

Chapter 5

Marine Meiofauna Diversity and Biogeography—Paradigms and Challenges



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Abstract Scientists studying the biodiversity and biogeography of meiofauna encounter many uncertainties regarding the causes and consequences of natural and anthropogenic-driven changes in biodiversity patterns they observe worldwide. Recently developed novel analytical and computational technologies are facilitating more systematic and integrated approaches to the study of meiofauna biodiversity. In this chapter, we reflect on the state of the art in biodiversity and biogeography research with a focus on the most abundant and diverse meiofauna taxa including nematodes and copepods. Other occasionally abundant meiofauna taxa such as carbonate-shelled crustacean ostracods and protist foraminiferans, which are present in the fossil record, allow meiobenthologists to understand the links between shifts in biodiversity and major historical events in the marine environment. Sample-size dependency and the lack of standardization across benthic surveys currently hamper the integration of disparate meiofauna studies into wider research of seafloor biodiversity and biogeography. We discuss habitat-specific meiofauna biodiversity patterns that are observed at different scales and identify the main drivers of such patterns. Important factors include physical characteristics of the seafloor, biogeochemical processes, ecosystem productivity, geographical location, but also the interactions of meiofauna with other ecosystem components including their prey, their predators, competitors,

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and habitat facilitators. We discuss the importance of meiobenthic biodiversity for ecosystem functioning and touch on the biogeography of dominant meiofauna taxa by looking at what we know about the importance of endemism versus cosmopolitanism, the growing insights in population genetics and cryptic speciation, the phylogenetic processes underpinning them, and critical gaps in our knowledge. We conclude by identifying some dynamic areas of research and inquiry for future generations of meiobenthologists studying the biodiversity and biogeography of meiofauna.

5.1 Why Study the Biodiversity and Biogeography of Meiofauna?

One of the major challenges in ecological research today is to identify the causes and effects of natural and human-driven changes in marine biodiversity patterns. Particularly urgent is the need to better understand and quantify different aspects of biodiversity and identify the role of anthropogenic activities and their consequences such as global warming, deoxygenation, acidification, eutrophication, overfishing, and pollution in local, regional, and global declines of biodiversity for all major components of the marine realm (Sala and Knowlton 2006; Mieszkowska et al. 2014; Luypaert et al. 2019), including the microscopically small meiofauna (see Chap. 7). The United Nation's Convention on Biological Diversity of 1992 defines biological diversity as "*the variability among living organisms from all sources including, inter alia, terrestrial, marine, and other aquatic ecosystems and the ecological complexes of which they are part: this includes diversity within species, between species, and of ecosystems*" (Josefsson 2018).

In ecological research on meiofauna, biodiversity is generally represented by the number of species and their equitability or evenness in a given sample, location, or area. Depending on the context, biodiversity is obviously much more than species counts and includes different sources of biological variability, such as genes, ecosystems, phylogeny, and functional traits (Turnhout and Purvis 2020). The metrics that represent biodiversity seem almost infinite, each of them emphasizing particular features of the biodiversity concept, which refers to a biological entity comprising multiple components (e.g., a community represented by different species) (Hill 1973; Ellison 2010; Chao et al. 2020). Biodiversity is studied in many different ways and at a variety of levels of biological organization. These range from counts of taxonomic or functional units per surface area or volume (for meiofauna traditionally expressed as number of taxa per 10 cm² surface area) to dominance (i.e., numbers of the most abundant taxon), and from alpha (sample or site) to beta (turnover) to gamma (large scale) diversity (Fig. 5.1), and include different temporal and spatial scales of sampling (Whittaker 1972).

Several abundant meiofauna taxa, especially nematodes and copepods, are known to comprise numerous co-occurring species (from about 10 to more than 100) in a relatively small sample of sediment (10 cm² surface area), yet many meiofauna

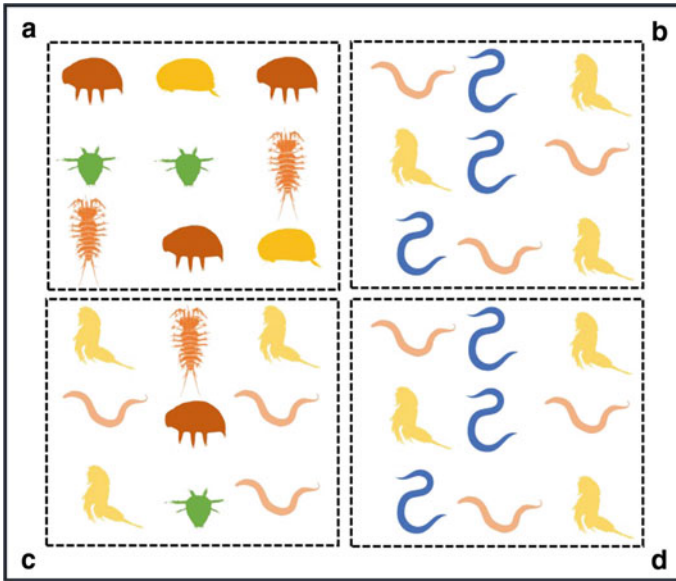


Fig. 5.1 Visualization of alpha, beta, and gamma diversity. The large box in solid line represents a region; the 4 small boxes labeled **a**, **b**, **c**, and **d** are samples from 4 different locations (sites) representative for the region. The different colored drawings illustrate different species or taxonomic units. Gamma diversity is calculated based on all species from within the large box representing the region. Alpha diversity is calculated for each small box separately and represents the site diversity. Beta diversity refers to differences between the sites (small boxes) and is a measure for how many species are shared between two sites. For example, sites **a** and **b** share no species and have a maximum turnover or beta diversity while sites **b** and **d** have a minimum beta diversity since they are identical in species composition

taxa are among the least known in terms of their diversity (Appeltans et al. 2012), suggesting that a large proportion of meiofauna species remains taxonomically undescribed. Understanding drivers of large-scale diversity patterns, i.e., the biogeography of meiofauna, requires knowledge of their dispersal, their evolutionary history, and their ability to adapt to prevailing environmental conditions (see Chap. 7). Is everything everywhere or do we find highly specialized taxa that are endemic to specific ecosystems in distinct areas? The high abundance of some meiofauna taxa, their ubiquitous presence, and their high taxonomic diversity have generated a set of interesting paradigms but also created challenges when interpreting contrasting patterns of meiofauna distribution.

