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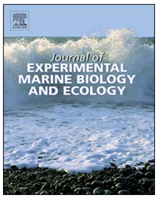

Addressing biodiversity shortfalls in meiofauna

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ABSTRACT

Technological advances throughout different fields of research have enhanced our understanding of biodiversity, especially for meiofaunal organisms, which are notoriously difficult to study because of their small size. Scanning and transmission electron microscopy, together with confocal laser scanning microscopy, has increased the amount of external and internal morphological information, improving the quantity and quality of species descriptions, as well as deepening our understanding of the evolutionary adaptations of meiofauna. In ecology, the characterization of molecules such as stable isotopes and fatty acids have permitted us to infer trophic niches of meiofauna species, enhancing our understanding of their functional role in the ecosystem. In parallel, advances in DNA sequencing techniques have allowed us to quantify with much higher accuracy the phylogenetic position of meiofaunal species. We here review the main biodiversity shortfalls in the studies of meiofauna, discussing how such shortfalls could be addressed, especially by merging different approaches. Important steps towards such interdisciplinary approach are to promote data sharing, to explore new technologies that combine disciplines, and to base studies on a clear theoretical framework. Working at the interface between different disciplines imposes several challenges and will require creative approaches, but well-designed studies making use of different methodologies will quickly contribute to address the main biodiversity shortfalls in the study of meiofauna.

1. Introduction

Small animals belonging to the meiofauna (here broadly defined as organisms smaller than 0.5 mm; Giere, 2009) are in the threshold of the optical resolution for routine identification, and our knowledge on their biodiversity is unfortunately still scarce compared to other groups of animals due to the inherent difficulties of working with microscopic organisms (Appeltans et al., 2012). Technological advances in optical and electronic microscopy provide us with the possibility to improve the quality and quantity of morphological data among meiofaunal groups, applying it for taxonomic descriptions (Boaden, 1963; Clausen, 1967; Di Domenico et al., 2013; Hummon, 1966; Martínez et al., 2013; Sterrer, 1998; Todaro, 2012), systematic classifications (Sørensen et al., 2015; Martínez et al., 2015; Sánchez et al., 2016), and studies on comparative morphology (Kirsteuer, 1976; Tyler and Hooge, 2004). In parallel, advances in molecular tools have dramatically improved our understanding of deep phylogenetic relationships within meiofaunal groups (Cannon et al., 2016; Dunn et al., 2008), including the distribution of meiofauna at different spatial scales (Curini-Galletti et al., 2012; Fonseca et al., 2014a; Scarpa et al., 2015), and of the potential speciation processes (Derycke et al., 2005; Fontaneto and Barraclough, 2015). A large number of molecular techniques can be applied in meiofaunal studies. Molecular data for meiofauna can be obtained from single individuals in the form of short target sequences (barcodes; Fontaneto et al., 2015) to that of entire genomes and transcriptomes (Bemm et al., 2016; Flot et al., 2013). In ecology, the use of dual stable isotopes and fatty acid analyses has allowed us to understand the role of meiofauna in the food web (De Troch et al., 2012; Guilini et al., 2013; Iken et al., 2001). In summary, we now have the power to scrutinize meiofauna in relation to species identity, phylogenetic position, trophic position, and ecological requirements.

The objective of this review is to use the framework of the seven global shortfalls in biodiversity knowledge suggested by Hortal et al. (2015) to identify how to address our lack of knowledge on meiofauna for: species identity, species distribution, species abundance, biological traits, evolutionary history, biological interactions, and environmental requirements (Table 1). Tackling these shortfalls in meiofauna is challenging given the large number of known and potential unknown meiofauna species (Appeltans et al., 2012). The integrated use of various methodologies could allow researchers to improve our knowl-

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Table 1
Global shortfalls of biodiversity, adapted from Hortal et al. (2015) to meiofauna.

Shortfall	Descriptor	Limitations
Linnean	Species identity	Large number of unknown species
Wallacean	Species distribution	Unknown distribution for the majority of the species
Prestonian	Species abundance	Quantitative studies are restricted to few taxa and regions
Raunkiaeran	Biological traits	Lack of knowledge on traits for most species
Eltonian	Biological interactions	Except for the parasitic forms, there is a lack of knowledge on species interactions
Hutchinsonian	Environmental requirements	Lack of knowledge on species environmental tolerance
Darwinian	Evolutionary history	Lack of knowledge on species evolutionary history

edge on meiofaunal biodiversity, answering interesting questions in order to have a better understanding of the general rules governing biodiversity in these small animals, especially in marine ecosystems (Zeppilli et al., 2015; Schratzberger and Ingels, 2017). Now being at the omic-, big-data-, and conservation-oriented era, the identification of the theoretical framework to organize different complementary methodologies will help focus our efforts to enhance our predictive power to address the biodiversity shortfalls throughout the meiofauna.

