolution imaging combined with machine learning could alleviate taxonomic impediments, ultimately enabling reliable assessments of meiofauna diversity (**Q#22**).

Meiofauna can be used to enhance awareness of Earth's ecosystems and the biodiversity crisis, through interactive talks, hands-on activities, and scientific workshops (**Q#57**)[251]. Meiofauna diversity has been highlighted in accessible books and fairy tales for children[252,253]. National Parks and UNESCO Geoparks can support dissemination efforts by integrating research with outreach initiatives[73,254,255]. Remarkably, some microscopic animals have gained popularity in internet culture through memes and videos: tardigrades are famous for their toughness[46], bdelloid rotifers for the lack of males[256], and mud dragons (kinorhynchs) or penis worms (priapulids) for their evocative morphologies[257]. Creative naming of new species after unique morphological features or famous artists might also bring them into the spotlight[258–260].

Table 3 | Summary of the top 5 questions for each Panel, along with the main problems as solutions extracted from the Panel's critical analyses of the selected questions

I	**Panel 1: Systematics and taxonomy**	
	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 meiofaunal researchers? [Q#60, 1988 points].	
	Main Problems	**Potential Solutions**
	Linnean shortfall in meiofauna *(P II, VI)*.	Training new taxonomists and developing agreed-upon standards[72,74,245].
	Inefficiency in species identification.	Speed-up species identification with technology (e.g., metabarcoding, machine learning).
	Challenges in surveys and DNA metabarcoding.	Collaborative biodiversity surveys (e.g., bioblitz)[57,65,99] and optimised protocols.
	Inaccessibility of type material and preservation challenge.	Photomicrography-based taxonomy.
	Cosmopolitan distribution dilemma *(P II)*.	Re-examining cosmopolitan species (P II)[22,80].
II	**Panel 2: Macroecology and Biogeography**	
	Can sampling protocols be standardised 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 dispersal/colonisation? [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].	
	Main Problems	**Potential Solutions**
	Lack of standardised sampling protocols.	Develop and test time-efficient sampling protocols (P I)[68].
	Taxonomic challenges *(P I)*.	See P I.
	Limited functional and genetic diversity information.	Align with the latest ecological multifaceted analysis standards[267].
	Limited availability of standardised, interoperable datasets.	Improving global databases and data papers following FAIR (findability, accessibility, interoperability, and reusability) principles[268,269].
	Strong geographical and taxonomic biases.	Joint initiative and workshops to fill regions and taxonomic groups[270]
III	**Panel 3: Morphology and adaptation**	
	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 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].	
	Main Problems	**Potential Solutions**
	Challenge of studying small, fragile specimens.	Implementation of advanced microscopy and imaging technologies.
	Problems disentangling convergent adaptation.	Integrating morphological and genomic data *(P IV)*[129].
	Lack of understanding on short-term acclimatisation.	Develop protocols for gene expression.
	Keeping alive animals for behavioural studies.	Development of experimental protocols, including cultures.
	Difficulties to perform undisturbed in-situ observations.	Technological developments on microsensing (*P V*).
IV	**Panel 4: Genome Biology and Evolution**	
	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, if any, explain the observed long branch lengths seen for meiofaunal taxa in many molecular phylogenies? [Q#101, 1798 points]	
	Main Problems	**Potential Solutions**
	Scarcity of genomic data.	Participation in international initiatives for genome sequencing and macrogenetics analyses[151,271].
	Technical difficulties of obtaining DNA due to small size.	Advancements in DNA library synthesis and genomic techniques[272].
	Challenges in resolving phylogenetic relationships.	Integration of genomic and experimental approaches.
	Disparity in the speed of molecular evolution and scarcity of fossils.	Test for evolutionary rates across groups to optimise molecular clocks[40].
V	**Panel 5: Anthropogenic impact and climate change**	
	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].	