Scientists studying the biodiversity and biogeography of meiofauna indeed encounter many uncertainties regarding the causes and consequences of changing biodiversity patterns they observe worldwide. Some of these uncertainties may remain unresolved in the short term. At the same time, innovative sampling approaches and recently developed novel analytical and computational technologies

are facilitating more systematic and integrated approaches to the study of meiofauna distribution and biogeography. In this chapter, we reflect on the state of the art in biodiversity and biogeography research with a focus on the most abundant and diverse meiofauna taxa including nematodes and copepods. Both taxa generally co-occur in the benthos under the same prevailing conditions despite being characterized by different functional traits linked to their distinctive morphology, life history, and physiology. Other occasionally abundant taxa composing the meiofauna are carbonate-shelled crustacean ostracods and foraminiferans, an important protist group. Generally present in the fossil record, studying those taxa allows meiobenthologists to understand the links between shifts in biodiversity and major historical events in the marine environment. Carbonate-shelled ostracods and foraminiferans are also susceptible to the effects of climate change and in particular ocean acidification (Yamada and Ikeda 1999; Fabry et al. 2008; see Chap. 7). Several additional permanent meiofauna taxa, including kinorhynchs, gastrotrichs, tardigrades, turbellarians, and loriciferans, are either rare in most environments or occur in such low abundances that they are largely outnumbered by the previously mentioned taxa in terms of their diversity. Nevertheless, poorly-studied rare taxa also represent interesting cases for comparison with the more abundant taxa to understand biodiversity and biogeography patterns, and the factors and processes driving them.

In this chapter, we

- Reflect on the biodiversity concept within the context of meiofauna biology and ecology, including generally applied approaches to measure biodiversity and some novel methodological and analytical developments, and identify the issues that currently hamper the integration of meiofauna biodiversity data across scales of space and time (e.g., sample size dependency, lack of standardization; Sect. 5.2);
- Discuss, for the most abundant meiofauna taxa, the biodiversity patterns that are observed at different biogeographical scales (Sect. 5.3);
- Reveal similarities and differences in meiofauna biodiversity patterns among habitats and identify the main drivers including physical characteristics of the substrate, biogeochemical processes, ecosystem productivity, water depth, geographic location, alongside biotic interactions of meiofauna with other ecosystem components including predator–prey relationships, competition, and facilitation (Sect. 5.4);
- Examine the importance of meiobenthic biodiversity for ecosystem functioning with an emphasis on the mediating role of meiofauna interacting with other ecosystem components from micro- to megabenthos (Sect. 5.5).
- Consider long-term changes of taxa for which we have a paleo-record (Sect. 5.6).
- Reflect on the biogeography of meiobenthic taxa by looking at what we know about the importance of endemism versus cosmopolitanism, the growing insights in population genetics and cryptic speciation, the phylogenetic processes underpinning them, and the gaps in our knowledge (Sect. 5.7).
- Finally, we put forward future perspectives and challenges and present some major opportunities for biodiversity and biogeography research of meiofauna (Sect. 5.8).

5.2 Studying an Invisible World: Sampling and Measuring Meiofauna Biodiversity

Nematoda is one of the most remarkable and widely studied invertebrate phylum on our planet. Still, many aspects of their biodiversity and biogeography in marine environments are poorly understood. Currently, one of the major research questions remains the reason behind the success of nematodes as one of the most abundant and diverse metazoan taxa across aquatic and terrestrial ecosystems (Schratzberger et al. 2019; Traunspurger 2021). Combining soil nematode habitat associations with a phylogenetic tree based on small sub-unit ribosomal DNA sequences, Holterman et al. (2019) showed that the phylum's success resulted from numerous habitat transitions followed by moderate diversification, rather than from extensive diversification after a limited number of major habitat transitions. Resolving the extent to which the same processes apply within the marine realm would deliver major insights for marine biodiversity research. While taxonomic research on marine nematodes began in the early twentieth century, quantitative biodiversity studies on meiofauna started in the late 1960s early 1970s (see reviews by Heip et al. 1985; Giere 2009). Although also present as epifauna or epibionts on hard substrata occasionally of biological origin (such as coral rubble or macroalgae), nematodes generally dominate invertebrate communities in soft sediments (Giere 2009). Soft sediment meiofauna is traditionally sampled with cores (diameter between 2 and 10 cm) to a sediment depth of 5 to 10 cm. Depending on the substrate, the majority of specimens are generally recorded in the upper 3–5 cm of the sediment, and nematode densities commonly lie between 100 and a few 1000s per 10 cm² surface area (varying between the extremes of about 10 to more than 10,000 individuals per 10 cm²; see below for examples). The second most abundant metazoan group tends to be copepoda, generally representing about 10% of the total meiofauna. This proportion is remarkably constant across water depths, only decreasing by a higher copepod sensitivity to oxygen depletion when oxygen becomes more limited (Kawano et al. 2021). Within the copepoda, the Harpacticoida dominate meiofauna samples in terms of abundance and diversity (George et al. 2020).

Because of their generally high abundances, identifying nematodes from an entire sample can be very time-consuming. For this reason, samples are traditionally sub-sampled (after randomization) to a maximum of a few 100s of nematode specimens that are subsequently identified at varying levels of taxonomic resolution. Most diversity metrics are sample size dependent, so unless sampling and sub-sampling techniques as well as taxonomic resolutions are standardized, data from different surveys are often not directly comparable (Soetaert and Heip 1990). Given the high nematode diversity, it is estimated that the majority of species remains undescribed to the present day (Mokievsky and Azovsky 2002). Consequently, many ecological studies tend to identify nematodes to genus level only. Although nematode genus composition often reflects macro-ecological patterns observed at species level (Vanreusel et al. 2010; Hauquier et al. 2019), several genera can be represented by numerous species in the same sample (high congeneric species richness), especially in the deep

sea (Muthumbi et al. 2011). Furthermore, the lack of species descriptions hampers biogeographic studies, and cryptic speciation is probably common in marine nematodes (although evidence is limited to mainly brackish and only a few marine species; Derycke et al. 2005, 2007, 2008; Bhadury et al. 2008; also see Sect. 5.3 below).

High throughput sequencing (HTS) approaches such as those based on metabarcoding are beginning to address these major drawbacks in meiofauna biodiversity research, while generating new uncertainties. No sub-sampling is required when sequencing sufficiently large samples after extraction from the sediment, and sequences can be analyzed at the highest (genetic) resolution. However, some taxa are still not sequenced or recognized in the bioinformatic pipelines currently used (Avó et al. 2017; Macheriotou et al. 2020; Brandt et al. 2021; Castro et al. 2021). Also, different conclusions can be drawn from analyses using different sequencing techniques (Leasi et al. 2018). DNA sequencing does not differentiate between dead and alive specimens, and therefore, the use of environmental RNA (eRNA), specifically targeting live organisms, is being explored as a tool in meiofauna studies. For instance, Broman et al. (2021) demonstrated a clear response of meiofauna to an organic enrichment gradient along the Baltic coast off Finland using eRNA targeting nematodes, foraminiferans, and ciliates.

