



Marine connectivity dynamics: clarifying cosmopolitan distributions of marine interstitial invertebrates and the meiofauna paradox

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Received: 25 September 2017 / Accepted: 2 July 2018 / Published online: 10 July 2018
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Abstract

Many interstitial species were first described as widely distributed, often cosmopolitan or amphi-oceanic, contrasting with descriptions of a sedentary life style and the general absence of pelagic dispersal stages. These inconsistencies became known as the “meiofauna paradox”. In this review, we present a literature review investigating these inconsistencies and address the assumptions of the meiofauna paradox. We break the paradox down to two aspects including species distribution and dispersal. Focusing on distribution, we demonstrate that wide distributions are seldom given and false records likely stem from biological phenomena like stasis or recent speciation. These phenomena account for morphological similarity, ultimately represented by the pronounced occurrence of cryptic species with restricted distribution ranges. Additionally, taxonomic artefacts such as the erroneous application of taxonomic keys contribute to the report of widely distributed species. Considering dispersal, we point out the mismatch between traditional assumptions of meiofaunal sedentarism and growing experimental and empirical evidences suggesting higher dispersal potential. These evidences include not only indications for dispersal by pelagic stages, but further consider ecological and life-history traits in shaping distribution ranges. We conclude that the meiofauna paradox *sensu stricto* most likely does not exist and provide a roadmap for future research, suggesting a focus on morphological similarity and marine connectivity. Meiofaunal research should concentrate on evolutionary factors resulting in morphological similarity, improving the taxonomic resolution of species complexes and conducting more sophisticated experimental experiments to meiofaunal dispersal. In all cases, meiofaunal research will benefit from high-throughput sequencing such as genome scanning approaches, metagenomics or metatranscriptomics.

Introduction

Few environments would seem more homogeneous and lifeless than an extensive area of sandy sediments. Accordingly, the interstitium or the space between the sand grains was overlooked as a potential source of biological diversity for

a long time. The first meiofaunal organisms were described in the 19th century (e.g., Lovén 1844; Dujardin 1851) and while this diversity was recognized it was not further considered (Giard 1904). The first naturalist who began to uncover this diversity was Remane (1933). He studied the fauna of the so-called coastal groundwater of sandy beaches by digging holes into the sand and collecting floating animals from the accumulating brackish ground water using small landing nets—the common collecting method in those times. Thus, owing to an error-prone sampling strategy, meiofauna organisms were assumed to only inhabit the groundwater. Later on, evidence accumulated suggesting that these organisms in fact inhabited the spaces between the sand grains in areas of moist sand and that the coastal groundwater itself only contained very few individuals, if any. These new findings initiated an intensive phase in meiofaunal research, leading to thousands of publications in many fields of zoology (for reviews see Higgins and Thiel 1988; Giere 2009) and uncovered an astonishing diversity, whereby a mere teaspoon of marine sediment or of sand in a beach could yield a

Responsible Editor: S. Connell.

Reviewed by Undisclosed experts.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s00227-018-3383-2>) contains supplementary material, which is available to authorized users.

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bewildering biological diversity (Fig. 1; Fenchel 1978; Giere 2009). Today we know that marine sediments anywhere in between the supralittoral to the deep sea are inhabited by a considerably diverse meiofaunal diversity. The fauna living in the space between sand grains is also generally known as interstitial fauna (Giere 2009), and the terms meiofauna and interstitial species are often used synonymously in the literature. In this way, although officially classified by sizes passing through sieves ranging from 22–44 μm to 500–1000 μm (Giere 2009; Zeppilli et al. 2015), these ranges represent just a convenient (yet arbitrary) definition. For instance, several interstitial species are considerably larger than 1000 μm such as the well-known annelid *Polygordius* and hence, strictly spoken, do not belong to the meiofauna. On the other hand, some meiofauna are not strictly interstitial, as they burrow through the sediment due to the small open space available. They are nonetheless referred to as interstitial (e.g., some *Nerillidae* species (Annelida) living in muddy sediments). In this review, we concentrate on both marine meiofaunal and interstitial species and consider them synonymously as it is the case in the literature. In the following sections, we refer to them as meiofauna for consistency with the literature, where this term is more commonly used than interstitial.

Out of the approximately 34 metazoan phyla, 23 have at least some meiofaunal representatives, and four, namely Gnathostomulida, Kinorhyncha, Loricifera and Micrognathozoa, are exclusively meiofaunal (Fenchel 1978; Sands et al. 2008; Giere 2009; Zeppilli et al. 2015; Figs. 1a–r, 2), but so far, no marine representatives are known for Micrognathozoa. Meiofauna is usually considered as an independent ecological evolutionary unit (Giere 2009) and its adaptation to the spatially restricted interstitial environment is the group's most prominent and distinctive feature. Indeed, the meiofauna's unique type of form has been coined the "meiofaunal syndrome" (Brenzinger et al. 2013; Jörger et al. 2014), which is generally characterized by an uniform, elongated, worm-like body shape and usually simplified external organization with adhesive structures for attachment to sand grains (Giere 2009). Hence generally, on first sight their appearance seems often to be that of simple-bodied organisms.

The combination of small size and the absence of pelagic larvae in some species have led meiofauna biologists to describe these organisms as sedentary (i.e., limited dispersal capacities) and to suggest severely restricted distribution rates (Giere 2009). At the same time, a substantial number of species were described with distribution ranges encompassing whole continental coast lines, amphioceanic, or even cosmopolitan (Sterrer 1973; Gerlach 1977; Westheide 1977, 2005; Westheide and Rieger 1987; Giere 2009; Jörger et al. 2012). This contradiction became known as the "meiofauna paradox" (Sterrer 1973; Gerlach 1977; Westheide 1977; Boeckner et al. 2009; Giere 2009). Several

alternative dispersal hypotheses were suggested to account for this inconsistency. For instance, dispersal models considering either stepping stone, or infrequent occasions of long-distance transport of a few individuals (such as bird-mediated dispersal, rafting on drifting material or recent accidental dispersal by humans) were suggested (Gerlach 1977; Westheide 1991; von Soosten et al. 1998). Alternatively, vicariance-driven hypotheses focusing on Pangea's division and subsequent continental drift (i.e., successive vicariance events) have been put forward to account for the meiofauna paradox (Sterrer 1973). Part of this discussion considers vicariance and dispersal as mutually exclusive. Following Giere (2009), this paradox can be summarized into two questions: (1) "Why are so many meiofaunal taxa from distant areas so similar despite their limited means of dispersal?" and (2) "How can meiofauna have bridged oceans and occupied distinct shores in the absence of large populations and competitive propagative stages?"

