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Nematode diversity patterns in mangroves: a review of environmental drivers at different spatial scales

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Abstract

Mangroves are among the most productive ecosystems on Earth, yet they are disappearing at a dramatic rate. Mangrove sediments harbor microscopic nematodes, which show specific responses to variations of sediment physicochemical conditions, thus being potential bioindicators for conservation purposes. Nematode communities are subject to the strong heterogeneity of mangroves and predicting their distribution remains laborious at global and regional scale, thus hampering final statements about bioindication. In this review, we analyze relevant research on mangrove nematode diversity in order to identify the ecological mechanisms shaping the nematode community at the global, local and micro scales, and to hierarchize the environmental drivers responsible for nematode genera sorting. At the global scale, nematode genera richness is positively influenced by latitude and community composition changes according to geographical regions. At the local scale, nematode richness, density and community composition follow opposite patterns along a land-sea continuum and mangrove trees may be responsible for the variations of sediment chemistry leading to such community patterns. At the microhabitat scale, the community shows unexpected similarities between a priori different habitats. Epistrate and detritus feeders dominate mangroves, but except for trophic groups, the use of functional traits is inconsistent among studies, thus impeding conclusions. Further understanding of the role of environmental filters in shaping nematode diversity at different spatial scales cannot overlook data gaps in unexplored mangrove areas and the heterogeneity of microhabitats. Future studies should investigate nematode diversity with cutting-edge approaches, such as β-diversity partitioning, functional traits and metacommunity analysis, and eventually integrate nematodes, microbes and macrofauna in a comprehensive framework.

Keywords

meiofauna; tropical ecology; environmental filtering; microhabitats; functional traits; β-diversity

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1. Introduction

Mangrove forests grow along tropical intertidal coastlines, estuaries, lagoons and they penetrate inland as far as the tide can reach (Walsh 1974). Mangroves are made up of trees that thrive in unusual conditions, such as alternatively waterlogged and drained saline soils (Walsh 1974). Even though mangroves are able to store vast amounts of carbon and mitigate the effect of catastrophic climatic events on the shoreline, there is evidence they could disappear within the next century because of anthropogenic activities (Duke et al. 2007). A 20 to 35% decrease in worldwide mangrove surface areas has already been observed in the last 50 years (Polidoro et al. 2010). A moderate proportion of the world's mangrove forests also are to be greatly affected by seawater level and sediment subsidence (Alongi 2008 for review).

Mangrove forests cover about 137 760 km^2 of sheltered tropical and subtropical coastlines (Giri et al. 2011) and they offer extremely valuable services to both humans and biodiversity as a whole (Nagelkerken et al. 2008). The rate of mangrove primary production equals that of tropical humid evergreen forests, thus making mangroves vital contributors in C sequestration (Alongi 2009). Carbon dynamics, storage and mineralization are hot topics for mangrove research, and some gaps persist in knowledge regarding the role of the benthic compartment in those processes (Lee et al. 2014). Mangroves' soft sediments are colonized by macrofaunal organisms, such as crabs and polychaetes, and many other small invertebrates among which meiofauna is numerically dominant (Alongi 1989; Netto and Gallucci, 2003; Nagelkerken et al. 2008; Zeppilli et al. 2018 for review; Michaud et al. 2022).

Although meiofauna plays an important role in litter degradation and acts like a critical link between microorganisms and higher levels of the food web (Gee, 1989), its role in mangrove carbon dynamics and fluxes is not yet quantified (Schratzberger and Ingels 2018 and references therein).

Metazoan meiofauna includes 24 of the 35 animal phyla, plus several protist groups as well as the taxon Foraminifera, and it encompasses all benthic metazoans with an upper size limit of 1000 µm and a lower of 20 µm (Giere 2009). Because of its short life cycle, high diversity and density, ubiquitous distribution in soft (sediments) and hard (roots, animal tubes) substrates, and sensitivity to environmental changes, meiofauna has already been used to test the effects of natural and anthropogenic forcings and it proved to be a good indicator for climate change and anthropogenic impacts in shallow waters and deep sea, in tropical, temperate and polar ecosystems (Zeppilli et al. 2015a). Nonetheless, the lack of taxonomic information from poorly explored areas such as mangroves, together with the scarcity of studies integrating environmental monitoring and biological datasets, hinder our understanding on meiofauna dynamics and functioning in such areas and its routine use in impact studies (Zeppilli et al. 2015a). Nematodes could be good candidates for impact studies in mangroves since they represent over 90% of total meiofauna abundance in mangrove sediments, with high densities (up to 5000 ind.10cm^{-2}) allowing the collection of small, yet statistically significant samples (Somerfield and Warwick 2013; Schenk et al. 2020; Venekey et al. 2016; Venekey et al. 2019).