The identification of copepods to species level can only be achieved by studying the adult specimens. Copepodites and nauplii are therefore generally excluded from biodiversity comparisons using traditional morphological methods. With the rise of molecular methods such as barcoding and metabarcoding, identification of all developmental stages is theoretically possible (Rossel et al. 2019). However, as for nematodes, the lack of suitable reference libraries is still greatly reducing the applicability of molecular methods (only 12% of the 122 species sequenced in Rossel and Martínez Arbizu 2019 are currently present in GenBank). Most of the species found in the abyss (> 99%) are thought to be new to science (George et al. 2013), but even in relatively well studied areas such as the North Sea, many copepod species remain undescribed (Huys et al. 1992) with only a few recent species descriptions added since 1992. Moreover, molecular methods revealed that 19% of the harpacticoid species in the German Bight, a part of the North Sea, are new to science, and > 8% represent species complexes with high cryptic genetic diversity which is not reflected in the morphology (Rossel and Martínez Arbizu 2019). Lack of comprehensive identification keys for marine harpacticoids also hampers the understanding of species ranges and biogeographical patterns of meiobenthic copepods.

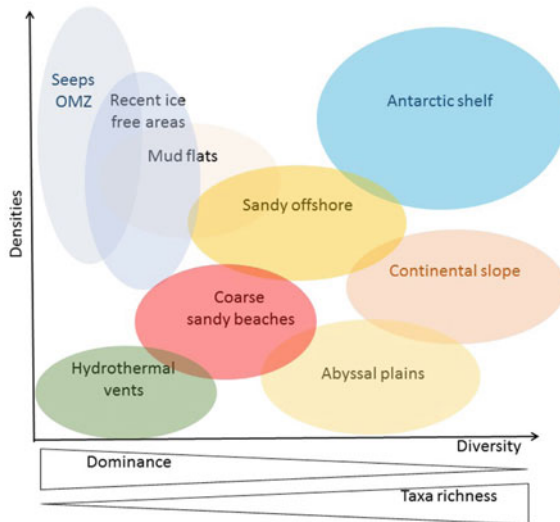
Lacking calcareous skeletal structures, nematodes and copepods, do not generally leave a fossil record that could be used to study past biodiversity changes. Conversely, the shelled ostracods and foraminiferans (alive and as fossils) have been well studied since the nineteenth century, although originally with a focus on taxonomy. They both are an important meiobenthic taxon of interest in most aquatic environments, not only for their living specimens, but especially for their fossil records. Quantitative ecological and paleoecological studies were initiated in the 1950s (e.g., Benson 1959; Benson and Kaesler 1963, Walton 1955). Similar to other meiobenthic taxa, most soft sediment ostracods and foraminiferans live in the top few centimeters of the

sediment (Gooday 1986; Jöst et al. 2017), and are therefore sampled in the same way as other meiofauna taxa.

5.3 Meiofauna Biodiversity Patterns Across Benthic Habitats

Single locality (sample, site, or station), or alpha, diversity patterns observed for nematodes and copepods range from samples with a very high number of rare taxa (often occurring as singletons or doubletons in a sample) to samples dominated (> 50% or more of total abundance) by a single or few high-abundance species. Intermediate between these extremes, we often observe assemblages composed of a few abundant species and a significant number of taxa with low abundances. Figure 5.2 illustrates some of the density-biodiversity patterns observed for alpha diversity of nematodes and copepods across habitats. While this figure generalizes the main trends, in each of the habitats shown, specific environmental gradients result in within-habitat shifts of density-diversity relationships. For instance, abyssal plains are generally characterized by low densities (from less than 10 to about 100 individuals per 10 cm²) and high species richness with no dominant nematode or copepod species present (Hauquier et al. 2019; Rose et al. 2005). However, a gradual increase in particulate organic carbon (POC) fluxes to the seafloor along a surface productivity gradient tends to result in higher abyssal densities because of the higher food input. This often corresponds with an increase in species richness for both copepods and nematodes (Fig. 5.3).

Fig. 5.2 Generalized patterns of density-biodiversity relationship for alpha diversity of marine nematodes and copepods in different habitats (OMZ: Oxygen Minimum Zones)



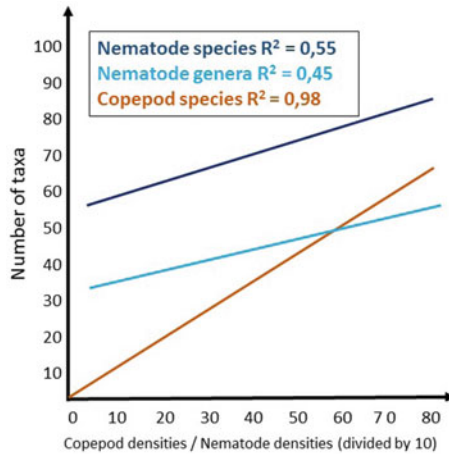


Fig. 5.3 Relationship between nematode species and nematode genera counts and densities (individuals per 10 cm²) in the abyssal NE Pacific along a particulate organic carbon (POC) gradient in the abyssal North East Pacific (based on data from Hauquier et al. 2019) combined with the relationship between copepod species versus densities from two locations (same depth) in the Angola Basin. Samples with copepod densities below 20 individuals per 10 cm² are from an extreme oligotrophic site while samples with densities above 20 individuals per 10 cm² are from a site influenced by Benguela Upwelling System (based on George et al. 2013)

Areas that have been depleted of organic matter (OM) for long periods of time, such as permanently ice-covered areas (Rose et al. 2014) or the deepest areas of shallow-water marine caves (Janssen et al. 2013; see Chap. 11), closely resemble abyssal communities in terms of low abundance and high evenness. This contrasts with cold seeps, where methane emanates from soft sediments. Its anaerobic oxidation is coupled to sulfate reduction producing high sulfide concentrations. In these reduced environments, occasionally, very high densities of a single nematode species (up to 10,000 individuals per 10 cm²) were found, such as *Halomonhystera hermesii* (originally identified as *H. disjuncta*) which was recorded on the subarctic Håkon Mosby mud volcano (Van Gaever et al. 2006; Tchesunov et al. 2014). The high bacterial production on this volcano seems to feed a single opportunistic species that is tolerant to, and even thrives in, extreme sulfidic and anoxic sedimentary conditions. However, not all seeps show the same elevated densities although diversity is in most cases reduced since only a few species seem to survive (Van Gaever et al. 2009; Pape et al. 2011). Also, sediments near shallow hydrothermal vents, such as off Milos (Greece), exhibit low diversity and the dominance of a single nematode species tolerant to the reduced sulfide-rich conditions. Although densities are not of the same magnitude as in the subarctic mud volcano, here too a single free-living marine nematode, *Oncholaimus campylocercoides*, occurred with abundances of up to 600 individuals per 10 cm² at the fringe area of the vents, coping with high sulfide concentrations and developing sulfur inclusions in the epidermis (Thiermann et al. 1994, 2000).

While some nematode species may thrive, most copepods and ostracods do not tolerate oxygen depleted sediments (see Chap. 10). Their densities in oxygen-poor sediments are generally very low, and assemblages are represented by a few species only. Copepod assemblages from seeps are often characterized by widely distributed taxa, such as species from the genus *Tisbe* which, for example, was the dominant taxon in chemosynthetic mussel beds in the Gulf of Mexico (Plum et al. 2015). In deep-sea hydrothermal vents, Gollner et al. (2015) reported decreasing copepod species diversity with increased hydrothermal activity. Noticeable is that the functional copepod diversity may increase under intense hydrothermal influence despite the seemingly challenging environmental conditions at vent sites compared to surrounding areas not influenced by vent emissions (Alfaro-Lucas et al. 2020). It is likely that local biochemical conditions and fluid flow intensity resulting from seepage or venting, in combination with the capacity of the dominant species to colonize the reduced environments, are responsible for different diversity patterns observed at different seeps and vents.