2. Current theoretical framework merging ecology and evolution

In the past, ecology and evolution were often studied in parallel, as studies in the two fields usually addressed different questions (Mouquet et al., 2012). These studies were under the assumptions that evolutionary processes require a long time to be detected, whereas ecological processes may happen at small temporal and spatial scales. Yet, the legacy of evolutionary history is printed in current ecological patterns (Cavender-Bares et al., 2009). The field of evolutionary ecology addresses such eco-evolutionary interactions, merging tools, approaches, methods, and rationales from different fields of ecology and evolution, bridging temporal dimensions and linking evolutionary history with ecological processes (Cavender-Bares et al., 2012). The inclusion of such disparate approaches and questions in studies on meiofauna is the key to addressing the biodiversity shortfalls in our knowledge.

Species co-occurrence in communities is driven by four fundamental processes: dispersion, drift, selection (through environmental filtering and species interaction), and speciation (Fig. 3; Vellend et al., 2014). These processes operate simultaneously at local scales (e.g. species interactions) and regional scales (e.g. environmental tolerances). They also occur in short time scales (e.g. competitive exclusion at single patches), and at an evolutionary scale (e.g. speciation). The challenge today for meiofauna studies is on how to incorporate these processes over ecological and evolutionary time scales in a unified experimental framework as it has been done for other organisms (Mouquet et al., 2012).

Most of the experimental evidences linking ecology and evolution come from small-bodied organisms, such as prokaryotes, protists, and also some model meiofauna taxa (Faillace and Morin, 2016; Gravel et al., 2012; Jousset et al., 2016). Small size and fast reproduction time represent an advantage for laboratory and field manipulation of multiple species and populations over several generations (Simonini and Prevedelli, 2003a, 2003b). For instance, high diversity promoted evolutionary diversification by means of resource competition in experiments on microbes (Jousset et al., 2016); whereas growth rates in an experiment with protists and rotifers depended on the history of the interactions between species (Faillace and Morin, 2016). These studies approached simultaneously the 'Darwinian', 'Prestonian' and 'Eltonian' shortfalls (Table 1). Studies on meiofauna tested so far how ecological processes could affect evolutionary patterns, focusing on the role of niche differentiation in explaining long-term coexistence of cryptic species (Derycke et al., 2016; Gabaldón et al., 2016; Grosemans et al., 2016). These studies were particularly interested in combining the 'Darwinian' and 'Wallacean' shortfalls (Table 1).

Thus, ecologists, taxonomists, molecular biologists, physiologists, morphologists, theoreticians, experimentalists, and other researchers working on meiofauna have the potential to successfully interact addressing the different facets of biodiversity in order to diminish the shortfalls on meiofauna. Here we review how different methods can address the different shortfalls and which are the current challenges, focusing on meiofauna.

3. Methodological advances to address biodiversity shortfalls

3.1. Morphology

Detailed acquisition of morphological structures is a requirement for species identification and for understand the ecological adaptations of small taxa (Artois et al., 2011). Small body size and apparent morphological stasis in meiofauna may mask the actual complexity of the group (Vinther, 2015). Thus, addressing morphological diversity in meiofauna with high-quality morphological data would allow targeting the 'Linnean' shortfall by describing species, the 'Raunkiaeran' shortfall by defining morphological traits, and the 'Darwinian' shortfall by understanding the evolution of shape and form (Table 1). Given that 29 out of 35 phyla of the metazoans are present in the meiofauna, addressing these shortfalls in the meiofauna will allow inference throughout the vast majority of animal groups.

Taxonomy of meiofaunal groups are based on both external and internal structures (Schmidt-Rhaesa, 2007). Detailed morphological information on the external and internal morphology is obtained by microscopy techniques such as scanning electronic microscopy (SEM), transmission electronic microscopy (TEM), confocal laser scanning microscopy (cLSM) combined with immunohistochemistry (Kerbl et al., 2015; Neuhaus, 1994), and X-ray microtomography (Micro-CT) (Dunn et al., 2014; Paterson et al., 2014). Each of these techniques explores one or more morphological aspects of the animal. The SEM provides very fine details of cilia, tips of chaetae, epidermal glands, jaws after dissection or any other external structure. The TEM is a powerful technique for ultrastructural data acquisition, giving fine details of the tissue and cells, connections, commissures, blood vessels, and nerve cords. The cLSM incorporates compound microscopes, laser techniques, and *Z*-stacks (axis); giving internal and external resolution in an integrative 3D approach when combined with immunohistochemistry. Micro-CT is most useful for anatomical studies, without damaging the animal, particularly for large-scale comparative projects (Paterson et al., 2014). Despite a lack of meiofauna studies with micro-CT, new technologies are advancing, improving our understanding of the anatomy at higher resolution in real time functional anatomical analyses (Paterson et al., 2014). The combination of techniques in an integrative approach will include most of the details, but requires multiple specimens. Micro-CT approach instead has an additional advantage of working on a single specimen.

Some groups as meiofauna hydrozoans (Polte and Schimidt-Rhaesa, 2011), acoels (Hooge and Smith, 2004; Reuter et al., 2001), nemertodermatids (Raikova et al., 2016), hemichordates (Worsaae et al., 2012), loriciferans (Neves et al., 2013), kinorhynchs (Altenburger, 2016; Herranz et al., 2014; Neuhaus, 2004), rotifers (Leasi et al., 2012),