The environmental factors structuring nematode diversity in a variety of aquatic ecosystems (e.g. deep sea, intertidal, freshwater) have been investigated for decades, resulting in a common set of drivers (food availability, substrate type, physical disturbance, physico-chemical characteristics as the salinity, grain size, redox potential), which can be differently hierarchized according to the ecosystem and spatial scales (Giere 2009; Vanreusel et al. 2010; Venekey et al. 2010; Sahoo et al. 2013; Abdullah and Lee, 2017; Rosli et al. 2018 ; Michelet et al. 2021). Recent research in tropical mangrove forests addressed whether environmental filtering is the most powerful mechanism regulating nematode diversity compared to dispersal-based ones, regardless of the spatial scale (Brustolin et al. 2021). At the landscape scale, habitat selection shapes nematode community and metacommunity organization in mangroves is most likely the result of the interaction between species sorting and patch-dynamics (Brustolin et al. 2021). An effective but poorly explored way to unravel patterns of species sorting (intended as the effect of environmental variables, dispersal and stochasticity on the capacity of a given species to colonize a given habitat) is analyzing the β-diversity of a community by partitioning it in its nestedness (species loss) and turnover (species replacement) components (Baselga, 2010). Nestedness occurs between two assemblages when the less rich is a subset of the richest, which entails an overall loss of richness (Legendre et al. 2005). Turnover implies the replacement of species between two assemblages as a result of either environmental forcing, spatial or historical constraints (Legendre et al. 2005). The β-diversity concept can be applied to explore the functional diversity of the community as well, by substituting species with functional traits (Cardoso et al. 2014; Martini et al. 2021). Although there is still no widely acknowledged and validated set of functional traits for marine nematodes, the literature usually refers to life strategy (Bongers 1990; Bongers et al. 1991, 1995), tail shape (Thistle et al. 1995), body cuticle (Pinto et al. 2013; Raes and Vanreusel 2006 ; Semprucci et al. 2014 , Semprucci et al. 2018), body size and shape (Schratzberger et al. 2007; Alves et al. 2014), shape of amphideal fovea (Semprucci et al. 2018) and morphology of the buccal cavity (Wieser, 1953; Moens and Vincx 1997; Hodda 2022). The two approaches have been used for macrofauna diversity in mangroves (Menegotto et al. 2019; Cannicci et al. 2021) and for nematodes in temperate estuaries (Alves et al. 2014; Sroczynska et al. 2021), but they are still unexplored for nematodes in mangroves.

Besides, nematodes can provide a complementary tool relevant for conservation purposes as they may serve as a cost-efficient biological indicator of environmental quality status (Moreno et al. 2011). Nematodes show some peculiar physiological adaptations in response to specific stress in extreme environments (e.g. deep sediments), such as highly sulphidic and anoxic conditions, for instance *Halomonhystera disjuncta* ovoviviparous strategy (Van Gaever et al. 2006; Zeppilli et al. 2015b) and Oncholaimidae sulfur droplets (Thiermann et al. 2000). These adaptive characteristics allow researchers to detect distinctive community features in response to different kinds of stressors (Semprucci et al. 2015). In mangroves, nematodes have been used to characterize several anthropogenic contexts in the Indian, Pacific and Atlantic regions (Della Patrona et al. 2016; Capdeville et al. 2018; Michelet et al. 2021). Nematodes' potential role as bioindicators has been widely discussed (Semprucci and Balsamo 2014; Semprucci et al. 2015; Zeppilli et al. 2015a; Ridall and Ingels 2021), yet their use in mangroves is still hampered by the lack of data, namely on unexplored areas. A bioindicator should consider the natural variability of the ecosystem and exclude it as a driver of the community to give a straightforward and unequivocal signal of anthropogenic pressure. Hence, characterizing nematode community structure in response to mangrove natural variability first is essential to avoid misinterpretation of the factors responsible for their presence or absence at a given location. The scientific community has been stressing the need of management and conservation strategies for sustainable mangroves, which so far have been realized both locally and globally (see Romanach et al. 2018 for review).

Nonetheless, such initiatives sometimes fail to integrate mangrove ecosystem services to their social benefits and human necessities (Romanach et al. 2018). Hence, a management plan integrating fisheries , aquaculture, timber exploitation, tourism and all other mangrove-related human activities should be designed considering every component of the mangrove ecosystem (trees, water column and sediments, with their flora and fauna) in order to reverse the dramatic rate of forest loss (Ellison 2008). In this review, the available studies on the biodiversity, the ecology and the adaptations of nematodes to mangrove ecosystems are analyzed in order to understand: i) how mangrove environmental filters are acting on nematode communities in terms of diversity, density and functional traits, and ii) if the ecological mechanisms shaping nematode communities change according to the spatial scale of observation. Then, strategies to improve current knowledge and overcome limitations in mangrove nematode research are discussed. Eventually, the present review suggests further avenues of nematode research in order to legitimize their use as bioindicators, in view of the elaboration of future sustainable management plans.