Antarctic shelves too can be characterized by very high nematode densities (> 5000 individuals per 10 cm²; Veit-Köhler et al. 2018). Depending on the local conditions, nematode assemblages comprise either a few dominant species (Ingels et al. 2006) in addition to several rare taxa or no obvious dominant taxon (Pantó et al. 2021). The availability of food and oxygen seems to drive the patterns observed (Pasotti et al. 2014), as does disturbance from past and present ice scouring (Lee et al. 2001). Moreover, when new ice-free habitats appear as a consequence of glacier and ice shelf collapses, succession can cause shifts in densities and diversity (see Chap. 9). Recently ice-free areas along the Antarctic shelf, for instance, are initially characterized by low densities of colonizing nematodes. Densities of a single or a few rapidly colonizing nematode species then increase before, often after decades, species-rich, highly abundant assemblages develop (Raes et al. 2010; Hauquier et al. 2011, 2015). This observation is in accordance with empirical studies from other habitats, recording the dominance of generalist species at an early stage of succession, followed by colonization of specialists when a diverse resource base has accumulated (Yeakel et al. 2020). The above cases illustrate some of the extreme biodiversity values in Fig. 5.2. Most environments, including sandy or muddy shelf areas, exhibit more moderate average diversity and density. Biodiversity will vary within habitats, depending on local gradients related to different environmental conditions (see Sect. 5.3).

Beta and gamma diversity of meiofauna is less well understood due to the lack of species descriptions and limited numbers of larger-scale studies. Spatial turnover is generally high between distinct habitats. Habitat heterogeneity has a strong positive effect on beta and gamma diversity, both at genus and at lower taxonomic levels (Danovaro et al. 2009; Zeppilli et al. 2011; Leduc et al. 2012a; Schratzberger and Somerfield 2020). A recent regional-scale study of soft sediment nematode communities by Liao et al. (2020), assessing the structuring roles of regional (e.g., dispersal) versus local (e.g., environmental habitat) processes, confirmed the importance of the environment as the first filter that selects a subset of species from the regional

species pool. Distance between locations seemed of lower importance for the surface-dwelling species, but when subsurface-dwelling nematodes are included in variation partitioning analyses, the importance of spatial descriptors such as geographical coordinates increases, in addition to the environmental filter (Hauquier et al. 2018).

Metabarcoding methods are being used to reduce limitations resulting from the large number of undescribed species and the unknown degree of cryptic diversity. Using HTS, Macheriotou et al. (2020) evidenced the importance of environmental filtering for nematodes in relatively homogenous abyssal sediments along a 2000 km POC gradient in the North East Pacific. In addition, sympatric speciation and affinity for overlapping habitats were suggested as important processes for diversity based on observations of aggregation and phylogenetic clustering in abyssal nematode amplicon sequence variants (ASVs).

5.4 Environment-Related Drivers of Meiofauna Diversity Patterns

Here we focus on important natural drivers of meiofauna biodiversity. What do we know about the relationship between specific environmental factors and their effect on the diversity of meiofauna taxa?

Substrate type: Sediment granulometry has been one of the most frequently evoked proxies correlating with patterns of nematode and copepod community composition. Multivariate analyses often group (or differentiate) samples based on their species and genus composition according to sediment type (Heip et al. 1985; Vanaverbeke et al. 2011; George et al. 2020). Changes in sediment characteristics are, at least partly, responsible for both nematode and copepod species turnover, because species are highly adapted to the substrate in which they live. For example, more slender copepod species dominate in sandy sediments, living in the interstices between sand grains, while adapted appendages help some copepod and even nematode species such as the members of the families Epsilonematidae and Draconematidae, to attach to hard substrates (Raes et al. 2008). In contrast to taxonomic composition and species turnover, the correlative relationship between granulometry and alpha diversity is less straightforward to explain empirically. Reviewing the wider literature on animal-sediment relationships, Snelgrove and Butman (1994) found little evidence that animal distributions are determined by any of the sediment variables derived from grain size alone. This also applies to meiofauna. Sediment-related primary drivers for biodiversity rather include biochemical processes related to oxygen supply and food input (Vanaverbeke et al. 2011). Shallow silty, organically enriched sediments are often associated with higher densities and lower meiofauna diversity due to the dominance of opportunistic species. Conversely, meiofauna species tend to be more evenly distributed in clean sands, but density is lower because of the generally lower organic matter content in those sediments. Meaningful and predictive explanations for meiofauna distributions are likely to emerge if

these are also evaluated relative to the suite of hydrodynamic and sediment transport processes that are responsible for sediment distributions. Also, offshore it seems important to investigate the physical form of the sediments (e.g., bedforms) at a range of spatiotemporal scales, including the details of the grain size distribution when aiming to provide meaningful explanations for the associations of nematodes with their sedimentary environment (Schratzberger and Larcombe 2014).

Organic matter supply and oxygen concentrations: In deep waters, nematode and copepod diversity generally increase with food availability, provided oxygen is not a limiting factor (Bianchelli et al. 2013; George et al. 2013; Hauquier et al. 2019). As shown in Fig. 5.3, both nematode genus and species numbers tend to increase with increasing food densities along a gradient of surface productivity in the North East Pacific abyss. It is likely that the general absence of opportunistic taxa in these food-limited environments prevents an overall increase in dominance, so that an increase in OM content at the seafloor is beneficial to many species. Also, copepod abundance in the abyssal study area in the South East Atlantic is mainly controlled by OM input to oxygen-rich sediments (George et al. 2013). A northern station, influenced by the Benguela upwelling system, had 5 times higher abundances and approximately 3.5 times more species than a southern station located outside the influence of the upwelling system. Remarkably, copepod evenness was only slightly (but significantly) lower in a more productive area, evidencing a clear linear relationship between abundance and diversity of copepods (at nearly constant evenness) in these well oxygenated deep-sea sediments (George et al. 2013). According to several studies, there is not a linear but a parabolic response of diversity to food availability in the deep sea. This is in accordance with the species richness energy hypothesis which suggests that both low and high food availability results in a low local or alpha meiofauna diversity (Leduc et al. 2012b). Indeed, studies from high productivity areas, such as parts of the Southern Ocean (Lins et al. 2018), documented a decrease in diversity due to the dominance of particular nematode species at locations with high food input, despite its abyssal depths. To what extent the decrease in biodiversity is determined by food supply only, or also by an associated decrease in oxygen concentrations or other factors such as shifts in species interactions, is not yet established. In eutrophic environments, oxygen limitation may favor a limited number of more opportunistic nematode species which can thrive on the available food and achieve high densities. However, highly refractory OM content in oxygen-poor sediments, as found in mud flats and mangroves, can depress both diversity and density since both variables may vary from high (Sharma et al. 2021) to very low (Cai et al. 2020). In contrast to nematodes, most other meiofauna taxa, including copepods and ostracods, are often absent or occur in very low abundance in hypoxic and anoxic sediments (Yasuhara and Irizuki 2001; Yasuhara and Yamazaki 2005; Yasuhara et al. 2012a; Yasuhara 2019). Crustaceans are much more sensitive to oxygen depletion and will decrease in density and diversity much more quickly along an oxygen gradient than nematodes (Elmgren 1975; see Chaps. 7 and 11). Neira et al. (2018) recorded a decrease of copepod densities along a gradient of oxygen depletion at the oxygen minimum zone (OMZ) off Costa Rica. No copepods were found at the site with lowest oxygen dissolved concentration (0.05 ml/L) at