Table 3 (continued) | Summary of the top 5 questions for each Panel, along with the main problems as solutions extracted from the Panel's critical analyses of the selected questions

	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].	
	Main Problems	**Potential Solutions**
	Selecting the appropriate metric to detect impact.	Increase theoretical and experimental work on meiofauna interactions with the environment at species and community level.
	Poor understanding of species-specific responses to perturbation and how it influences ecological interactions.	Perform experimental essays of pollutants.
	Quantification of non-linear responses to perturbations (resistance and resilience).	Incorporate methods from quantitative biology (e.g., network-based frameworks)
	Limited availability of long-term temporal series.	Incorporate meiofauna into monitoring protocols.
VI	**Panel 6: Population and community ecology**	
	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].	
	Main Problems	**Potential Solutions**
	Difficulties to perform undisturbed in situ observations *(P III)*.	See P III
	Taxonomic inefficiency *(P I, II)*.	See P I
	Limited connection between individual behaviours and emergent spatial patterns *(P III)*.	See P III
	Limited understanding on the level of connectivity across populations *(P IV)*.	See P IV
	Limited connection between morphology and functions.	Integrating trait-based studies in the meiofauna research agenda[96,215].
	Limited understanding of species interactions.	Experimental studies on living animals (local scale) and study of co-occurrence patterns (broader scale).
VII	**Panel 7: Biogeochemistry and applied topics**	
	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].	
	Main Problems	**Potential Solutions**
	Largely underexplored field (e.g., the role of meiofauna's role in carbon and nutrient cycling).	Increase collaborations between ecologists and biogeochemists.
	Historical bias towards benthic and shallow marine ecosystems, oppose to the deep sea	Increase awareness of the importance of meiofauna across a broader range of habitats[28].
VIII	**Panel 8: Communication and other topics**	
	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].	
	Main Problems	**Potential Solutions**
	Most meiofauna are invisible to the naked human eye.	Incorporate technological advances to show the invisible (3-D printing, imaging).
	Public's lack of familiarity and inefficient public engagement.	Incorporation of meiofauna into public outreach programmes and science communication initiatives[245,251].
	Limited mention of meiofauna in public initiatives, books, educational programmes.	Aim at general questions to increase the impact of meiofaunal research (see the text for inspiration!)
	Lack of students interested in meiofauna	Incorporate meiofauna into university curricula or organising courses and workshops including meiofauna

Issues that are transversal to more than one panel are indicated in brackets using abbreviations (e.g., P II = *Panel II*).

Discussion and future directions: the next generation of meiofauna research

Are we exploiting the full potential that meiofauna offer as a model to address questions of broad scientific and societal importance? The answer is no, or at least not yet. There are a number of key challenges and biases that adversely affect our current knowledge of meiofauna (Table 3). Nevertheless, integrative approaches and technological developments have been creating opportunities to use these fascinating organisms to address broad and important questions[28] (Fig. 3). Meiofauna have been used as models to understand fundamental adaptive processes, they have contributed to unravelling the animal Tree of Life[39], they are predicted to contain a treasure trove for future genomic studies[125], they play key roles in ecosystem functioning and integrity[30,31], and they have been used as models to understand human diseases[47]. Meiofauna also represent a valuable biomonitoring tool for freshwater and marine environments alike, even where larger-sized fauna have become depleted or absent[34,35,261]. This very broad spectrum of topics is just the tip of the iceberg, with new ideas and research avenues continuing to emerge as technological developments and accumulation of information shed light on the fascinating life of the microscopic, ubiquitous animals around us.

What are the critical research priorities? Our research agenda should balance the investigation of general questions—sparking the interest of a broad audience—and address specialised research topics focusing on theoretical aspects concerning meiofauna (Fig. 3). The latter aspects, which often involve generating primary data on distribution, taxonomy, traits, and DNA sequences, are not only critical to address some of the knowledge shortfalls that pervasively affect the development of the field[59], but are also 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. Survey responses were not influenced by the background of the voters (Fig. 2A; Supplementary Methods), nor by the linguistic features of the questions (readability, length, use of jargon and acronyms). Whether survey responses were influenced by other factors not controlled for in our analysis, such as the current funding landscape or the growing eco-anxiety, rests in the mind of each voter. Regardless, survey results should not be accepted uncritically as a roadmap guiding research priorities; rather, they should be viewed as a diagnosis of how broad international audiences perceive the importance of the different topics addressed traditionally in meiofauna research.

Which biases currently affect meiofauna research and how can we overcome them to move forward with the research agenda? Geographical and taxonomic biases, as well as biases inherent to the small size of meiofauna, have affected meiofauna research[37]. Therefore, it is unsurprising that they were the focus of many top priority questions of each panel (Fig. 3).

Technological innovation might alleviate some of those biases. New imaging and microscopy technologies, for example, have provided unprecedented insights into meiofauna. 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 optimising sequencing technologies for small meiofaunal organisms. Whilst reduced genome representation methods and transcriptomics can offer interim solutions[262,263], the full potential lies in generating complete reference genomes. To achieve this, greater collaborative and development efforts are essential.