2. Environmental filters acting at different spatial scales

2.1 Global scale drivers

Mangrove forests are mainly found in river deltas, lagoons and estuarine zones throughout the coastlines of tropical regions between 30°N and 30°S (Robertson and Alongi 1992). Because of the Earth's plate separation, two biogeographic areas of distribution are distinguished nowadays, the Atlantic-Caribbean-East Pacific (ACEP) and the Indo-West Pacific (IWP) (Alongi 2016). IWP hosts the greatest tree diversity (36 species), whereas in ACEP there are 15 species, of which 2 were introduced by man (Day et al 2013). These two areas only share 3 common genera of mangrove trees (*Acrostichum*, *Rhizophora* and *Avicennia*)   (Ellison et al. 1999). According to a typical zonation pattern for IWP area, the low intertidal zone is colonized by *Aegiceras*, *Avicennia* and *Sonneratia*, the mid-intertidal by *Bruguiera* and *Rhizophora*, and the high intertidal by *Heritiera* and *Xylocarpus* (Robertson and Alongi 1992). Along estuaries, mangroves species differ mainly according to salinity conditions (Bunt et al. 1982). In the ACEP, mangrove forests are quite homogeneous in structure: *Laguncularia* and/or *Avicennia* dominate pioneer seafront and riverine forests, whereas *Rhizophora* appears in a minor proportion in mature coastal and riverine mangroves (Fromard et al. 1998). *Avicennia* tolerates wide salinity ranges and its propagules efficiently settle in mudcracks, thus it can grow in areas with high porewater salinities and evaporation and it can colonize unstable mudbanks (Marchand et al. 2004; Fiot and Gratiot 2006). *Rhizophora* is less tolerant to salinity variation and its seedlings cannot colonize unstable coastal sediments (Lambs et al. 2008). Consequently, in Brazil and French Guiana, weak salinity variations characterize the estuaries for several km inland and mangroves are dominated by *Avicennia*, which often forms monospecific forests, followed by *Rhizophora*. However, mangrove tree zonation patterns are not universal and they cannot be generalized from local observations (Bunt and Williams, 1981). Therefore, mangrove ecologists extensively use a functional classification of mangrove forests, which includes overwash, fringe, riverine, basin, scrub and hammock mangroves (Lugo and Snedaker 1974).

In order to understand the drivers of nematode richness and community composition, two macroecological studies tested the influence of latitude, biogeographical region and presence of mangrove trees using data from all over the world. According to Fonseca and Netto (2015), who compared estuaries at different latitudes and regions, the presence or the absence of mangroves does not significantly affect nematode genus richness. Considering exclusively mangroves, Brustolin et al. (2018) stated that mangrove tree richness cannot explain nematode genus richness. Indeed, nematode genus richness increases towards the Equator but not from the ACEP to the IWP, while mangrove trees richness is much higher in the Indo-Pacific area (Brustolin et al. 2018). While the presence itself of mangrove trees doesn't increase nematode richness, it influences community composition, which changes gradually towards higher latitudes by decreasing turnover (Fonseca and Netto 2015). In other words, nematode assemblages at higher latitudes are poorer in number of genera and their composition can be a subset of lower latitudes assemblages. Moreover, the increasing turnover from ACEP to IWP means that two nematode communities from those two regions will have a highly different genera composition despite having the same genera richness. Three geographical areas were determined according to community composition (first North America and Europe, then Africa, India and East Asia, and lastly South America and Australia), inside which mangrove nematodes were consistently characterized by the genera *Parodontophora*, *Desmodora*, *Trissonchulus* and *Terschellingia* (Fonseca and Netto 2015).

Despite the differences in the analytical methods, both Fonseca and Netto (2015) and Brustolin et al. (2018) highlighted latitude as the most significant factor structuring nematode richness and community composition in estuaries (with or without mangroves) and in mangrove ecosystems (Fig 1). They hypothesized that patterns of nematode distribution might be related to temperature gradients, which suggest the roles of regional environmental and climatic factors in structuring nematode richness at large scales, as also observed for the terrestrial nematodes (Song et al. 2017). Biogeographical region didn't affect genus richness, but it influenced nematode genus composition (Fonseca and Netto 2015) (Fig 1).

However, as the previous authors noted, such meta-analyses at global scale suffer from other limitations, namely the absence of data from some geographical areas (Caribbean Islands, Indonesia, Cambodia), the lack of key environmental parameters (e.g. salinity, oxygen, organic matter content) essential for the interpretation of nematode data, the exclusion of rare genera (only the dominant ones, i.e. >1% of relative abundance, are considered), analytical methods changing between studies, and the representativeness of local (small scale) datasets when considering the whole heterogeneity of a given mangrove area (see Online Resource 1). To our knowledge, none of these meta-analyses tested the influence of the type of vegetation (mangrove tree species), nor the impact of variable environmental conditions within the same vegetation type, on nematode density, richness and community composition at a global scale.