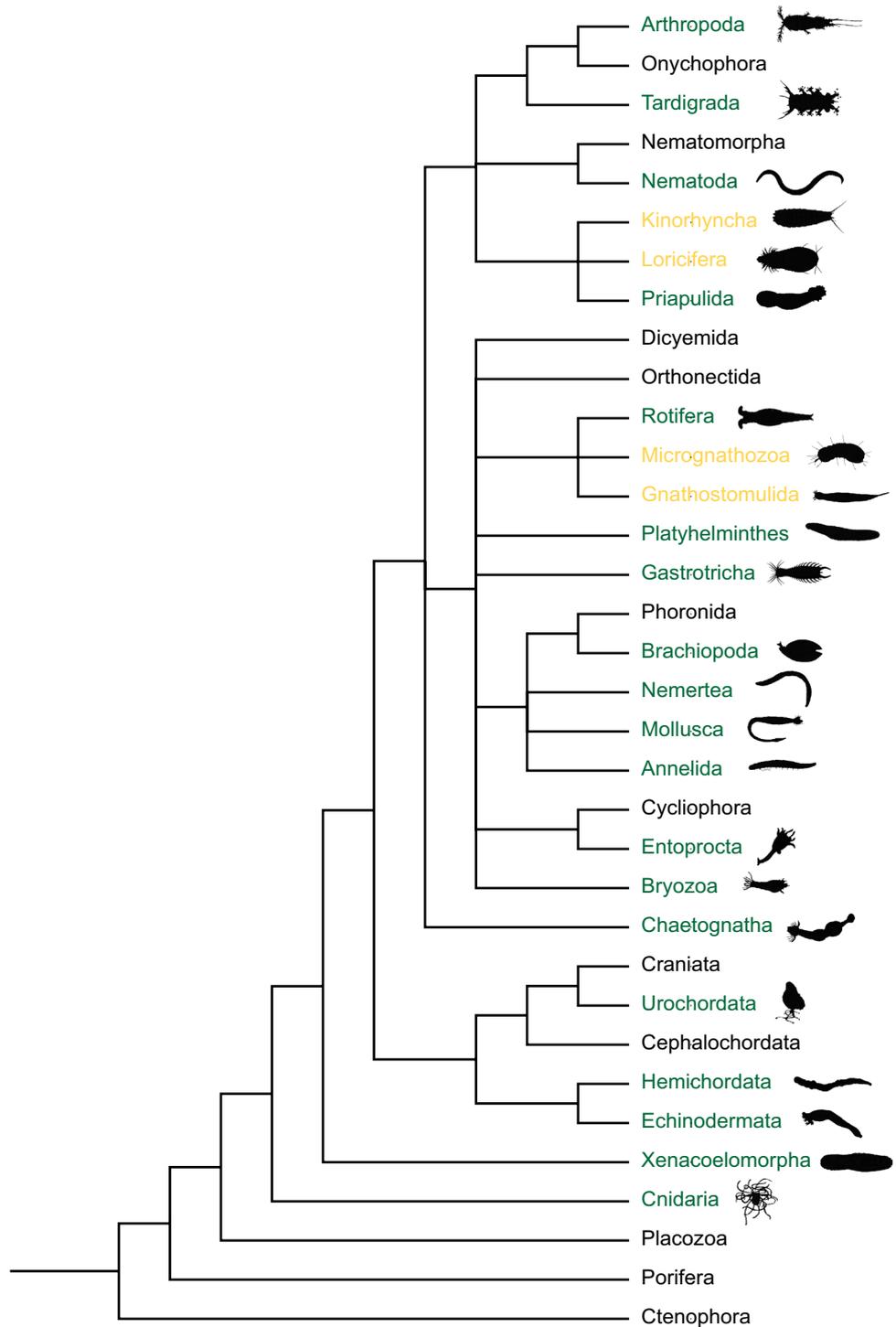
In this review of the meiofauna paradox, we present a literature survey focusing on distribution ranges and meiofaunal dispersal and how these contribute to a modern understanding of this paradox. We consider marine metazoan species from beach shores to the deep sea. Additionally, we consider the distribution range of a species as the geographic area within which a species has genetic cohesiveness is maintained by gene flow (Klautau et al. 1999). Having Giere's (2009) questions in mind, we address this paradox into two slightly more general questions both relating to dispersal and distribution range of meiofauna species. First, we ask: "Why are so many meiofaunal taxa from distant areas so similar?". We reframe this question considering that morphological similarity across wide distribution ranges might not hinge only upon dispersal capacity, but also on other biological phenomena, as well as non-biological aspects like observers' bias. By tackling morphological similarity, we discuss that distribution ranges are often inflated as a synergistic by-product of taxonomic challenges, sampling biases and the occurrence of cryptic species. Second, we address "How can meiofauna have bridged oceans and occupied distinct shores in the absence of propagative stages?". Meiofaunal population sizes are largely unknown as their local distribution is often patchy and possibly subject to enhanced extinction–colonization dynamics (i.e., metapopulation dynamics) and hence it cannot be determined if large populations are present. Moreover, dispersal over long distances does not depend exclusively on large populations. Considering this question, we address the disparity between historical literature on dispersal and vicariance and the recent experimental and empirical evidence of meiofauna dispersal. We demonstrate that both our empirical and experimental knowledge about meiofauna dispersal is still relatively limited for general conclusions. Based on these evidences, we conclude that the meiofauna paradox in the strict sense most



Fig. 1 Meiofauna diversity shown by examples from a variety of higher taxa. Light micrographs from living animals, originals. **a** Cnidaria: *Halammohydra octopodides* Remane, 1927 (Hydrozoa). **b** Xenacoelomorpha: *Symsagittifera roscoffensis* (Graff, 1891) (Acoela, Bursalia). **c–f** Ecdysozoa. **c** *Metepsilonema hagmeieri* (Stauffer, 1924) (Cycloneuralia, Nematoda, Chromadorea). **d** An undetermined Kinorhynch (Cycloneuralia, Kinorhyncha). **e** *Batillipes mirus* Richters, 1909 (Tardigrada, Heterotardigrada). **f** *Halacarellus subterraneus* Schulz, 1933 (Arthropoda, Chelicerata, Acari). **g–r** Spiralia. **g** *Turbanella* sp. Schultze, 1853 (Gastrotricha, Macrodasysida). **h** *Dactylopodola baltica* (Remane, 1926) (Gastrotricha, Macrodasysida). **i** *Proschizorhynchus gullmarensis* Karling, 1950 (Platyhelminthes,

Neophora, Kalyptorhynchia). **k–r** Lophotrochozoa. *Prostomatella arenicola* Friedrich, 1935 (Nemertini, Monostylifera). **l** undescribed *Pholidoskepia*. **m** *Microhedyle glandulifera* (Kowalevsky, 1901) (Mollusca, Gastropoda, Opisthobranchia). **n** *Trilobodrilus axi* Westheide, 1967 (Annelida, Sedentaria, Orbiniidae). **o** *Stygocapitiella subterranea* Knöllner, 1934 (Annelida, Sedentaria, Orbiniidae). **p** *Hesionides arenaria* Friedrich, 1937 (Annelida, Errantia, Phyllococida). **q** *Protodriloides chaetifer* (Remane, 1926) (Annelida, Errantia, Protodrilida). **r** *Nerilla antennata* Schmidt, 1848 (Annelida, Errantia). Scales in **a, b, f, i, m, n, o, p** 250 μm ; in **c, d, e, g, h, l** 100 μm ; in **k, q, r** 500 μm

Fig. 2 Meiofaunal representatives across the animal phylogeny. Clades with meiofaunal representatives are highlighted in green. Exclusively meiofaunal clades are highlighted in yellow. Tree topology reproduced after Dunn et al. (2014)



likely does not exist and provide a roadmap for future directions of research on meiofauna dispersal and distribution.

Literature survey: description and general results

On June 6, 2018 we searched ISI Web of Science using the following combination of search terms: “(meiofauna* OR meiobenth* OR Gnathostomulida OR Kinorhyncha OR Loricifera) AND (marine OR Atlantic OR Pacific OR

Indian OR Arctic OR Antarctic OR “Southern Ocean”) AND (molecular OR cryptic OR paradox OR taxonom* OR dispersal OR phylo* OR biogeo* OR distribut*)”. This search yielded 1069 publications. While we were unable to obtain 16 articles mostly due to the presence of paywalls and indexed meeting abstracts on ISI, we assessed the abstracts and results of the remaining 1053 (Supplementary Table 1). After this preliminary assessment, we excluded 302 publications because they did not focus on marine, metazoan or meiofaunal organisms or they were not written in English (for a through list of criteria see Supplementary Material). The remaining 751 contributions were scored for taxa, discipline, use of molecular or morphological methods, occurrence of cryptic and pseudocryptic species, geographical location including depth and habitat description, as well as if there was an experimental approach to test for meiofauna dispersal (for a complete list of scoring criteria see Supplementary Material).

The majority of the captured papers corresponded to taxonomic (235) or ecological studies (488; Table 1). Surprisingly, only seven studies focused specifically on the evolution of meiofaunal species (one on Annelida, two on Arthropoda, two on Kinorhyncha, one on Nematoda and one on Platyhelminthes; Table 1). Herein, we consider publications as “evolution” in the strict sense of the discipline “Evolutionary Biology” by focusing on understanding evolutionary processes such as speciation and on population genetics (i.e., performing explicit tests of demography and gene flow). This allows us to differentiate these publications from studies of other disciplines like taxonomy or systematics also addressing the species’ evolution. Similarly, development (12 papers), physiology (15) and palaeontology (4) were also underrepresented. Most studies focused on nematodes and arthropods, primarily harpacticoid copepods (Table 1), reflecting their overall abundance and their availability as ecological indicators (407 out of 447 papers dealing with nematodes and 303 out of 357 of the studies on Arthropoda were ecological studies).