400 m depth. Some Harpacticoid families like the Cletodidae, however, show some resistance to low oxygen levels, being the only family able to survive during a two months long anoxic event (Grego et al. 2014).

Temperature: Temperature is a major driver of marine biodiversity (Tittensor et al. 2010). Even in the deep sea, temperature plays an important role in controlling meiofauna biodiversity (Yasuhara et al. 2009; Yasuhara and Danovaro 2016; Jöst et al. 2019; Doi et al. 2021). Physiological tolerance drives the temperature diversity relationship, with fewer species being able to tolerate very cold temperatures (Currie et al. 2004; Yasuhara and Danovaro 2016). Paleontological and biological time series, and modern spatial distribution records of ostracods, foraminiferans, and nematodes all show significant temperature diversity relationships (Cronin and Raymo 1997; Danovaro et al. 2004; Hunt et al. 2005; Yasuhara et al. 2009, 2014; Yasuhara and Danovaro 2016; Jöst et al. 2019). A recent paleontological time series deep-sea benthic Foraminifera by Doi et al. (2021) supported the causality of temperature on diversity, suggesting a major role of bottom-water temperature. For shallow water environments where the effects of global warming are expected to be more prominent, laboratory experiments with nematodes revealed that thermal stress from elevated temperature not only affects the fitness of selected species, but also species interactions, thereby impacting species coexistence and consequently biodiversity (De Meester et al. 2015; Vafeiadou and Moens 2021). Both the amplitude and frequency of diurnal temperature fluctuations affected nematode species interactions (Vafeiadou and Moens 2021). Multiple stressor experiments also demonstrated a combined effect of acidification and warming on meiofauna and nematode structural and functional community descriptors (Meadows et al. 2015; see Chaps. 7 and 11).

Bathymetry: Rex (1973) revealed a parabolic relationship between alpha diversity and water depth for specific macrobenthic taxa such as gastropods. According to this and other studies, diversity reaches a maximum at mid-water depth between 1500 and 2000 m. Some nematode studies evidenced increasing diversity from the shelf break to mid-slope depths (Muthumbi et al. 2011), while others showed that diversity decreases from the mid-slope into abyssal depths (Gambi et al. 2010). Rex et al. (2005) suggested that low abyssal biodiversity resulted from the fact that the benthic fauna there was only a spill-over (sink) from the shallower slope fauna and not a province on its own. However, the presence of abundant nauplii, copepodites, and egg-carrying females was indicative of self-sustaining copepod populations that do not depend on spill-over of individuals from slopes to survive. The vent endemic copepod family Dirivultidae (> 65 species) also diversified in the mid-ocean ridges and not on the slopes (Gollner et al. 2010). For nematodes, biodiversity data spanning the whole bathymetric range from shelf to abyss is limited. The increase of nematode species and genus diversity with increased POC flux in the abyss up to a certain level (Fig. 5.3) is also likely the process responsible for biodiversity increases from the abyss to mid-slope depths (1500–2000 m). From mid-slope to the upper slope, depending on surface productivity, the oxygen minimum (between 1500 and 500 m water depth in general) may impinge on the seafloor which can reduce diversity at the core of the oxygen minimum area and increase the dominance of species adapted to low oxygen concentrations. Furthermore, the presence of strong selective pressures related to gradients of food and oxygen availability, in combination with predation

and competition, may have led to an increase in habitat specialization in the lower reaches of oxygen-minimum zones at about 1500 m. This may have supported an increased rate of speciation at mid-water depths (Rogers 2000) and explain the peak in biodiversity at mid-slope depths. For copepods, data on diversity-depth relationships across continuous transects from the shelf to the abyss are also currently lacking. We can only infer from the small volume of diversity-productivity data that does exist that diversity will be attenuated along a transect of increasing depth, following the productivity gradient. Remarkably, meiofauna abundance and diversity increased in several hadal trenches, as these environments act as accumulation areas for OM triggered by lateral transport (Schmidt and Martínez Arbizu 2015; Schmidt et al. 2018; see Chap. 9). Ostracods tend to show a similar parabolic depth diversity relationship. The peak of the curve is shallower in the Arctic and Nordic Seas (several hundreds of meters) than in the North Atlantic (1500–2000 m; Yasuhara et al. 2012b; Jöst et al. 2019).

Disturbance: Measures of nematode diversity have been proposed as potential indicators for disturbance (see reviews by Balsamo et al. 2012; Zeppilli et al. 2015 and Chap. 7 for further references), but such metrics are not always reliable as single indicators of stress. Different natural environmental variables strongly affect meiofauna biodiversity (see sections above), leading to disturbance-biodiversity relationships that are habitat-specific and difficult to unravel. Emerging modeling studies using artificial neural networks may provide new insights. Merckx et al. (2010) modeled both the predictability of free-living marine nematode diversity on the Belgian Continental Shelf (North Sea) as well as the environmental dynamics affecting it, using a large historical database. Reliable predictions were made for evenness and species richness, which were mainly related to the clay and sand fraction of the sediment, and the minimum annual total suspended matter. Variation in species richness was partly explained by disturbance from sand extraction and the amount of gravel of the seabed. To our knowledge, no further attempt has been undertaken to date using such modeling approaches, despite a major development in modeling tools during the last decade. Metabarcoding approaches too have the potential to help identify a baseline against which future changes in meiofauna diversity, both natural and anthropogenic in origin, can be evaluated. On the condition that reference databases are available, metabarcoding can provide a comprehensive and multi-taxon assessment of meiobenthic biodiversity while avoiding the labor-intensive sorting and expert-based morphological identification.