2.2 Local scale drivers

If at the global scale, nematode diversity doesn't mirror the two main biogeographical areas of mangrove distribution (ACEP and IWP) (Fonseca and Netto 2015; Brustolin et al. 2018), at the local scale, nematodes do respond differently according to tree type, which influences density, richness and community composition (Boucher and Gourbault 1990; Vanhove et al. 1992; Netto and Gallucci 2003; Chinnadurai and Fernando 2007; Xuan et al. 2007; Venekey et al. 2019; Mokievsky et al. 2011; Abdullah and Lee 2017; Ghosh and Mandal 2019; Cai et al. 2020 ; Michelet et al. 2021) (Fig 1). Mangrove tree type not only affects the morphology and the chemistry of the sediment, but it also provides different vegetal substrates available for meiofauna colonization (i.e. leaf litter and roots) (Gee and Somerfield 1997; Gwyther and Fairweather 2002; Gwyther 2003; Torres Pratts and Schizas 2007; Gallucci et al. 2020). The spatial heterogeneity due to tree diversity, together with the overall geomorphological and hydrological setting of a given area, can result in different microhabitats even in a single sampling site (Pinto et al. 2013). In those microhabitats, direct (competition, predation) and indirect (bioturbation, microbial degradation) biological interactions are important structuring factors for the nematode community (Alongi 1988; Gwyther 2003). Thus, the interpretation of nematode diversity patterns at local scale should consider both the environmental context and biological interactions.

2.2.1. Vegetation type

The effects of mangrove tree species and habitat heterogeneity on nematode distribution have not been considered in most macroecological studies available in literature, but there is evidence of their influence on nematode diversity and density patterns at a smaller scale. The few studies that take into account the presence of the different types of tree as independent in a given forest patch are all situated in the IWP, whereas to our knowledge there is no such study in the ACEP. In Nha Trang Bay (Vietnam) for instance, nematode density progressively increased along a land-sea continuum from *Rhizophora* (avg 184 ind.10 cm^{-2}) to *Avicennia* (avg 328 ind.10 cm^{-2}) and eventually bare mud (avg 435 ind.10 cm^{-2}). In addition, the various genera exhibited similar relative abundances in the *Rhizophora* site, while dominances were observed in the other biotopes (Mokievsky et al. 2011). Similar patterns were shown elsewhere in Vietnam (Can Gio mangrove), with increasing density from the *Rhizophora* site (1090 ± 334.6 ind.10 cm^{-2}) to the *Avicennia* (1354.7 ± 400 ind.10 cm^{-2}) and bare mud (1759 ± 437 ind.10 cm^{-2}) sites, while the mixed *Avicennia-Rhizophora* sites exhibited the lowest nematode density (968 ± 151.7 ind.10 cm^{-2}) (Xuan et al. 2007). In the Pichavaram estuary (India), *Avicennia*-dominated stations showed the highest nematode density (890 ind.10 cm^{-2}) compared to *Rhizophora* (257 ind.10 cm^{-2}), and genus composition was different (Chinnadurai and Fernando 2007). In the Matla estuary (India), *Sonneratia* occupied the lowest intertidal and sustained the highest nematode density (3100 ± 62 ind.10 cm^{-2}) and richness (17 genera). The *Avicennia* station was second in density (1735 ± 52 ind.10 cm^{-2}) and richness (14 genera), whereas the *Aegiceras*, *Bruguiera* and *Rhizophora* stations exhibited much lower density and diversity (Ghosh and Mandal 2019). By contrast, in Gazi Bay (Kenya), the highest nematode density (4500 ind.10 cm^{-2}) was found in *Bruguiera* stands, followed by *Rhizophora* and then *Avicennia*, *Sonneratia* and *Ceriops* (lowest density: 1700 ind.10 cm^{-2}) (Vanhove et al. 1992). In Australia, nematode density is not consistently higher at low intertidal *Avicennia* stations, for instance in Terranora and Tallebudgera creek there is a decrease in density at mid-intertidal *Rhizophora* stations and an increase at high intertidal *Aegiceras* stations (Abdullah and Lee 2017). Thus, this land-sea gradient in nematode density and diversity, common among different areas in the Indo-Pacific, cannot be generalized. Bare mud nematode communities are nested to *Avicennia* ones overall, while the turnover increases between *Avicennia* and *Rhizophora* communities, except for some dominant genera such as *Paracomesoma* and *Terschellingia* (Xuan et al. 2007; Mokievsky et al. 2011; Cai et al. 2020).