The uneven representation of arthropods and nematodes is not as pronounced in taxonomy or biogeography as in ecological research. In total, 48 studies focused on biogeography and 235 focused on taxonomy (Table 1). This survey was unable to detect any taxonomic or biogeographical study focusing on Chaetognatha or Echinodermata. Most taxonomic studies were performed in Arthropoda (46), Gastrotricha (50), Kinorhyncha (26), Nematoda (39), Platyhelminthes (23) and Tardigrada (21). Studies in biogeography included Annelida (7), Arthropoda (15), Chordata (1), Cnidaria (2), Gastrotricha (6), Gnathostomulida (1), Kinorhyncha (3), Loricifera (1), Mollusca (2), Nematoda (13), Nemertea (3), Platyhelminthes (5), Rotifera (3), Tardigrada (2) and Xenacoelomorpha (2). Most of the studies were performed around European (327), North and Central American (157)

and Asian (141) coastlines and waters. Coastlines and waters adjacent to Antarctica (35), Africa (54), Australia (51) and South America (75) are less well-studied. Regarding depth distribution, 359 papers focused on shallow-subtidal to a depth of 200 metres, 212 focused on the deep sea (below 200 m) and 202 intertidal areas. In contrast, only 14 studies investigated species from supralittoral areas (Table 1).

Most taxonomical studies described new species (135), while relatively few, often only implicitly, reported on the distribution range of meiofaunal species (Table 2). Of these, 40 papers reported an unchanged distribution of some of the focal taxa (accounting for 82 species), 25 reported an increase of distribution (including 112 species) and 22 a decrease of distribution (including 160 species). Only 27 papers used a combination of molecular and morphological data to assess species delineation (Todaro et al. 1996, 2014; Curini-Galletti and Puccinelli 1998; Westheide and Hass-Cordes 2001; De Ley et al. 2005; Sterrer and Sørensen 2006; Suatoni et al. 2006; Leasi and Todaro 2007; Casu et al. 2009; Neusser et al. 2011; Eder et al. 2011; Kieneke et al. 2012; Jörger et al. 2012; Leasi et al. 2013; Jörger and Schrödl 2013; Rundell and Leander 2014; Di Domenico et al. 2014; Kånneby et al. 2015; Smythe 2015; Dal Zotto 2015; Kajihara et al. 2015; Karanovic et al. 2016; Sánchez et al. 2016; Tanaka and Ohtsuka 2016; Kieneke and Nikoukar 2017; Atherton and Jondelius 2018; Van Steenkiste et al. 2018), with 16 additional papers using molecular data only (Schmidt and Westheide 2000; Bhadury et al. 2006; Todaro et al. 2006; Casu and Curini-Galletti 2006; Bik et al. 2010, 2012; Gruber-Vodicka et al. 2011; Tulchinsky et al. 2012; Baldrighi et al. 2013; Yamasaki et al. 2014; Fonseca et al. 2014; Leasi and Norenburg 2014, 2016; Meyer-Wachsmuth et al. 2014; Scarpa et al. 2015; Sahraean et al. 2017). Moreover, 14 papers mentioned difficulties in morphological characterization of the considered taxa (we refer to this issue as the low-morphology problem, see below). The occurrence of cryptic or pseudocryptic species was reported in 32 papers. Finally, only 25 studies performed experimental approaches to understand meiofaunal dispersal (Supplementary Table 2).

These results point to several trends in meiofaunal research. European, North and Central American and Asian coastlines are the most well-studied, potentially as an outcome from scientific traditions in these continents. Additionally, deep-sea research is well-represented with about 20% of the works focusing on this area, yet the majority of works was still done on shallow-subtidal areas (from low-water line to 200 metres depth). Taxonomy and ecology are the most vibrant disciplines in meiofaunal works. The potential skew towards Nematoda and Arthropoda research is most pronounced in ecological surveys, while Gastrotricha, Kinorhyncha, Platyhelminthes, and Tardigrada are especially well-represented in taxonomy. Moreover,

Table 1 Number of scored papers per taxon in the literature survey

| Taxon | Total number of papers | Discipline | | | | | Study area | | | | | Depth distribution | | | | | | | | | |
|-----------------|------------------------|------------|------------|----------------|-----------|--------------|--------------|--------------|------------------------|-----------------|--------|--------------------|------|------------|--------|---------------------------|----------------|----------------|---------------|---------------------------------------|-------------------|
| | | Ecol-ogy | Evo-lution | Bio-geog-raphy | Tax-onomy | Devel-opment | Phys-i-ology | Phys-i-ology | Review or per-spective | Pal-aeon-tology | Africa | Ant-arc-tica | Asia | Aus-tralia | Europe | North and Center Amer-ica | South Amer-ica | Supral-ittoral | Inter-ittoral | Shallow-subtidal (low-water-line—200) | Deep sea (>200 m) |
| Annelida | 195 | 177 | 1 | 7 | 12 | 1 | 1 | 0 | 0 | 0 | 16 | 7 | 36 | 13 | 93 | 27 | 18 | 3 | 42 | 98 | 69 |
| Arthropoda | 357 | 303 | 2 | 15 | 46 | 2 | 4 | 1 | 2 | 30 | 18 | 64 | 19 | 148 | 71 | 29 | 4 | 93 | 148 | 124 | |
| Chaetognatha | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 |
| Chordata | 3 | 3 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 1 | 1 | 0 |
| Cnidaria | 28 | 25 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 5 | 0 | 14 | 2 | 3 | 0 | 0 | 5 | 15 | 10 |
| Gastrotricha | 125 | 74 | 0 | 6 | 50 | 2 | 0 | 0 | 0 | 6 | 2 | 20 | 8 | 66 | 20 | 18 | 2 | 27 | 64 | 31 | |
| Gnathostomulida | 12 | 5 | 0 | 1 | 5 | 2 | 0 | 0 | 0 | 1 | 0 | 2 | 2 | 3 | 3 | 2 | 0 | 4 | 4 | 3 | |
| Hemichordata | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 |
| Echinodermata | 5 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 1 | 4 | 2 |
| Entoprozoa | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 |
| Kinorhyncha | 132 | 99 | 2 | 3 | 26 | 3 | 1 | 1 | 0 | 5 | 4 | 21 | 6 | 60 | 25 | 12 | 0 | 20 | 66 | 65 | |
| Loricifera | 25 | 18 | 0 | 1 | 7 | 0 | 1 | 0 | 1 | 1 | 2 | 7 | 1 | 13 | 1 | 2 | 0 | 0 | 8 | 18 | |
| Mollusca | 85 | 76 | 0 | 2 | 6 | 2 | 1 | 0 | 0 | 6 | 3 | 17 | 7 | 41 | 10 | 8 | 1 | 17 | 41 | 35 | |
| Nematoda | 447 | 407 | 1 | 13 | 39 | 0 | 3 | 1 | 1 | 29 | 19 | 83 | 27 | 209 | 60 | 42 | 5 | 109 | 194 | 166 | |
| Nemertea | 18 | 15 | 0 | 3 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 1 | 9 | 4 | 4 | 0 | 3 | 12 | 6 | |
| Platyhelminthes | 129 | 110 | 1 | 5 | 23 | 0 | 1 | 0 | 0 | 5 | 6 | 22 | 8 | 66 | 16 | 9 | 2 | 44 | 63 | 33 | |
| Priapulida | 25 | 21 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 1 | 1 | 4 | 2 | 13 | 3 | 1 | 0 | 4 | 17 | 8 | |
| Rotifera | 37 | 33 | 0 | 3 | 3 | 0 | 1 | 0 | 0 | 1 | 1 | 7 | 2 | 22 | 9 | 1 | 2 | 9 | 12 | 17 | |
| Tardigrada | 88 | 66 | 0 | 2 | 21 | 0 | 2 | 0 | 0 | 5 | 4 | 19 | 5 | 45 | 6 | 9 | 1 | 15 | 39 | 38 | |
| Xenacoelomorpha | 7 | 1 | 0 | 2 | 4 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 2 | 5 | 3 | 0 | 0 | 0 | 5 | 0 | |
| Total | 752 | 488 | 7 | 48 | 235 | 12 | 15 | 4 | 4 | 54 | 35 | 141 | 51 | 327 | 157 | 75 | 14 | 202 | 359 | 212 | |

The number of papers in a category (discipline, area or depth) can add up to more than the total number as more than one subcategory could be scored (see Supplementary Tables 1 and 2 for a thorough description and the detailed dataset)