Geographical gaps will only be overcome through the establishment of international collaborations[264]. The International Association of Meiobenthologists plays an important role, including periodically organised conferences and thematic sessions at international meetings. Summer schools and regional workshops have proven useful as well, especially in engaging local students and researchers from areas with limited resources available to study meiofauna. Improving communication skills is crucial in reaching diverse audiences and making the research community even more international and diverse.

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

Material and Methods

To identify fundamental questions addressable using meiofauna[52], we applied a horizon scanning methodology, proven effective in similar studies[54,55]. Two survey coordinators defined eight panels, each with a panel coordinator (Table 1) to form an international expert panel tasked with drafting initial questions. Each panel included two renowned meiofauna experts, an early-career researcher, and an external expert with relevant expertise on the topic of the panel outside meiofauna.

Panels assembled an initial list of 253 questions, which was first reduced to 194 questions after removing duplicates and improving readability (see Supplementary Methods)[50,51,265]. Then, 32 panel members and 2 survey coordinators (total 34 voters) scored questions in List #1 from 1 to 10. The scores ranged from 266 (top-voted question) to 120 (least-voted question). Based on a bimodal distribution of scores, the best 117 questions scoring above 205 were included in List #2.

List #2 underwent public voting via an online survey, targeting a broad audience, including meiofauna specialists, non-specialists, students, and stakeholders. The survey was promoted through direct emails, social media (Facebook, Twitter, ResearchGate), workshops, meetings, newsletters (e.g., International, Brazilian and Japanese Association of Meiobenthologist), and mailing lists (e.g., rotifer-family@listserv, Annelida, International Society for Subterranean Biology, Italian Ecological Society, Ecological Society of India). Panel members also shared it with students in their courses.

Caveats of horizon scanning surveys and our countermeasures in the statistical methods are discussed in the Supplementary Material.

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

Data availability

The code is available at https://github.com/amartinezgarcia/Meiofauna50Questions, whereas the complete list of questions and the metadata of the voters are stored in the Open Science Foundation repository (https://doi.org/10.17605/OSF.IO/7G2QX)[266]. Any remaining information can be obtained from the corresponding author upon reasonable request.

Alejandro Martínez[1] ✉, Stefano Bonaglia[2], Maikon Di Domenico[3], Gustavo Fonseca[4], Jeroen Ingels[5], Katharina M. Jörger[6], Christopher Laumer[7], Francesca Leasi[8], Daniela Zeppilli[9], Elisa Baldrighi[10], Holly Bik[11], Diego Cepeda[12], Marco Curini-Galletti[13,14], Asher D. Cutter[15], Giovanni dos Santos[16], Simone Fattorini[17], Dagmar Frisch[18], Sabine Gollner[19], Ulf Jondelius[20], Alexandra Kerbl[21], Kevin M. Kocot[22], Nabil Majdi[23], Stefano Mammola[1,14,24], José M. Martín-Durán[25], André Menegotto[26,27,28], Paul A. Montagna[29], Francisco J. A. Nascimento[30], Nicolas Puillandre[31], Anne Rognant[32,44], Nuria Sánchez[33], Isaac R. Santos[2], Andreas Schmidt-Rhaesa[34], Michaela Schratzberger[35], Federica Semprucci[36], Mauricio Shimabukuro[37], Paul J. Sommerfield[38,45], Torsten H. Struck[39], Martin V. Sørensen[40], Andreas Wallberg[41], Katrine Worsaae[42], Hiroshi Yamasaki[43] & Diego Fontaneto[1,14]

[1]Molecular Ecology Group (MEG), Water Research Institute (CNR-IRSA), National Research Council, 28922 Verbania Pallanza, Italy. [2]Department of Marine Sciences, University of Gothenburg, Gothenburg, Sweden. [3]Center for Marine Studies (CEM), Federal University of Paraná (UFPR), Pontal do Paraná, Paraná, Brazil. [4]Marine Science Institute, Federal University of São Paulo, Santos, Brazil. [5]National Institute of Water and Atmospheric Research, 301 Evans Bay Parade, Hataitai, 6021 Wellington, New Zealand.