To our knowledge, such relationships between the occurrence of a specific mangrove tree and nematode diversity have not been studied (or shown) for the ACEP. Most of the research on this area is located in Brazil (Netto and Gallucci 2003; Venekey et al. 2019), French Guaiana (Michelet et al. 2021) and Guadeloupe (Boucher and Gourbault 1990). In Ratones estuary (Santa Catarina, Brazil), nematode density and richness decrease and increase inconsistently along the land-sea continuum. Along the Piratuba Reserve coast (Brazil), nematode density and richness were consistently higher in non-vegetated intertidal bare muds rather than in mangroves and the overall diversity was lower compared to other Brazilian locations (Pinto et al. 2013; Netto and Gallucci 2003, Venekey et al. 2019). In the Cayenne estuary (French Guiana) the diversity pattern is more straightforward, since both nematode density and richness increase inland (Michelet et al. 2021). No land-sea transect was realized so far in Guadeloupe, but diversity seems to be generally lower compared to the mentioned studies (Boucher and Gourbault 1990).Such trends in nematode diversity along the land-sea continuums we cited are most likely explained by the physico-chemical gradients specific of every land-sea transect (Fig. 1). For instance, *Avicennia marina* sediments have a higher ratio of silt and clay particles, and clay is known for storing carbon which can be more or less readily available for microbial degradation (Yang et al. 2021). Nematodes may profit from this carbon desorption both directly by feeding on the dissolved organic matter released and indirectly by grazing on the growing bacteria population. Granulometry is known to affect size and composition of the nematode community. Indeed, nematode body shape and consequent locomotion strategy relate to grain size (and oxygen availability) since a long and slender body allows effective movements between particles and displacement between sediment layers. Moreover, an increased ratio of body surface to body diameter supports intensive transepidermal oxygen uptake, useful in harsh conditions (Giere 2009). Nematode diversity can also be shaped by sediment chemistry, which can be altered by the presence of decaying vegetal material, such as wood and leaves and the consequent production of secondary metabolites, such as tannins, which are toxic for meiofauna (Alongi 1987b). Compared to *Avicennia*, the leaves of *Rhizophora*, *Bruguiera* and *Ceriops* release a higher amount of tannins during their decay process. Furthermore, the dissolved organic matter they produce is more refractory compared to *Avicennia* leaves, meaning that it is not readily consumed by nematodes (Gee and Somerfield 1997).

Site-specific environmental conditions may be responsible for the high structural and functional turnover in nematode genera composition between *Avicennia* and *Rhizophora* communities, which indeed share few common genera (Fig. 2). *Avicennia* supports similar relative abundances of epistrate feeders (2A) (Wieser 1953), such as *Dorylaimopsis*, *Hopperia*, *Ptycholaimellus*, *Desmodora* and *Monoposthia*, and detritus feeders (1A, 1B), such as *Terschellingia*, and *Sabatieria*. *Rhizophora* is characterized by detritus feeders (1A, 1B), such as *Daptonema*, *Theristus*, *Sabatieria*, and *Terschellingia*, and omnivores/predators (2B), such as *Metachromadora* and *Viscosia* (Chinnadurai and Fernando 2007; Ghosh and Mandal 2019). Different types of vegetation in a given area can result in the dominance of different trophic groups, for instance at Matla (India), Rhizophora forest patches are mostly colonized by detritus feeders (1A, 1B) and Avicennia by epistrate feeders (2A), despite belonging to the same mangrove forest (Ghosh and Mandal 2019) (Fig. 2). The same type of vegetation in two geographically distinct areas can host the same dominant trophic group. *Avicennia* sites in Zanzibar, in Vietnam and in India are all dominated by group 2A (and secondarily 1B), with the genera *Spirinia*, *Microlaimus* and *Desmodora* (Ólafsson, 1995), *Chromadorella*, *Ptycholaimellus* and *Tripyloides* (Mokievsky et al. 2011), and *Desmodora*, *Monoposthia* and *Sabatieria* (Ghosh and Mandal 2019), respectively (Fig. 2). Regardless of the geographical position of the

Avicennia-dominated forest, its physico-chemical environment filters for nematodes of the group 2A, which can be represented by different genera at the various locations, yet all adopting the same trophic strategy. Hence, taxonomically distinct communities may exhibit some degree of redundancy in their functionality, specifically concerning the trophic group trait. Besides, nematodes with the same trophic habits may differ regarding cuticle ornamentations, tail shape and/or body morphometrics. For instance, *Desmodora* and *Tripyloides* have the most different *habitus*: the first has a strongly striated cuticle, a conical tail and a relatively slender body, while the second has a smooth cuticle, a clavate tail and an overall larger body (de Man 1886, 1889).