Table 2 Range change of species and occurrence of reported cryptic species in the literature survey

| Taxon | Distribution range | | | | Detection of cryptic species | | | | | | | | | |
|-----------------|-----------------------------------|--------------------|---------------------|--------------------|------------------------------|--------------------|---------------------|-------------------------|---|---------------------------------|--------------------------|---------------------------|--------------------------------|---------------------------------|
| | New species ^a (papers) | Unchanged (papers) | Unchanged (species) | Increased (papers) | Increased (species) | Decreased (papers) | Decreased (species) | Molecular data (papers) | Molecular and morphological data (papers) | Low-morphology problem (papers) | Cryptic species (papers) | Cryptic species (species) | Pseudocryptic species (papers) | Pseudocryptic species (species) |
| Annelida | 6 | 3 | 3 | 0 | 0 | 3 | 5 | 10 | 3 | 1 | 3 | 4 | 1 | 1 |
| Arthropoda | 25 | 8 | 14 | 2 | 6 | 1 | 2 | 11 | 2 | 1 | 3 | 11 | 0 | 0 |
| Chaetognatha | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Chordata | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Cnidaria | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Gastrotricha | 30 | 9 | 12 | 3 | 19 | 4 | 9 | 9 | 5 | 5 | 4 | 4 | 3 | 8 |
| Gnathostomulida | 3 | 0 | 0 | 1 | 11 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 |
| Hemichordata | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Echinodermata | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Entoprozoa | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Kinorhyncha | 18 | 3 | 15 | 3 | 11 | 1 | 5 | 8 | 2 | 0 | 0 | 0 | 0 | 0 |
| Loricifera | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Mollusca | 3 | 3 | 5 | 0 | 0 | 2 | 12 | 8 | 4 | 3 | 3 | 25 | 0 | 0 |
| Nematoda | 19 | 1 | 1 | 6 | 27 | 1 | 6 | 11 | 2 | 0 | 2 | 10 | 0 | 0 |
| Nemertea | 0 | 2 | 13 | 0 | 0 | 3 | 72 | 3 | 0 | 3 | 3 | 93 | 0 | 0 |
| Platyhelminthes | 12 | 3 | 4 | 2 | 7 | 4 | 18 | 13 | 5 | 2 | 4 | 5 | 2 | 13 |
| Priapulida | 2 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| Rotifera | 0 | 2 | 4 | 1 | 1 | 2 | 21 | 2 | 2 | 1 | 2 | 14 | 0 | 0 |
| Tardigrada | 9 | 5 | 9 | 5 | 28 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 |
| Xenacoelomorpha | 2 | 1 | 2 | 0 | 0 | 1 | 10 | 2 | 1 | 1 | 1 | 20 | 0 | 0 |
| Total | 135 | 40 | 82 | 25 | 112 | 22 | 160 | 61 | 27 | 17 | 26 | 189 | 6 | 22 |

Numbers refer to either the number of papers or species as indicated in the column heading (see Supplementary Tables 1 and 2 for a thorough description and the detailed dataset; supplementary Table 2 also includes cryptic species and range changes of the different entities (OTU/MOTU/cryptic/pseudocryptic) found)

^aNew species were scored as “distribution before unknown (NA); afterwards (local/regional)” and were not included in the “increase” column

the surveyed ecological studies did not at all focus on or address geographical distribution as well as the meiofauna paradox. Hence, these studies were irrelevant with respect to the subject of this review. Given the considered studies, the incidence of cryptic species seems high and few studies have explicitly focused on uncovering the distribution of meiofaunal species (Table 2). In the next section, we discuss some of these results more exhaustively.

“Why are so many meiofaunal taxa from distant areas so similar?”

A considerably high number of meiofaunal species descriptions include distribution ranges encompassing whole continental coastlines, amphi-oceanic, or even cosmopolitan (Sterrer 1973; Gerlach 1977; Westheide 1977, 2005; Westheide and Rieger 1987; Giere 2009). While many of these descriptions were registered in early decades of meiofauna research, valuable insights provided by detailed morphological reanalyses and approaches such as molecular taxonomy and phylogeography clearly contrasted these records. Hence, Giere’s first question (2009) of “similarity” between meiofaunal taxa is here considered based on biological phenomena resulting in the lack of accumulation of morphological differences between reproductively isolated species as well as difficulties in characterization and identification of meiofauna.

In recent years, the unveiling of “cryptic species” has become commonplace in meiofauna taxa, especially for those with presumed wide geographic ranges (Todaro et al. 1996; von Soosten et al. 1998; Schmidt and Westheide 2000; Rocha-Olivares et al. 2001; Casu and Curini-Galletti 2004; Derycke et al. 2005, 2006, 2012, 2013, 2016; Suatoni et al. 2006; De Meester et al. 2012; Tulchinsky et al. 2012; Jörger et al. 2012; Kieneke et al. 2012; Leasi and Norenburg 2016; Meyer-Wachsmuth et al. 2014; Van Campenhout et al. 2014; Leasi and Norenburg 2014). We consider cryptic species as species which demonstrate a high degree of molecular divergence, despite no recognizable morphological differentiation (Struck et al. 2018b). The presented literature survey showed that most of the studies using both molecular and morphological data detected either cryptic or pseudocryptic species (Table 2). In total, 189 cryptic species within Annelida, Arthropoda, Gastrotricha, Mollusca, Nematoda, Nemertea, Platyhelminthes, Rotifera and Xenacoelomorpha were recorded (Curini-Galletti and Puccinelli 1998; Schmidt and Westheide 2000; Rocha-Olivares et al. 2001; Westheide and Hass-Cordes 2001; Casu and Curini-Galletti 2006; Suatoni et al. 2006; Jouin-Toulmond and Gambi 2007; Casu et al. 2009; Leasi and Todaro 2009; Neusser et al. 2011; Kieneke et al. 2012; Tulchinsky et al. 2012; De Meester et al. 2012, 2015; Jörger et al. 2012; Leasi et al. 2013; Jörger

and Schrödl 2013; Leasi and Norenburg 2014, 2016; Meyer-Wachsmuth et al. 2014; Karanovic et al. 2016; Muentner and Kieneke 2017; Sahraean et al. 2017; Kieneke and Nikoukar 2017; Van Steenkiste et al. 2018). Interestingly, the number of cryptic species is highly uneven across the studied taxa. While some studies captured an overwhelming number of cryptic species within established morphospecies or species complexes of Acoelomorpha, Nemertea, Mollusca and Rotifera (Suatoni et al. 2006; Jörger et al. 2012; Leasi et al. 2013; Leasi and Norenburg 2014, 2016; Meyer-Wachsmuth et al. 2014), other studies found only a few cryptic species within complexes of Annelida, Gastrotricha and Platyhelminthes (Schmidt and Westheide 2000; Casu et al. 2009; Kieneke et al. 2012; Kieneke and Nikoukar 2017) (Table 2). However, the uneven discovery of cryptic species does not necessarily reflect differences in occurrence of cryptic species between taxa, but rather the study’s efforts. For example, the two papers addressing cryptic species in Nemertea (Leasi and Norenburg 2014, 2016) investigate several species complexes, while the ones on rotifers (Suatoni et al. 2006; Leasi et al. 2013) focus on a single species complex each (Supplementary Table 2).

Following the aforementioned definition of cryptic species, these can be considered as the result of phenomena such as recent speciation, parallelism, convergence and morphological stasis (Wada et al. 2013; Swift et al. 2016; Struck et al. 2018a, b). Several of these have been reported in meiofauna, highlighting these species as possible systems addressing questions of phenotypic conservation. Cases of recent speciation where morphological differentiation lags behind reproductive isolation have not yet been explicitly proposed in meiofauna, but numerous cases of cryptic species in our survey are likely to represent such cases (Casu et al. 2009; Jörger et al. 2012; Kieneke et al. 2012; Leasi et al. 2013; Leasi and Norenburg 2014, 2016; Meyer-Wachsmuth et al. 2014; Karanovic et al. 2016; Kieneke and Nikoukar 2017). In contrast, parallelism and convergent evolution have been explicitly suggested for some interstitial gastropods (Brenzinger et al. 2013; Jörger et al. 2014). Morphological stasis arises as the most common explicit explanation, possibly resulting from stabilizing selection on morphology due to the restricted space available in the interstitial environment (Sterrer 1973; Westheide and Rieger 1987; von Soosten et al. 1998; Schmidt and Westheide 2000; Hansen and Houle 2004; Futuyma 2010).