Salinity: Sharp transition zones along strong environmental gradients such as those caused by salinity are known as ecotones. The extent to which ecotones harbor more or fewer meiofauna species than the adjacent environments, which they are connecting, is habitat-specific. For marine nematodes, there is occasional evidence of increased taxonomic distinctness at upper sandy beaches where freshwater and marine species coexist (Gheskiere et al. 2005). Meiofauna diversity patterns along estuarine gradients are not always consistent, but river mouth areas with higher salinity generally have a higher biodiversity of most meiofauna taxa compared to the more brackish and freshwater parts (Soetaert et al. 1995; Whitfield et al. 2012; Broman et al. 2019; Horne et al. 2022). To what extent nematodes species are truly

brackish or just tolerant of decreased salinity is unclear at present. It is clear, however, that salinity can limit the dispersion of both marine and freshwater species. Understanding physiological tolerance of these species is a prerequisite to interpret biodiversity patterns along estuarine gradients (see Chap. 7). A noticeable observation was made in the Baltic Sea, where nematode genera classified as predators prevailed under more saline conditions. Network analysis demonstrated more prominent meiofauna-macrofauna associations which were correlated to the higher biodiversity of both size groups (Broman et al. 2019). However, the total number of meiofauna species in estuaries is temporally and spatially variable, and reasons for this are complex. Using eDNA data, Fais et al. (2020) revealed that intertidal meiofaunal communities in the Lima estuary (Portugal) comprised marine taxa, even under oligo- or mesohaline conditions, suggesting they went through a large adaptive effort, compared to the limnetic meiofauna.

Interaction with other ecosystem components: Larger animals belonging to macro- and megafauna affect meiofauna community composition by bioturbating and bio-irrigating the seafloor (Braeckman et al. 2011), providing habitat (Raes et al. 2008; Degen et al. 2012), grazing (Ólafsson 2003), and/or competing with meiofauna for food (Ólafsson 2003; Nascimento et al. 2011; Ingels et al. 2014). The resultant, combined effect on meiofauna diversity is challenging to ascertain. Meysman et al. (2006) suggested that bioturbation increases the number of habitable niches and the variety of food sources, resulting in higher meiofauna diversity. Recently developed ecological models for larger fauna supported the idea that ecological engineers may enhance community diversity by facilitating colonization and limiting competitive exclusion (Yeakel et al. 2020). To what extent this is applicable to meiofauna is not yet clear. The benthic environment harbors different size classes and is continuously reshaped by larger organisms interacting with their smaller co-inhabitants. Interesting in this context are results from microcosm experiments investigating the effect of meiofauna and their activities on sediment properties and inter- and intraspecific interactions of sediment-dwelling fauna. For example, Piot et al. (2013) found that in the presence of a natural meiofauna community, the interactions between macrofaunal species changed, which subsequently led to modifications of ecosystem properties such as oxygen and nutrient fluxes in the sediment but also microbial abundances.

5.5 The Function of Meiofauna Biodiversity

Positive relationships between nematode biodiversity and benthic prokaryotic activity as a proxy for ecosystem functions in deep-sea sediments suggested that marine diversity loss could have adverse effects on ecosystem functioning (Danovaro et al. 2008; Pusceddu et al. 2014). To what extent these relationships are causal rather than due to other, confounding variables, or are a consequence of reverse causation, remains unclear and requires further experimental testing. However, manipulating the biodiversity of microscopically small organisms in a laboratory approach is not

a sinecure. Bonaglia et al. (2014) controlled meiofauna abundances and biodiversity in laboratory microcosms and measured resultant effects on sediment biochemistry. Interactions between meio-, macrofauna and bacteria contributed significantly to the nitrogen cycling in soft sediments. However, the role of biodiversity versus abundance was not disentangled in this experiment. Other experiments also evidenced the effects of meiofauna abundance on specific aspects of ecosystem functioning such as oxygenation of hypoxic sediments and sulfide removal, although the effects of biodiversity were less clear (Bonaglia et al. 2020; see Chap. 2). Mathieu et al. (2007) showed that the activity of nematodes enhanced the net productivity of diatom biofilms, while natural meiofauna communities enhanced the mineralization of organic matter in another experimental setup (Nascimento et al. 2012). Schratzberger and Ingels (2018) reviewed the role of meiofaunal activities in regulating ecosystem processes that provide or support ecosystem services. While empirical evidence is growing on the importance of meiofauna, the specific role of diversity remains a critical knowledge gap. Interesting is the observation that not only biodiversity, but even more so the presence of specific functional traits appears to be crucial for maintaining specific ecosystem functions.

5.6 Looking into the Past to Understand the Future: Fossil Records

Studying temporal variation in marine benthic communities requires continuous and regular sampling. Consequently, long-term studies on benthos including meiofauna are rare (Kitazato et al. 2000; Danovaro et al. 2004; Ruhl et al. 2008; Smith et al. 2009). Currently, the only way to explore temporal variation beyond decadal time scales is by using fossil records. Meiofaunal foraminifera and ostracods are the only groups that have hard, mainly calcareous parts (i.e., shells) that are fossilized and provide good fossil records. In the deep sea, ostracod and foraminiferal fossil diversity changes in accordance with climatic change (Cronin and Raymo 1997; Hunt et al. 2005; Yasuhara and Cronin 2008; Yasuhara et al. 2009, 2014; Doi et al. 2021). Species diversity is generally higher during warmer periods on 10^2 to 10^4 time scales (Yasuhara and Cronin 2008; Yasuhara and Danovaro 2016). Global climate and deep-sea biodiversity curves are remarkably similar on glacial-interglacial time scales, indicating a climatic control of deep-sea biodiversity (Fig. 5.4; Yasuhara et al. 2009). Major climatic events affect meiofauna diversity. There is increasing evidence that the Mid-Brunhes Event (MBE; a major climatic mode shift at approximately 400 to 350 thousand years ago) has affected deep-sea ecosystems substantially, especially in marginal seas such as the Arctic and the Sea of Japan (DeNinno et al. 2015; Cronin et al. 2017; Huang et al. 2018, 2019). In contrast to the majority of marine species, deep-sea benthic foraminifera did not have a major extinction at the Cretaceous/Paleocene (K/Pg) boundary (D'Hondt 2005). Mass extinction of marine

foraminifera occurred in the Paleocene-Eocene Thermal Maximum (PETM: approximately 55.5 million years ago; Thomas 2007) during the Cenozoic. An extinction event of certain deep-sea foraminiferan taxa is also known for the Mid-Pleistocene Transition (MPT: approximately 1.2–0.55 million years ago; Hayward et al. 2007). Evidence from bathyal and abyssal foraminiferan fossils indicates that the origin of a latitudinal diversity gradient was at approximately 37 million years ago (Thomas and Gooday 1996; Stuart et al. 2003; Yasuhara et al. 2020). Because of high sedimentation rates in marginal marine environments, highly resolved young meiofaunal fossil records are available, allowing us even to depict the effects of anthropogenic activities. For example, in Osaka Bay and the Gulf of Mexico, man-induced eutrophication and its associated deoxygenation via urbanization and industrialization caused a substantial diversity and/or abundance decline of benthic foraminifera and ostracods (Rabalais et al. 2007; Yasuhara et al. 2007, 2012b, 2019; Tsujimoto et al. 2008; Pitcher et al. 2021).