In the ACEP, we are not able to establish any causal relationship between a particular mangrove tree species and nematode trophic activity. In the referenced literature, the main tree species (*Avicennia*, *Rhizophora* and *Laguncularia*) are reported to occur together, though with a dominance of *Avicennia*. ACEP mangroves host mostly epistrate-feeders (2A) and detritus-feeders (1A) in a minor proportion in French Guiana and Guadeloupe (Michelet et al. 2021; Boucher and Gourbault 1990) and detritus-feeders (1B, 1A) in Brazil (Netto and Gallucci 2003; Venekey et al. 2019). As for the IWP, different nematode genera, yet belonging to one specific trophic group colonize sites apart from each other, thus taxonomic diversity is enhanced compared to the functional one. For instance, detritus-feeders (1B and 1A) dominating in Brazil are represented by either *Haliplectus*, *Anoplostoma* and *Terschellingia* (Netto and Gallucci 2003) or *Daptonema*, *Elzalia*, *Hypodontholaimus*, *Neochromadora*, *Dichromadora* and *Thalassomonhystera* (Venekey et al. 2019). The dominance of either 2A or 1B-1A depends on the availability of the respective food sources and oscillations of their relative abundances can be observed in mangroves according to season, canopy cover, amount and origin of organic matter. Epistrate-feeders graze on bacteria, protozoa and microphytobenthos and such food sources are more abundant in the warmest months and where water transparency and canopy cover allow light penetration for photosynthesis (Netto and Gallucci 2003). The dominance of this trophic mode in mangroves has been related to chlorophyll *a* and other pigment parameters (Michelet et al. 2021), though the origin of such chlorophyll is yet to be clarified. To our knowledge, the role of mangrove trees in providing epistrate-feeders food sources has not been quantified. Detritus-feeders rely on the high amount of organic matter which deposits in muddy sediments, but the extent to which nematodes feed directly on mangrove-derived low palatable detritus is yet to be quantified.

Trophic group is the most used functional trait in mangroves, but the apparent redundancy of epistrate feeders across spatial scales arises questioning about the sensibility of the trophic group in detecting functional diversity patterns for nematodes in mangroves. Trophic groups could be further subdivided in other functional traits to get more specific traits combinations (mouth morphology for instance), but having more significant results this way is unlikely, because of the relatedness of those traits (Schratzberger et al. 2007). Different functional traits should be tested in a consistent way in order to enhance their liability and efficiency in detecting spatial patterns. So far, nematode functional redundancy in mangroves has not been tested.

According to the aforementioned literature, the decrease in nematode density and diversity is more or less consistent with the presence of *Rhizophora* trees. One could argue that this trend might be simply due to the tidal regime that contributes in driving the zonation of mangroves and benthic fauna and flora. Lower intertidal stations may be more suitable for nematodes than higher intertidal zones because of longer inundation time and subsequent higher turnover of dissolved oxygen and food availability in sediment porewater. Indeed, along the northeast coast of Australia and in Unguja Island (Zanzibar), regardless of the location and the different environmental settings, the low-intertidal sites are consistently the most densely populated by nematodes (Alongi 1987a; Ólafsson 1995). At the opposite, nematode assemblages colonizing high-intertidal sites, such as Muwanda (Zanzibar), which are only inundated during spring tide, show no relevant variation after a single inundation event (Ó lafsson et al. 2000). Muwanda is characterized by hypersalinity due to the evaporation of water after tidal inundation. The nematode assemblage at this site remains stable in density and diversity regardless of the tide, which suggests adaptive metabolism to hypersaline conditions (Ó lafsson et al. 2000). Nematodes showed successive changes from dry to wet season rather than from one tide to another, most likely because tidal inundations didn’t affect salinity as much as rainfall did on a much longer time span (Ó lafsson et al. 2000). In response to high salinity variation (from 0.3 to 6%), marine nematodes up-regulate genes for damage control, osmolytes and collagen production and they reduce neural signaling adopting a quiescent behavior (Xie et al. 2021). So far, *Daptonema*, *Sabatieria*, *Dichromadora* and *Oncholaimus* have been found in association to hypersaline conditions in different localities (Red Sea, India, Zanzibar) (Gerdes et al. 1985; Ó lafsson et al. 2000; Pandiya rajan et al. 2022) and occasionally *Terschellingia* (Alongi 1988) and *Microlaimus* (Ó lafsson et al. 2000).

2.2 .2. Substrate type

Although mangrove sediments may offer the greatest colonizable surface for nematodes, the latter can develop on fallen and rotting mangrove leaves and on pneumatophores as well. Gallucci et al. (2020) tested the influence of either the kind of biological substrate or its position in different environments on the nematode assemblage of Araçà Bay (Brazil). Pneumatophores of *Laguncularia racemosa*, colonized by the macroalgae *Bostrychia* sp. hosted a nematode community dominated by detritus feeders (*Thalassomonhystera* (46%) and *Araeolaimus*

(19%)). The authors didn’t take into account trophic groups, but the high abundance of selective and non-selective detritus feeders can be due to either a decompositional state of the roots or to the sediment that is trapped by the algae, which consequently stores more organic matter. Gwyther and Fairweather (2002) analyzed the nematode community of real *Avicennia*, mimic (wooden-made) and transplanted pneumatophores. Genera richness on natural pneumatophores wa s lower (7 species) compared to the other substrates (23 and 8 species respectively) and the only common genera were *Tri pyloides*, *Diplolaimella* and *Metachromadora*. The reason for the lower nematode richness in natural and transplanted pneumatophores could be found in the production of toxic secondary metabolites (i.e. phenols) by the roots (Gwyther and Fairweather 2002). Nematode genera richness increased with time during the colonization of the pneumatophores and Chromadoridae was the pioneer family. Epistrate feeders (2A), well represented by Chromadoridae were the most abundant trophic group, followed by detritus feeders. 2A nematodes graze on the vegetal cells of the algae growing on the pneumatophores by piercing and sucking their content. Late stages of colonization were characterized by the presence of Monhysteridae, which can be associated with pneumatophores' decomposition processes, since they feed on bacteria.