Although the pronounced phenotypic similarity opens venues in evolutionary research, the occurrence of cryptic species or overlooked diversity can also stem from the difficulty of characterizing and identifying meiofauna. For instance, the general paucity of traits with systematic value or inadequate morphological criteria poses a challenge to morphology-based taxonomic practices, eventually resulting in the synonymization of several species into a widely

distributed, cosmopolitan species (Sterrer 1973). This problem has been framed as the “low-morphology problem” and has been thoroughly discussed in algae and corals where molecular approaches have been suggested as a more reliable approach to species delimitation (van Oppen et al. 1996; Klautau et al. 1999). Indeed, 17 studies applying explicitly molecular and/or morphological methods directly reported or discussed issues related to difficulties of morphological-oriented practices in species delimitation in meiofauna. These studies spanned several phyla, including gastrotrichs, annelids, platyhelminths, nemerteans, molluscs, rotifers, xenacoelomorphs and arthropods (Todaro et al. 1996; Casu and Curini-Galletti 2006; Jouin-Toulmond and Gambi 2007; Casu et al. 2009; Leasi and Todaro 2009; Neusser et al. 2011; Tulchinsky et al. 2012; Jörger et al. 2012; Kieneke et al. 2012; Leasi et al. 2013; Jörger and Schrödl 2013; Meyer-Wachsmuth et al. 2014; Leasi and Norenburg 2014, 2016; Karanovic et al. 2016; Muentner and Kieneke 2017; Kieneke and Nikoukar 2017); Table 2).

Similarly, although the presence of cryptic species should be considered alongside with a strict sense of absence of morphological differentiation between species, re-analyses of meiofaunal species have uncovered overlooked morphological differences for some species (e.g., Pietsch and Westheide 1985; Westheide and Rieger 1987; Curini-Galletti and Puccinelli 1998; Rocha-Olivares et al. 2001; Casu and Curini-Galletti 2006; Jouin-Toulmond and Gambi 2007; Casu et al. 2009; Leasi and Todaro 2009; Garlitska et al. 2012; Muentner and Kieneke 2017; Struck et al. 2017). Species with morphological differences found after reinvestigations are usually named ‘pseudocryptic species’ (which can be considered as morphologically unrecognised species). For example, differences in setation were found within the cosmopolitan harpacticoid copepod *Nannopus palustris* (Arthropoda; Garlitska et al. 2012). Likewise, overlooked differences in the muscular system correspond with genetic differentiation within the *Xenotrichula intermedia* species complex (Gastrotricha; Leasi and Todaro 2009; Muentner and Kieneke 2017). For the annelid *Stygocapitella subterranea* complex slight differences in the chaetal composition of the first two chaetigers were re-evaluated as constituting species-specific differences in the light of molecular data and in contrast to previous conclusions (Struck et al. 2017).

The breadth of changes in distribution range before and after a study captured by the literature survey also revealed trends in meiofaunal research (Supplementary Table 3; Table 2). In the survey, we report 25 studies whose focus species increased its distribution (considering the established categories, including regional, amphi-oceanic and cosmopolitan). In common, none of these studies employed molecular approaches and relied explicitly or implicitly on morphological data only (e.g., Villora-Moreno and Grimaldi 1993; Chatterjee et al. 2000; Delogu et al. 2008; Dal Zotto and Todaro 2016;

Clausen 2000; Prasath et al. 2017). In sharp contrast, studies reporting a decrease of a range distribution generally employed molecular methods (Table 2; Supplementary Tables 2–3; e.g., Curini-Galletti and Puccinelli 1998; Schmidt and Westheide 2000; Jörger et al. 2012; Leasi et al. 2013; Meyer-Wachsmuth et al. 2014; Karanovic et al. 2016; Leasi and Norenburg 2016; Kieneke and Nikoukar 2017; Sahraean et al. 2017). For example, the six cryptic species uncovered within the *Terschellinia longicaudata* species complex (Nematoda) decreased the overall distribution of a formerly cosmopolitan species to two clades occurring in Bahrain, one in Taiwan, one in the UK and Mexico (amphi-oceanic), one in the UK and one cosmopolitan. 40 studies reported unchanged distributions (Table 2). A conclusion from these results is the necessity of molecular-oriented methods in species identification. Additionally, changes in distribution rather reflected the usage of methods than taxa. Within Xenacoelomorpha, Mollusca, Nemertea, Platyhelminthes, and Rotifera, there was a tendency for decreased or unchanged distribution ranges. In contrast, for Gastrotricha, Kinorhyncha, Nematoda and Tardigrada we found an increase. Yet, this cannot be related to the taxa themselves, but rather to the methodology used. Taxa with reduced ranges are also the ones with high numbers of cryptic or pseudocryptic species (Table 2).

Added to the limited available morphological traits for species delimitation and the presence of morphologically similar species, sampling biases might also contribute to the erroneous assumption of a cosmopolitan distribution of a species. Information on species distribution is often biased by sampling localities and intensity (Leasi and Norenburg 2016; Garraffoni and Balsamo 2017; Rinaldo et al. 2017). For instance, the higher diversity of meiofaunal species from European waters likely reflects a sampling artefact due to research traditions (Fontaneto et al. 2009; Jörger et al. 2014). Due to this bias, the report of species from understudied areas is often based on the inappropriate usage of species descriptions or taxonomic keys from Europe due to lack of such information for the study area. This is a common problem in modern taxonomy and not restricted to meiofauna only. Application of keys originating from different regions is likely to result in inappropriate assignment of species (Hutchings and Kupriyanova 2018). For instance, our survey potentially captured some papers wherein British keys were used following surveys in India and Thailand (Zawierucha et al. 2013; Ansari et al. 2015a, b, 2016, 2017; Prasath et al. 2017) and, maybe not surprisingly, these suggest an increased species distribution (Supplementary Table 3).

Conclusions regarding “Why are so many meiofaunal taxa from distant areas so similar?”

Considering the prevalence of cryptic species complexes and the subsequent reduction in distribution ranges in studies employing molecular investigations, the distribution of most meiofauna species seems clearly inflated as complexes of cryptic species consists of several, independent distributions, currently interpreted as a single distribution range (Casu and Curini-Galletti 2004; Derycke et al. 2005; Andrade et al. 2011; Tulchinsky et al. 2012; Leasi and Norenburg 2014). Our survey showed that cosmopolitan or, at least, amphi-oceanic distributions of most meiofauna species seldom occur and that increases in distribution range are not supported by molecular approaches. Therefore, the taxonomic identity and assumed wide distribution ranges of many meiofauna species assumed to be examples of the ‘meiofauna paradox’ is not verified (Schmidt and Westheide 2000; Casu and Curini-Galletti 2006; Suatoni et al. 2006; Casu et al. 2009; Tulchinsky et al. 2012; Jörger et al. 2012; Kieneke et al. 2012; Leasi et al. 2013; Leasi and Norenburg 2014, 2016; Meyer-Wachsmuth et al. 2014; Karanovic et al. 2016; Sahraean et al. 2017; Kieneke and Nikoukar 2017). Careful reinvestigations, including detailed morphological and molecular analyses should resolve the paradox of widespread species. Hence, in the strictest sense the meiofauna paradox, that meiofauna species with limited dispersal capacities exhibit wide distribution ranges, does not seem to exist or only to a substantially lower degree than assumed before.

Nonetheless, the original observations associated with the meiofauna paradox, that widely distributed complexes of species exhibit very high degrees of morphological similarity, poses intriguing research topics. Clearly, morphological and genetic diversity seem to evolve at different paces in meiofaunal species, as suggested by the high degree of morphological conservatism. Although the provided discussions did not directly give a single and clear answer to the overall similarity between meiofaunal species complexes, it suggests that this question is indeed prominent. First, this requires that the evolutionary history and hence the taxonomy of the study system is firmly established as the basis for future research efforts. While many taxonomists have been aware of these problems, species identifications should include DNA sequences as molecular fingerprints as well as ideally the determination of the level of gene flow at the genomic level.

Additionally, besides the presence of restricted gene flow it has also to be shown that the degree of morphological similarity is as high as assumed (Struck et al. 2018b). Some degree of assumed similarity might arise

from neglecting certain morphological character traits a priori (e.g., due to taxonomic tradition), that might actually help to delimitate the species and hence decrease the morphological similarity. Indeed, new developments and approaches in morphological measurements such as detailed anatomical examinations and 3D modelling, other high-resolution microscopy techniques or morphometrics might provide further resolution (Leasi and Todaro 2009; Neusser et al. 2009, 2011; Jörger et al. 2014; Struck et al. 2017). Additional and so far overlooked characters might also decrease the overall similarity in some cases (Knowlton 1993; Méndez et al. 2000; Andrade et al. 2011; Garlitska et al. 2012). Revalidation of characters in this respect could also include other phenotypic characters such as chemical traits, as most marine species rely on chemical cues for mate choice and ecological interactions (Knowlton 1993; Derycke et al. 2008) or the microbiome (Derycke et al. 2016).