Recent extensive benthic foraminiferal research resulted in a synthetic Cenozoic paleobiogeographic framework known as the Hopping Hotspots Model (Renema et al. 2008), suggesting that the biodiversity hotspot has moved through the Cenozoic. During the Eocene, highest diversity occurred in the western Tethys (present Mediterranean). Then, the hotspot shifted to the Arabian region from the late Eocene through the Oligocene. By the mid-Miocene, both hotspots had collapsed, the Indo-Australian Archipelago (IAA) hotspot in the southeastern Asian (aka Coral Triangle) emerged and remains until today. Some ostracod data are consistent with this model (Yasuhara et al. 2017a; Shin et al. 2019). Although further data and studies are needed, meiobenthic ostracods and foraminiferans help to understand deep-time diversity and biogeography dynamics by taking advantage of their excellent (i.e., continuous and high abundance) fossil records.

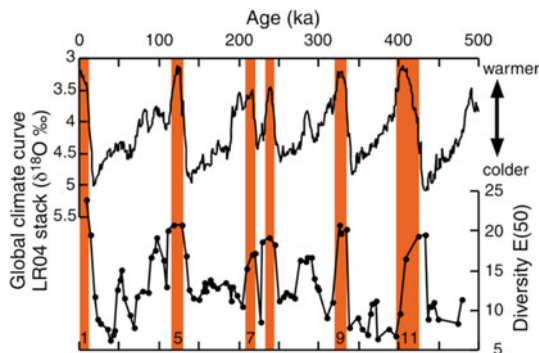


Fig. 5.4 Global paleoclimate (top: oxygen isotope; Lisiecki and Raymo 2005 versus deep-sea ostracod species diversity; bottom: as a standardized diversity measure, rarefaction E(50)) in the Atlantic Ocean. Note the remarkable similarity between global climate and deep-sea diversity curves. Orange areas indicate peak interglacials (warm climate peaks). Modified after Yasuhara et al. (2009)

5.7 Biogeography of Meiofauna: Hypotheses and Evidence

The degree to which meiofauna biodiversity differs between oceans and seas is largely unknown. The lack of biodiversity estimates at species level hampers comparisons of alpha diversity, while the general lack of species descriptions (Appeltans et al. 2012) hampers comparisons of beta and gamma diversity across oceans and seas. Also, latitudinal trends in biodiversity of nematodes are not always straightforward to establish and interpret (Danovaro et al. 2009; Gambi et al. 2010), not even at higher taxonomic levels (Kotwicki et al. 2005). A meta-analysis by Hillebrand (2004) revealed only weak geographical gradients for Nematelminthes, mainly represented by nematodes. Also, Gobin and Warwick (2006) found that nematode species colonizing artificial hard substrates did not show a trend based on latitude, as diversity was similar for the northern and southern temperate and the tropical areas under investigation. However, in contrast to these shallow water studies, counts of nematode species in the abyssal North Atlantic increased with latitude between 13 to 56°N and were related to the productivity gradient in the North Atlantic (Lamshead et al. 2000). Both, ostracods and foraminiferans show standard latitudinal diversity gradients in shallow-marine and deep-sea systems (Culver and Buzas 2000; Buzas et al. 2002; Yasuhara et al. 2009; Jöst et al. 2019; Chiu et al. 2020). Marginal seas (e.g., Arctic Ocean) tend to lack certain faunal elements (DeNinno et al. 2015). Shallow marine ostracods have more genus-level endemism among oceans and seas compared to largely cosmopolitan deep-sea ostracod genera.

Since the early days of marine research, it has been acknowledged that many of the small benthic organisms are surprisingly widespread, even to the extent that biogeographical patterns seem absent (Costello et al. 2017; Fontaneto 2019). This observation is commensurate with the ubiquity hypothesis or among meiobenthologists known as the meiofauna paradox: despite their low mobility and their lack of planktonic larval stages, microscopic benthic organisms are often cosmopolitan. Now, we know that there is a wide variety of meiobenthic distribution patterns, ranging from cosmopolitan to endemic. We also know that, depending on specific morphological and life history characteristics, meiobenthic species disperse to varying degrees. According to Fontaneto (2019), important traits for long-distance dispersal in small organisms include dormancy capability, long-term resistance of dormant stages, and the ability to colonize new habitat rapidly. The meiobenthic sized annelid *Dinophilus vorticoides* is a widely distributed species, which lives buried in sediments and lacks pelagic larvae. However, it is also found on macroalgae and ice, likely surviving by forming dormant encystment stages during long-distance rafting (Worsaae et al. 2019). Previously presumed mechanisms for passive transport of meiofauna are now supported by empirical evidence, including resuspension and drifting in the water column, attachment to other fauna (e.g., turtle shells) and flora (e.g., drifting algae), and even survival as aeroplankton (Corrêa et al. 2013; Ptatscheck et al. 2018; Buys et al. 2021). For instance, an unexpectedly dense epibiont community was observed on the back of loggerhead turtles migrating over large distances for reproduction and feeding (Ingels et al. 2020a). Considering the evolutionary age

of the taxa involved, dispersal of meiobenthic taxa through turtles is very likely contributing to the cosmopolitan distribution of meiobenthos (Corrêa et al. 2013).

Studying harpacticoid copepods belonging to the deep-sea family Argestidae, Menzel et al. (2011) sampled 113 stations across 12 abyssal regions. They found that many species had a long-range distribution across the Atlantic Ocean and that submarine ridges were not a barrier for dispersal. Pointner et al. (2013) found the same species of deep-sea Paramesochridae distributed in the Atlantic and Pacific abyssal plains.

In addition to limited knowledge on dispersal of meiobenthic taxa, there is also a lack of information on genetic structuring of populations. Given the originally presumed limited dispersal capacity of marine nematodes, prominent genetic differentiation between geographically isolated species was expected previously. However, shared haplotypes and multiple admixture events (when previously diverged or isolated genetic lineages mix) in the population of a *Sabatieria* species (Nematoda) at several widely separated cold seeps in the East Mediterranean revealed gene flow, most likely facilitated by water current transport of individuals and/or eggs (De Groot et al. 2017). In contrast, in the Southern Ocean off the Weddell Sea, gene flow between *Sabatieria* populations and *Desmodora* species was restricted at large geographic distances, questioning the efficiency of transport via currents (Hauquier et al. 2017). However, genetic structuring differed between nematode species from the same geographic area, but with different habitat preferences. Nematodes from surface sediments had a different population genetic structure than those from the deeper layers with the latter exhibiting more complex haplotype networks.

Also, cryptic species are found among several meiofauna groups including not only nematodes and copepods but also nemertean (Leasi and Norenburg 2014), turbellarians (Tessens et al. 2021) gastrotrichs (Todaro et al. 1996, but Kieneke et al. 2012), and even microscopically small sea slugs (Jörger et al. 2012). Derycke et al. (2016) reported the sympatric occurrence of cryptic nematode species. The coexistence of different bacterivorous cryptic species of the nematode species complex *Rhabditis (Pellioiditis) marina* was explained by substantial differences in their associated microbiomes and feeding strategies (Derycke et al. 2016). Their performance in combined cultures was compared with that in monospecific cultures at two different salinities, showing that three of the four cryptic species were able to coexist. Salinity had an effect on their interactions, suggesting that abiotic conditions may play an important role in facilitating coexistence between cryptic nematode species and can alter the interspecific interactions between them (De Meester et al. 2011).