In the Merbok estuary (Malaysia), *Rhizophora* and *Bruguiera* leaves experimentally placed under *Rhizophora* or *Bruguiera* trees, respectively hosted different nematode communities (Gee and Somerfield, 1997). However, the two kinds of leaves hosted different nematode communities under *Rhizophora* but not under *Bruguiera*, meaning that the environment may be a stronger driving factor under *Bruguiera* (Gee and Somerfield 1997). Despite similar granulometry, tidal height and inundation time between the two biotas, the nematode assemblages were significantly different , suggesting that tree species was a strong driver of nematode community composition . Under *Bruguiera* trees, the sediment surrounding the leaves was a more powerful driver for nematode communities rather than the type of leaf , but the specific responsible sediment variables are yet to be clarified. In order to disentangle the effects of tree-derived and sediment-derived factors on nematode community structure, one could compare leaves samples and cores of the surrounding sediment and trace the origin and composition of the organic matter ingested by the nematodes. .

Leaf decay process would not significantly affect nematode community structure over time. For instance, in Puerto Rico’s *Rhizophora mangle* forest, the nematode communities were quite nested whatever the decay time, with *Adoncholaimus* and *Dichromadora* being dominant and no significant shift in dominance over time (Torres- Pratts and Schizas 2007). Similarly, *Rhizophora* leaves decay stages only differed for relative abundances of the dominant genera *Perspiria, Theristus, Diplolaimella* and *Terschellingia* in the study of Gee and Somerfield (1997).

The taxonomical difference between the nematode communities of the two aforementioned studies was mirrored by a functional one: omnivores-predators (2B) dominated in Torres- Pratts and Schizas (2007), whereas epistrate (2A) and non selective deposit feeders (1B) prevailed in Gee and Somerfield (1997).

It has been suggested that nematode assemblages might be more influenced by the microbial communities developing on the various vegetal substrates (i.e. leaves and roots) than by the substrate itself (Gwyther 2003). Indeed, Alongi (1988) found *Terschellingia longicaudata* to be positively correlated with bacterial growth rates and inversely with bacterial densities. *Oncholaimus brachycercus* (2B group) was positively correlated with flagellates and the overall epistrate-feeders with chlorophyll *a* (Alongi 1988). To our knowledge, there is no study integrating microbes, meiofauna and macrofauna in mangroves, thus the trophic dynamics between the biotic components of the benthos are yet to be clarified.

2.2 .3. Microhabitats

Eventually, the literature agrees on the pitfalls of examining nematode diversity at large scale because of the lack of information and the difficulties in integrating studies using different methodologies (Fonseca and Netto 2015; Brustolin et al. 2018). On the other hand, the former studies highlighted the importance of considering medium and small scale patterns, in order to depict the whole local heterogeneity of the environment. The word “microhabitat” is often used in mangrove studies to refer to any small scale combination of physical and/or chemical feature of the sediment, which constitute a niche for macrofauna, meiofauna and bacteria (Hsieh 1995; Netto and Gallucci 2003; Ross 2006; Cleary et al. 2012; Kon et al. 2011). Netto and Gallucci (2003) refer to microhabitat as the micro conditions generated by the presence of mangrove detritus in the sediment, which is more palatable for meiofauna than for macrofauna. Pinto et al. (2013) tested the hypothesis that nematode assemblages varied significantly among mangrove microhabitats in a 3000 m^2 area in Northeastern Brazil (Pernambuco). The authors compared four intertidal patches of different sediment granulometry (i.e. sandy mud, mud flat, cyanobacterial mat, and mud associated with *Rhizophora mangle*), four epibenthic habitats all including roots closely associated with microbenthic algae and/or sponges and/or sediments, and one single subtidal site in a stream composed of sandy sediments only. The various microhabitats showed significantly different nematode assemblages, with only 5 genera out of 73 common to all sites: *Anoplostoma, Desmodora, Paracanthonchus, Terschellingia* and *Viscosia*. Nonetheless, the genera *Daptonema, Gomphionema* and *Linhomoeus* were dominant in both the sediments associated with microalgae-covered roots and near to *Rhizophora mangle*. Likewise, *Sabatieria*, *Spirinia* and *Terschellingia* were highly specific to both sandy mud and sediments associated with sponge-covered roots. Thus, the presence of sediments on either epibenthic substrate is more important than the substrate itself in defining the nematode community composition (Pinto et al. 2013). Nematode functional traits didn't mirror the taxonomical dissimilarities between microhabitat couples in the latter study: indeed, the grouping could have been different if based on cuticle type or feeding guilds. For instance, the above-cited pairs of microhabitats showed low dissimilarity concerning cuticle types and they contained more than 50% of deposit feeders. It was hard to to identify a specific trophic group as characteristic of a given microhabitat, whereas the type of cuticle ornamentation was related to specific microhabitats, for instance punctuated cuticle was the dominant type at the mudflat, whereas the rows of dots pattern was the most common at the sponge and the rows of structures at the pneumatophores covered by algae microhabitats.