If it can be shown that the homogenising effect of gene flow is not present or minimal due to the presence of reproductive isolation, the shown overall morphological or even phenotypic similarity could indicate an adaptive value of this conservatism. As suggested, phenomena such as recent speciation, parallelism, convergence and morphological stasis might account for this (Wada et al. 2013; Swift et al. 2016; Struck et al. 2018b), but further research is needed to unveil the contributions of these phenomena and the selective forces driving them as well as to determine the adaptive value of morphological conservatism (for further details please see the road map below).

“How can meiofauna have bridged oceans and occupied distinct shores in the absence of propagative stages?”

Dispersal and vicariance are generally discussed as the two major forces underlying the distribution range of meiofauna species. Both hold a fundamental role in shaping ecological and evolutionary dynamics of populations and species as they influence habitat colonization, genetic cohesion of species across space, competition and, in the case of dispersal, facilitate or hamper local adaptation (Knowlton 1993; Ronce 2007; Derycke et al. 2013; De Meester et al. 2015; Baco et al. 2016; Mevenkamp et al. 2016). Ronce (2007) defined dispersal as “any movement of individuals or propagules with potential consequences for gene flow across space”. Vicariance can be regarded as the establishment of barriers, whether biotic or abiotic, to dispersal and hence gene flow.

Several lines of evidence provide support for dispersal ability in meiofauna. The presented survey included 25 works which directly tested for meiofauna dispersal with experimental approaches (Supplementary Table 2).

Generally, these experimental and empirical evidences show that certain meiofauna organisms (including annelids, arthropods, gastropods, kinorhynchans, nematodes, molluscs, platyhelminths, rotifers and tardigrades; Supplementary Table 2) are regularly found drifting in the water column, rafting on algae or ice or are able to colonize sediment traps and have a selective settlement (Pugh 1996; Schratzberger et al. 2000; Commito and Tita 2002; Thistle 2003; Ullberg and Ólafsson 2003a, b; Teasdale et al. 2004; Cristoni et al. 2004; Gwyther and Fairweather 2005; Arroyo et al. 2006; Gobin and Warwick 2006; Hooper and Davenport 2006; Junkins et al. 2006; da Fonsêca-Genevois et al. 2006; Gallucci et al. 2008; Boeckner et al. 2009; Guilini et al. 2011; Thomas and Lana 2011; Callens et al. 2012; De Meester et al. 2012, 2015; Lins et al. 2013; Mcfarlane et al. 2013; Cuvelier et al. 2014; Mevenkamp et al. 2016).

Presence in the water column can result from sediment erosion (Hagerman and Rieger 1981; Palmer 1988) or through active dispersal as a response to unexpected threats (such as predator attack), changing conditions (such as environmental deterioration, overcrowding, competition), winter migration or nocturnal emergence (Palmer and Gust 1985; Armonies 1990, 1994; Giere 2009). For example, polychaetes and harpacticoid copepods colonize nearby cages more rapidly and abundantly than those farther away (Boeckner et al. 2009). Rates of up to 80% of emergence were reported in harpacticoid copepods (Sedlacek and Thistle 2006). While in the water column, meiofauna can be transported as far as 10 kilometres by erosive tidal currents (Hagerman and Rieger 1981) and members of all meiobenthic taxa have been found in the water column (Armonies 1990). However, all these experimental studies are hampered by the fact that they could not differentiate between local recruitment and long-distance dispersal as they were based on morphological data only. Generally, the conclusions in these studies were therefore conservative and assumed that the detected meiofauna species were only locally recruited from the adjacent sediments.

Besides water column transport, meiofauna dispersal can occur by drifting macroalgae, ice, large floating islands and marine snow (microbial processes and mucus secretions; Fenchel 1978; Westheide 1991; Shanks and Walters 1997; Barnes 2002; Derycke et al. 2008; Giere 2009; de Meester et al. 2012; Tulchinsky et al. 2012; Mcfarlane et al. 2013; Mevenkamp et al. 2016). The dispersal of eggs attached to sand grains (Fenchel 1978) or “buoyant” eggs rather than individuals has also been suggested (Giere 2009; Zeppilli et al. 2011). For example, marine gastrotrichs attach their fertilized eggs directly to sand grains, making dispersal via current sediment plausible (Giere 2009; Kieneke et al. 2012). Considering the evidence for both water column transport and drift, water movements such as currents and flows could become invaluable sources of information when

studying meiofauna distribution and dispersal. For example, currents influence genetic structuring in marine nematodes, where population genetic differentiation (i.e., F_{ST} values) is often uncorrelated with distance (Derycke et al. 2013). Additionally, wet ballast sand in ships potentially influences meiofaunal dispersal by human activities and could account for dispersal over hundreds of kilometres, but evidence thus far is sparse (Radziejewska et al. 2006; Giere 2009). Moreover, the possibility of stepping-stone dispersal using sea mounts has also been discussed (George and Schminke 2002; George 2013; Packmor and Riedl 2016). However, the evidence for dispersal in these studies was only indirect as they were derived from biogeographic patterns without direct testing of the means of dispersal using, for example, experimental approaches.

In contrast to all this cumulating direct or indirect evidence of dispersal, meiofaunal organisms are often considered to be one of the most sedentary of the marine faunas with virtually no capacity for dispersal (Sterrer 1973; Christiansen and Fenchel 1979; Westheide and Hass-Cordes 2001; Kieneke et al. 2012). For example, Sterrer (1973) stated that the “development, morphology and biology all seem designed to assure one thing: that the organism never leaves its interstitial environment”; while Danielopol and Wouters (1992) suggested that “they are supposed to disperse very slowly and only with or through the sediments as they have no pelagic life stages”. Hence, ideas stating that meiofaunal organisms are poor dispersers influenced the general understanding, hypothesis testing and discussion of meiofaunal dispersal modes (Giere 2009). This viewpoint is further supported by the above finding that the supposed wide distribution ranges of meiofaunal are indeed the cumulated distribution ranges of species complexes and the distribution range is often substantially reduced for each species in this complex when molecular data are applied (see above, Table 2 and Supplementary Table 3).

Along this trend, antagonising views were often either dismissed, neglected or ignored (Palmer and Gust 1985) and the dispersal-distribution discussion narrowed to focus almost exclusively on the absence of pelagic larvae. This is generally in accordance with the remaining marine biology literature. Marine species without pelagic larval dispersal are generally expected to have smaller distribution ranges and higher genetic differentiation between populations than species with such stages, which are thought to ultimately connect populations at larger spatial scales and thus lowering genetic differentiation (Knowlton 1993; Kelly and Palumbi 2010; Baco et al. 2016). As a result, much research has been dedicated to understand larval developmental patterns, duration of pelagic larval stage and larval behaviour (Jokiel 1990; Bhaud and Duchêne 1995). However, evidence against the general applicability of this intuitive scheme (pelagic vs. non-pelagic) has accumulated over the

years. Several studies demonstrated cases of non-pelagic dispersed organisms with highly homogeneous haplotype networks occupying surprisingly wide ranges; on the other hand, other studies reported pelagic dispersed species with clear population structuring, for example, due to local settlement of larva within in the vicinities of the parents (Jokiel 1990; Kyle and Boulding 2000; Colborn et al. 2001; Sponer and Roy 2002; Lester and Ruttenberg 2005; Johnson and Black 2006; Cowen et al. 2007; Lester et al. 2007; Hellberg 2009; Boissin et al. 2015). Hence, dispersal is not the sole, perfect proxy of the distribution range of marine species in general and several other circumstances and particularities can impact distribution ranges such as niche breadth, environmental tolerance, body size, population abundance, latitude, environmental variability at different spatial and temporal scales like substrate type or wave exposure, occurrence of environmental gradients, reproductive strategy, fecundity, lifecycle duration, and physiological constraints (Gaylord and Gaines 2000; Lester and Ruttenberg 2005; Lester et al. 2007; White et al. 2009; Sanford and Kelly 2011). Focusing on meiofauna, some of these factors and concepts have been discussed in the literature, mostly following discoveries of inconsistent and confounding patterns in species' range distribution (Andrade et al. 2011; Tulchinsky et al. 2012). For example, Derycke et al. (2013) suggest that life-history characteristics are important in determining the genetic structure of nematode populations. Similarly, the genetic structure of *Pellioditis marina* might be best explained by its life-history characteristics of a short generation time, high colonization potential and evolutionary potential for local adaptation (Derycke et al. 2005). Furthermore, evidence for rare long-distance dispersal events stems also from the highly similar composition and high diversity of the meiofauna of the Galapagos Islands with other parts of the world (Westheide 1977, 1991). The same may hold truth for colonization of other islands of volcanic origin.