[6]SNSB-Bavarian State Collection of Zoology, Munich, Germany. [7]The Natural History Museum, Department of Life Sciences, London, UK. [8]Department of Biology, Geology, and Environmental Science, University of Tennessee at Chattanooga, Chattanooga, TN, USA. [9]UMR6197 Biologie et Écologie des Ecosystèmes Marins Profonds, University Brest, CNRS, Ifremer, 29280 Plouzané, France. [10]Department of Biology, The University of Nevada, Reno, NV, USA. [11]Department of Marine Science & Institute of Bioinformatics, University of Georgia, Athens, GA, USA. [12]Department of Life Sciences, University of Alcalá (UAH), Ctra. Madrid-Barcelona Km.33, 600. 28805 Alcalá de Henares, Madrid, Spain. [13]Department of Veterinary Medicine, University of Sassari, Sassari, Italy. [14]National Biodiversity Future Center (NBFC), Palermo, Italy. [15]Department of Ecology & Evolutionary Biology. University of Toronto, Toronto, ON, M5S3B2, Canada. [16]Zoology Department, Federal University of Pernambuco, 50670-901 Recife-PE, Brazil. [17]Department of Life, Health & Environmental Sciences, University of L'Aquila, Via Vetoio – Coppito, 67100 L'Aquila, Italy. [18]Department of Evolutionary and Integrative Ecology, IGB Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany. [19]Department of Ocean Systems (OCS), Royal Netherlands Institute for Sea Research (NIOZ), Landsdiep 4, 1797 SZ 't Horntje, Texel, The Netherlands. [20]Swedish Museum of Natural History, Department of Zoology, POB 50007, SE-104 05 Stockholm, Sweden. [21]Department for Evolutionary Neurobiology, Centre for Organismal Studies, University Heidelberg. Im Neuenheimer Feld 230, 69120 Heidelberg, Germany. [22]Department of Biological Sciences, University of Alabama, Tuscaloosa, AL, USA. [23]Réserve Naturelle Nationale de la Forêt de la Massane, Sorbonne Université, UPMC Université Paris 06, Observatoire Océanologique de Banyuls, 66650 Banyuls-sur-Mer, France. [24]Laboratory for Integrative Biodiversity Research (LIBRe), Finnish Museum of Natural History (LUOMUS), University of Helsinki, Helsinki, Finland. [25]School of Biological and Behavioural Sciences. Queen Mary University of London. Mile End Road, E1 4NS London, UK. [26]Department of Ecology, Research Centre for Biodiversity and Global Change, Autonomous University of Madrid (CIBC-UAM), C/ Darwin 2, 28049 Madrid, Spain. [27]Terrestrial Ecology Group (TEG-UAM), Department of Ecology, Autonomous University of Madrid, 28049 Madrid, Spain. [28]Department of Ecology, ICB, Federal University of Goiás, Goiânia, 74690-900, Brazil. [29]Harte Research Institute, Texas A&M University-Corpus Christi, Corpus Christi, TX, USA. [30]Department of Ecology, Environment and Plant Sciences, Stockholm University, Stockholm, Sweden. [31]Institut Systématique Evolution Biodiversité (ISYEB), Muséum national d'Histoire naturelle, CNRS, Sorbonne Université, EPHE, Université des Antilles, 57 rue Cuvier, CP51, Paris, France. [32]Océanopolis. Port de Plaisance du Moulin blanc. B.P. 91039. Brest Cedex 1, Brest, 29210, France. [33]Facultad de Ciencias Biológicas, Departamento de Biodiversidad, Ecología y Evolución José Antonio Novais, 12. Planta 10. 28040 Madrid, Spain. Universidad Complutense de Madrid, Madrid, Spain. [34]Leibniz Institute for the analysis of biodiversity change (LIB), Hamburg, Germany. [35]Centre for Environment, Fisheries and Aquaculture Science (Cefas), Lowestoft, UK. [36]Dipartimento di Scienze Biomolecolari., Università degli Studi di Urbino Carlo Bo, Marche, Italy. [37]Universidade Federal do Rio Grande (FURG) - Instituto de Oceanografia, Rio Grande, Brazil. [38]Plymouth Marine Laboratory, Plymouth, UK. [39]Natural History Museum, University of Oslo, 1172 Blindern, 0318 Oslo, Norway. [40]Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark. [41]Department of Medical Biochemistry and Microbiology, Uppsala University; Husargatan 3, 751 23 Uppsala, Sweden. [42]Marine Biological Section, Department of Biology, University of Copenhagen, Universitetsparken 4, 2100 Copenhagen, Denmark. [43]Faculty of Arts and Science, Kyushu University, Fukuoka, Japan. [44]Deceased: Anne Rognant. [45]Deceased: Paul J. Sommerfield. ✉e-mail: alejandro.martinezgarcia@cnr.it