5.8 The Future of Meiofauna Biogeography and Biodiversity Research: Gaps in Our Knowledge and Research Frontiers

Biogeography is a multifaceted, multidisciplinary field of study aimed at answering two fundamental questions in science: *How and why are organisms distributed as they are on Earth?* (Wen et al. 2013). Addressing these questions from the perspective of meiobenthology is challenging, not only because of the animals' small size and their seemingly wide geographical distribution, but also because many questions concerning the systematics, ecology, and paleontology of meiofauna remain unanswered (see previous sections of this chapter). Yet, meiofauna diversity and biogeography offer many dynamic areas of research and inquiry for future generations of meiobenthologists.

The chapters comprising this book have emphasized the importance of meiofauna as an integral part of marine benthic ecosystems. Although they are not currently considered a major component in food web models in terms of metabolic activity and carbon flow (Gontikaki et al. 2011; Braeckman et al. 2013), their ubiquitous distribution across the globe, their high taxonomic and functional diversity and proven interaction with mega- and macrofauna, and microbiota makes them a non-negligible component of multidisciplinary marine biodiversity research (see Ingels et al. 2020b as a reply to Danovaro et al. 2020). Furthermore, several meiofauna taxa act as excellent model organisms both for experimental research and for modeling approaches to understand fundamental drivers and consequences of biodiversity change.

Many questions in meiofauna diversity and biogeography remain unanswered, offering horizons for future research and posing challenges for rapidly developing methodology. Most frontiers pertain to the difficulty of generating sufficiently large volumes of reliable distributional, genetic, and phylogenetic meiofauna data:

- ***Overcoming taxonomic challenges:***

A critical knowledge gap in biodiversity and biogeography research on meiofauna currently is information on the distribution of species, the degree of turnover, population connectivity, and understanding the diversification process. This is mainly due to the identification burden which is, when centered on morphology, time-consuming and expert-based, and therefore not always feasible, affordable, or indeed reliable. Finding rapid, and at the same time standardized and sound, tools for estimating biodiversity at relevant spatial and temporal scales is essential. HTS is offering that first step but still requires a critical and cautious approach. Developing new investigation methods and standardizing them is still ongoing and needs further investments to optimize protocols and validate different techniques. Furthermore, not all questions can be answered with HTS, so training taxonomists with the necessary morphology-based skills remains a necessity for the future. Artificial Intelligence and machine learning may have a role to play in making taxonomy less dependent on the expertise of a limited (and declining) number of

taxonomists. By automatizing taxonomic identification through pattern recognition technologies, biodiversity research could become more accessible (MacLeod et al. 2010). The development of automated identification systems that are robust and reliable will take time, however, as has been shown in plankton research (Pastore et al. 2020).

- ***Overcoming analytical challenges:***

In the next decade, data analytical challenges are emerging as a result of increasing volumes of occurrence data and phylogenetic information. Even for extreme and remote environments, such as trenches and polar seas, access to samples and biodiversity data is growing. Fortunately, data sharing is being facilitated through research financiers, journals, and easy to access data platforms (e.g., Genbank, Barcode of Life Data Systems BOLD, Ocean Biodiversity Information System OBIS, World Register of Marine Species WORMS). It seems inevitable that data mining methods will become essential tools for future biogeographic research of meiofauna. The processes involved are not yet perfect due to the lack of standardization and sound quality control of data. Meiofauna phylogenies are increasing in size, and taxonomic breadth and new sequencing techniques generate increasingly vast phylogenetic datasets, yet tools for data mining and integrated analyses of meiofauna are in their infancy. Most existing parametric statistical approaches will need to be improved or developed to handle large and more complex meiofauna data. The need for input from computer scientists is becoming more urgent. As access to reliable big datasets is being ensured, innovative approaches to the study of meiofauna diversity and biography should allow to answer a whole range of crucial research questions beyond the specific meiofauna interest (see below).

- ***The continued search for general patterns of meiofauna diversity and biography:***

This is particularly challenging because of the tendency of diverse taxa responding differentially to local environmental conditions at varying scales of space and time. Meiofauna biodiversity and biogeography will undoubtedly become an increasingly multidisciplinary and integrative endeavor and become more closely linked to conservation biology (see concluding paragraph below). The current loss of biodiversity causes dramatic changes in the spatial distributions of many species, but the contribution of meiofauna to these global trends remains poorly understood and quantified. Many contemporary drivers of biodiversity change are also recognized as having driven such changes in the past. Therefore, paleobiological investigations reconstructing biogeographic patterns of meiofauna over geological time scales from their fossil records have been increasing steadily. This line of research should be further pursued, given the fact that fossils are the only direct evidence to understand the past biodiversity beyond biological monitoring of a few decades. Paleobiodiversity reconstruction across spatial and temporal scales,

using proxy records of paleoenvironment and paleoclimate (such as paleotemperature), will help our understanding of past, present, and future biodiversity and their drivers (Yasuhara et al. 2017b, 2019, 2008). Evidence generated from studies of contemporary and fossil meiofauna will provide the empirical underpinning for predictive models of biodiversity change to address questions including:

- Where are the highest/lowest levels of meiofauna diversity and what factors drive the patterns observed?
- Why are some meiofauna taxa found in certain locations and not others, and what are the processes that generate the patterns in their distribution?
- How have biogeographic patterns of meiofauna been altered in the past, and how are they likely to be altered under various future scenarios?
- Where are changes in meiofauna diversity most pronounced and why?

However, not only the access to large biodiversity datasets is a priority. The use of micro- and mesocosms under controlled conditions is providing us with crucial insights into the interactions of meiofauna with microbiota and macrofauna, while demonstrating the importance of their biodiversity for ecosystem functions such as primary production and mineralization. This kind of experiments would provide further evidence for the consequences of biodiversity loss and natural habitat degradation, and at the same time support the adjustments of model outputs to more realistic descriptions and predictions.

We cannot make meaningful decisions about the conservation of marine life if we do not know what species are where and why. It is clear that meiofauna has a role to play in the discovery and conservation of biodiversity. To some extent, predictive modeling can anticipate the expected impacts of natural and anthropogenic disturbance on seafloor functions coupled to meiofauna biodiversity. Uhlenkott et al. (2020a, b), for example, used random forest models to predict the meiofauna abundance and diversity across the whole German polymetallic nodule contract area in the abyssal Northeast Pacific. They were able to test the suitability of Preservation and Impact Reference Zones that will help in assessing the impacts of future deep-sea mining. Lessons learned from future meiofauna studies need to be applied not only to discover previously unknown species and report their distributions, but to put those findings into a broader ecosystem context. Only then can global biodiversity dynamics be understood in a more holistic, integrated, and consequently more meaningful way.

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