Vicariance has also been proposed not only to explain the establishment of barriers to dispersal as evidenced by the reduced distribution ranges (Table 2), but also as a responsible force underlying the present distributions of meiofaunal species. In specific, the distribution of meiofaunal taxa was suggested to reflect the movement of the tectonic plates and with that the continental landmasses with their coastlines (Sterrer 1973). Arguably, Sterrer overemphasized the importance of this mechanism, and dismissed dispersal (due to the absence of pelagic larval stages) as a viable mechanism, rendering both as mutually exclusive (Sterrer 1973). When considering variation of species distributions through time, the severe differences in geological and climatological events have to be accounted for (Norris and Hull 2012), as these influence population connectivity and distribution ranges in complex ways, both at macro- and microgeological scales.

For example, glacial periods resulted in a decrease of the sea level, leading to changes of coastal geography (e.g., increase in island mass) including closure of seaways which were open in interglacial periods. Likewise, temperature, oxygen and salinity gradients were affected by these changes. It is not surprising to assume that the evolutionary history, regardless of the dispersal abilities of ecological communities was severely affected throughout time by such events (Dawson 2001). Hence, considering the registered variance of climatological, sea level and geological changes throughout the last ~ 500 million years, focusing exclusively on vicariance is misleading. Accordingly, none of the studies mentioned above using molecular data supported the hypothesis that the distribution was exclusively the result of plate tectonic events. Indeed, climatic oscillations such as intermittent glacial–interglacial periods resulted in bottlenecks, recent founder-events, and local extinctions in some meiofaunal species (Taylor et al. 1998; Derycke et al. 2005, 2008, 2013; Casu and Curini-Galletti 2006; Tulchinsky et al. 2012). For the gastrotrich *Turbanella cornuta*, Kieneke et al. (2012) found that the most likely colonization to the Baltic Sea was via water connections and corresponding currents about 10,000 years ago rather than by the recent connectivity routes. Moreover, instances of long-distance dispersal within the Northeast Atlantic could be found in other *Turbanella* species. A recent study focusing on the annelid genus *Stygocapitella* demonstrated that considering a strict vicariance hypothesis does not fit meiofauna dispersal (Struck et al. 2017). Applying the vicariance hypothesis strictly would require that the southern species be separated 450 million years ago in the Ordovician with the beginning formation of the Paleo-Tethys Ocean (Fig. 3). Hence, ancient dispersal events (Fig. 3) are more likely, possibly in combination with vicariant events establishing barriers of dispersal (Struck et al. 2017). Furthermore, Derycke et al. (2013) discussed hypotheses considering dispersal and gene flow of free-living meiofaunal nematodes and stressed the importance of historical events in shaping the genetic pattern of marine nematodes, showing that land mass drift, sea level rise and glacial cycles influenced population structuring and distribution of the nematode *Litoditis marina*. From this, they concluded that the evolutionary history of this cryptic species complex is only thoroughly understood when historical events are considered alongside aspects of dispersal. In conclusion, climatological and geological events affect meiofauna distribution and dispersal.

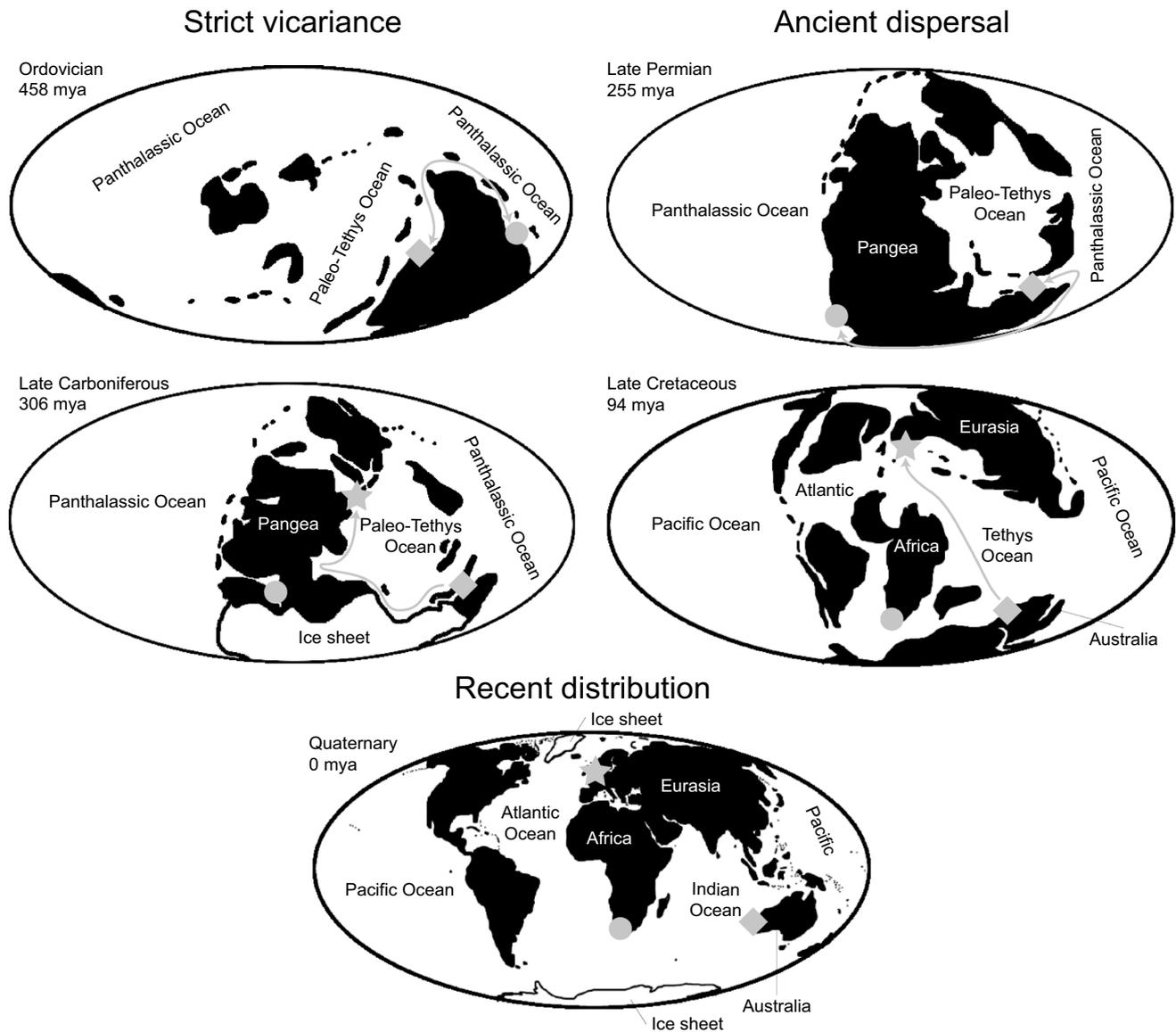


Fig. 3 Two scenarios explaining the distribution of three species of *Stygocapitella* investigated by Struck et al. (2017). The left upper two panels show a strictly vicariant scenario, the right upper two show ancient dispersal and the lowest the recent distribution. Arrows indi-

cate possible dispersal routes either via plate tectonics or long-distance dispersal. Paleomaps modified from Scotese (2002). Star, population of *S. subterranea*; diamond, population of *S. australis*; circle, population of *S. minuta*

Conclusions on “How can meiofauna have bridged oceans and occupied distinct shores in the absence of propagative stages?”

A cornerstone of the ‘meiofauna paradox’ is the expectation of low dispersal of meiofaunal invertebrates. There is an increasing body of experimental and empirical evidence, which clearly contrasts this view. Meiofaunal dispersal, not specifically tied to any restrained evolutionary lineage or taxonomic clade, has been clearly demonstrated. Dispersal abilities seem to account for the distribution of lineages throughout considerably large areas. Nevertheless, this

should not be confounded by the ability to maintain cosmopolitan distributions. The expectations of low dispersal seem to emerge from historical views based on the dichotomous presence/absence view on pelagic larval dispersal. The presence of pelagic dispersal plays a role in dispersal and species distribution, but it is not the only considered variable. Meiofaunal biologists should explore the ecological roles and life-history traits of the species to understand the distribution of a species. Ecological and life-history traits effectively affect dispersal and the range distribution of individuals and are seldom considered. Moreover, the inclusion of vicariant events and ancient dispersal routes can explain

the recent distribution of meiofaunal organisms. However, vicariance should not be considered the sole driver of meiofaunal distribution. Only few studies on meiofauna have been conducted so far, which accounted for both (Westheide 2005). Therefore, general conclusions for meiofauna dispersal as not being possible must be regarded as idiosyncratic for the time being.