Received: 5 August 2024; Accepted: 5 March 2025;
Published online: 17 March 2025

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Acknowledgements

We thank Marta García-Cobo, Jan N. Macher, Ana Milena Lagos, María Victoria León, Lenke Tödler, Nancy Mercado-Salas, Terue Kihara, and Guillermo García-Gómez for providing pictures for the manuscript. Kevin M. Kocot was funded by NSF DEB-1846174. Dagmar Frisch Deutsche Forschungsgemeinschaft DFG- German Research Foundation) – Project number 461099895. André Menegotto was supported by a "Juan de la Cierva—Formación" fellowship (FJC2020044080-I), funded by MICIU/AEI/10.13039/501100011033 and by "European Union NextGenerationEU/PRTR". The study received support from the National Recovery and Resilience Plan (NRRP) of the Italian Ministry of University and Research, funded by the European Union—NextGenerationEU, project code CN_00000033, National Biodiversity Future Center—NBFC, CUP B83C22002930006.

Author contributions

Alejandro Martínez, Stefano Mammola, and Diego Fontaneto. designed the study. Alejandro Martínez and Diego Fontaneto. acted as survey coordinators, selecting the panels and assigning panel coordinators. Stefano Bonaglia, Maikon Di Domenico, Gustavo Fonseca, Jeroen Ingels, Katharina M. Jörger, Christopher Laumer, Francesca Leasi, and Daniella Zeppilli served as panel coordinators. Stefano Bonaglia, Maikon Di Domenico, Gustavo Fonseca, Jeroen Ingels, Katharina M. Jörger, Christopher Laumer, Francesca Leasi, Daniela Zeppilli, Elisa Baldrighi, Holly Bik, Diego Cepeda, Marco Curini-Galletti, Asher D. Cutter, Giovanni dos Santos, Simone Fattorini, Dagmar Frisch, Sabine Gollner, Ulf Jondelius, Alexandra Kerbl, Kevin M. Kocot, Nabil Majdi, Stefano Mammola, José M. Martín-Durán, André Menegotto, Paul A. Montagna, Francisco J. A. Nascimento, Nicolas Puillandre, Anne Rognant, Nuria Sánchez, Isaac R. Santos, Andreas Schmidt-Rhaesa, Michaela Schratzberger, Federica Semprucci, Mauricio Shimabukuro, Paul J. Sommerfield, Torsten H. Struck, Martin V. Sørensen, Andreas Wallberg, Katrine Worsaae, and Hiroshi Yamasaki proposed the first set of questions. Alejandro Martínez analysed the poll data and prepared the figures. Alejandro Martínez and Diego Fontaneto wrote the first draft, with significant input from Stefano Bonaglia, Maikon Di Domenico, Gustavo Fonseca, Jeroen Ingels, Katharina M. Jörger, Christopher Laumer, Francesca Leasi, and Daniella Zeppilli in their respective panels. Stefano Bonaglia, Maikon Di Domenico, Gustavo Fonseca, Jeroen Ingels, Katharina M. Jörger, Christopher Laumer, Francesca Leasi, Daniela Zeppilli, Elisa Baldrighi, Holly Bik, Diego Cepeda, Marco Curini-Galletti, Asher D. Cutter, Giovanni dos Santos, Simone Fattorini, Dagmar Frisch, Sabine Gollner, Ulf Jondelius, Alexandra Kerbl, Kevin M. Kocot, Nabil Majdi, Stefano Mammola, José M. Martín-Durán, André Menegotto, Paul A. Montagna, Francisco J. A. Nascimento, Nicolas Puillandre, Anne Rognant, Nuria Sánchez, Isaac R. Santos, Andreas Schmidt-Rhaesa, Michaela Schratzberger, Federica Semprucci, Mauricio Shimabukuro, Paul J. Sommerfield, Torsten H. Struck, Martin V. Sørensen, Andreas Wallberg, Katrine Worsaae, and Hiroshi Yamasaki worked and improved the first draft. All authors approved the submitted version of the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s42003-025-07888-1.

Correspondence and requests for materials should be addressed to Alejandro Martínez.

Peer review information *Communications Biology* thanks Lara Macheriotou and the other, anonymous, reviewers for their contribution to the peer review of this work. Primary Handling Editors: Kaliya Georgieva. A peer review file is available.