Future empirical studies on the dispersal of meiofaunal organisms should concentrate on deciphering the contributions of dispersal and vicariance on the recent distribution at several geographic and temporal scales. This will allow more general conclusions regarding dispersal potential, time scales of dispersal and speciation as well as associated processes, especially if these studies are conducted for a broad range of the meiofaunal biodiversity. Empirical data providing indirect evidence of dispersal routes should be complemented by experimental approaches to directly test dispersal capacities, which allow assessing the difference between local recruiters and long-distance dispersers (for further details please see the road map below).

Moreover, analyses of metapopulation dynamics have gained popularity in marine ecological studies (Wares et al. 2001; Kritzer and Sale 2004; Cowen et al. 2007), and have been frequently applied to meiofaunal organisms (Derycke et al. 2006, 2007a, b, 2008; Andrade et al. 2011; Leasi and Norenburg 2016). The complexity and dynamics of meiofauna populations through time and space make them suitable for such analyses. Suitable habitats often consist of relatively small (metre scale) isolated patches of sediment, which are separated from each other by distances of several metres to even hundreds of kilometres of inhospitable habitat (Tulchinsky et al. 2012; Leasi and Norenburg 2016). This often results in mosaic-like population patterns, which are best addressed by taking metapopulation dynamics into account.

Roadmap for meiofauna research: directions of future research

The wide geographical distribution (including cosmopolitanism) of many marine species has puzzled researchers and resulted in the prevalence of several paradoxes. Examples are the extended pelagic stage of some species with restricted distributions (Colborn et al. 2001), the community composition of Rockall (Johannesson 1988) or the cosmopolitan distribution of marine species without free-living larvae (Sponer and Roy 2002). These paradoxes stem from sampling and taxonomic complications and the meiofauna paradox is no exception to these difficulties. Here, we discussed that the meiofauna paradox likely stems from pre-established, historically defined hypotheses, pre-concepts of sea connectivity dynamics and

the presence of cryptic species as well as difficulties and biases in meiofauna sampling and collection, identification and characterization. As pointed out in the literature survey, recent evidences indicate that the meiofauna paradox and its underlying assumptions including the wide distribution and low dispersal capability of meiofaunal organisms are not met. First, a considerable amount of studies focusing on cosmopolitan species and applying molecular methods uncovered underlying diversity (cryptic species) often with limited distribution ranges. Hence, the assumption of wide distribution is not given. Second, the limited dispersal capacity seems questionable and a remnant of historical literature. Nonetheless, even though the meiofauna paradox in its strictest sense does most likely not exist, certain aspects of the paradox pose interesting research venues. As such, facing the future we suggest that Giere's (2009) questions concerning the meiofauna paradox should be considered in terms of morphological similarity and marine connectivity.

To understand phenotypic conservatism, both evolutionary and taxonomic approaches are needed. Future studies should focus on unveiling the selective pressures resulting in phenotypic similarity of meiofaunal species. Overall similarity in meiofauna and its underlying processes warrants potentially interesting evolutionary phenomena (i.e., morphological stasis, recent speciation, parallel or convergent evolution). In the age of 'high-throughput sequencing', genomic scans such as RADseq, anchored hybrid enrichment (AHE), ultra-conserved elements (UCE) or genome re-sequencing in combination with de novo genome assemblies of meiofaunal species will open unprecedented gates to understand the evolutionary history, connectivity, adaptation and selective regimes affecting meiofaunal organisms. Surprisingly though, the provided literature survey captured only seven studies focusing on evolutionary biology (Schmidt and Westheide 1999; Rocha-Olivares et al. 2001; Denis et al. 2009; Yamasaki et al. 2014; Scarpa et al. 2015; Smythe 2015; Randsø et al. 2018) out of a total of 751 studies. Meiofaunal species represent ideal systems to understand selective pressures on cryptic species complexes and deceleration of phenotypic evolution (as generally suggested by Struck et al. 2018a, b). Even though meiofaunal organisms are of small size, recent advantages in whole genome amplification techniques allow working with individual specimens (e.g., Golombek et al. 2013, 2015). On the other hand, the small size can be a potential advantage when investigating the similarity of the whole phenotype as a more complete assessment of the whole phenotype is possible. If such studies are combined with nested sampling strategies of populations and species of a complex as well as of morphological slightly different sister species, selective regimes at different taxonomical levels such as between populations, cryptic species and non-cryptic species can be revealed.

In addition to this evolutionary approach, discovery and description of meiofaunal species should be prioritized, as only a broad taxonomic basis will allow for solid general conclusions about evolutionary processes, speciation and biogeographic history and selective regimes as well as provide the necessary phylogenetic framework for the evolutionary studies. Taxonomic efforts should include DNA sequences when describing species, as these allow a better detection of distribution ranges as discussed above. Guidelines for DNA taxonomy with a focus on meiofauna have been published (Fontaneto et al. 2015). Additionally, the overall phenotype of the meiofaunal species should be described in as much detail as possible, as this will provide the basis to assess similarities across species boundaries. Indeed, following our discussion, a thorough understanding of meiofaunal species' distributions is inevitable to understand the scale and range that meiofaunal species can maintain connectivity. The unravelling of cryptic species, resulting from the overall phenotypic similarity, will help understanding potential barriers of gene flow including historical barriers. Additionally, the discovery of cryptic species will open further research venues such as physiological variability (de Meester et al. 2011) and distribution along ecological gradients. Hence, investment in classical taxonomic research like species characterization and development of identification keys in understudied areas should be a priority of meiofaunal research, likely yielding the discovery of endemic species or species with a more restricted distribution (Garraffoni and Balsamo 2017).

To tackle marine connectivity, both empirical and experimental approaches should be adopted. Empirical research on dispersal and distribution of meiofaunal organisms can apply the methodology outlined above for evolutionary and taxonomic approaches. If an adequate sampling regime is performed, the produced data will be able to tackle questions concerning connectivity, demography and biogeography. Hence, the sampling strategy should be inclusive to both possible vicariance and dispersal events for the group of interest. The dispersal potential of meiofaunal organisms and the influence of vicariant events can then be addressed more thoroughly and systematically in time, space and taxonomic breadth. This includes assessing dispersal potential empirically at local and regional scales, which are potentially affected by historic events like glaciations, comparing sister species pairs with only very few differing biological properties as well as using metapopulation models to get a better fit of the reality of meiofaunal population structure. A strong focus of research is recently on intertidal to shallow-subtidal habitats. However, to achieve a more thorough understanding, marine connectivity research on supralittoral and deep sea habitats should also be emphasized, also having in mind that these could have been temporal habitats in the past. Moreover, genome-scale data are preferable over

few molecular markers if possible, as they allow a more accurate assessment of both recent and historic gene flow and hence dispersal capacity based on fewer specimens due to the increased sampling size.

In contrast, only a minority of the surveyed literature directly tested for meiofaunal dispersal in experimental settings. While challenging historical expectations, these works are vital to understand the means of meiofauna connectivity, dispersal and distribution. Considering recent technological advances, the inclusion of DNA sequences on species detection in such studies using metagenomic and metatranscriptomic approaches will enable future works to test for dispersal of meiofauna more accurately (Fonseca et al. 2014; Carugati et al. 2015; Leray and Knowlton 2015, 2016). For example, collecting environmental DNA samples of sediments at various depths and from the adjacent 'pelagic realm' can provide insights if the present meiofaunal species in the pelagic realm are only locally recruited or if specimens from more distant populations are also present. Additionally, metatranscriptomic approaches have the potential to determine which stages of development are responsible for dispersal. However, to validate such approaches, appropriate databases must be established, including genetic and transcriptomic markers specific for certain developmental stages. Therefore, at the present stage, priority should be given to projects compiling such comprehensive databases.

Acknowledgements The authors are indebted to two anonymous reviewers and Diego Fontaneto whose comments have considerably improved the original manuscript. JC is grateful to Zeca Afonso (among other thinkers) for inspiration ("Em cada esquina um amigo; Em cada rosto igualdade"). This is NHM Evolutionary Genomics Lab contribution No. 10.

Compliance with ethical standards

Ethical approval All authors have approved the submitted manuscript

Conflict of interest The authors declare that they have no conflict of interest.

Human animal rights statement This article does not contain any studies with animals performed by any of the authors.

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