Pinto et al. (2013) applied IndVal analysis (Dufrêne & Legendre 1997) to quantify the specificity of nematode genera to environmental settings. IndVal coefficient combines the relative abundance of a genus and its relative frequency of occurrence in a group of replicates. This index revealed a tight connection between nematode assemblages and mangrove microhabitats. Except for cyanobacterial mat and stream microhabitats, which were characterized by only one genus (respectively *Cobbia* and *Eurystomina*), the other ones exhibited three or four "faithful" genera. *Actinonema*, *Comesa*, *Anoplostoma* and *Pontonema* were specific to the mudflat, whereas *Acanthonchus*, *Araeolaimus*, *Chromadorita* and *Prochromadora* were typical of sediments associated with sponge-covered roots. Sediments associated with algae-covered roots were characterized by *Thalassomonhystera*, *Oncholaimus* and *Microlaimus*. The similarity in community composition between *a priori* different microhabitats led the authors to suggest that the spatial distribution of nematode genera was structured on a larger scale than initially thought. However, interpretation of qualitative data on nematode communities should be cautious when no environmental parameter has been measured. Ideally, microhabitats should be defined according to an accurate screening of environmental conditions prior to sampling the fauna in order to determine causal relationships between nematode composition and environmental forcing.

At the microhabitat scale, biological interactions between macrofauna, meiofauna, microbes and microalgae contribute in shaping the diversity of the nematode communities (Alongi 1988; Gee 1989; Hubas et al. 2010; D'Hondt et al. 2018; Wu et al. 2019). In mangroves, where food is generally not a limiting factor, one could hypothesize that predation is more important than competition in population regulation. However, experiments with crabs found evidence for the importance of both predation of crabs on meiofauna and competition for resources depending on the species of crab and the environmental settings of the study area (Ólafsson and Ndaro

1997; Schrijvers et al. 1997; Abdullah and Lee 2016). The soldier crab Mictyris longicarpus exerts a trophic top-down control on nematodes (Abdullah and Lee 2016), whereas other crabs (Uca spp., Dotilla fenestrata, Sesarma meinerti, Metopograpsus thukuhar) have rather a competitive or disturbance-related interaction with nematodes (Dye and Lasiak 1986; Schrijvers et al. 1995; Schrijvers et al. 1997), or no effect at all (Ólafsson and Ndaro 1997). Nematodes, and more generally meiofauna, are prey for fishes (Gee 1989; Coull et al. 1995) and crustaceans (Dittel et al. 1997) and especially for juveniles and larvae, but there is no evidence of this in mangroves to our knowledge. Competition effect can be confused with disturbance, as it has been the case with gastropods of the genera Terebralia and Cerithidea (Schrijvers et al. 1997; Carlén and Ólafsson 2002). Bioturbation is the main source of sediment disturbance in mangroves and it is mainly ascribed to crabs and to mesofauna (Aschenbroich et al. 2016, 2017), but to our knowledge its effect on nematodes has not been assessed yet. Nematodes could benefit from the micro-niches generated by the sediment reworking and the solute displacement, which take place as a consequence of bioturbation activity (Kristensen et al. 2012). The interaction between nematodes, microbes and microalgae can be direct (grazing), symbiotic and/or indirect, for instance nematodes can stimulate bacterial production thanks to the dispersal of mucus and the activation of geochemical fluxes through bioturbation (Aller and Aller 1992; Traunspurger 1997; Moens et al. 2005; D'Hondt et al. 2018). To our knowledge, the nematodes-microbes-microalgae interaction in mangroves has been investigated only in a correlative way, meaning that the effects they have on each other are only documented as a correlated increase or decrease in abundance (Alongi 1988; Tietjen and Alongi 1990; Faust and Gulledge 1996; Michelet et al. 2020). No direct ingestion rate, enrichment experiment, microscope observation supported by molecular analysis to actually understand such interaction have been performed in mangrove sediments yet. The effect of nematode grazing is not structuring for bacterial communities because of their rapid turnover rates and if available, nematodes seem to prefer microalgae, microphytobenthos and detritus (Giere 2009 and references therein). Those food sources being abundant in mangroves, one could speculate that the interaction nematodes-bacteria could be of an indirect and/or symbiotic origin, but there is no evidence to support this yet. On the other hand, Demopoulos et al. 2007 suggest a potentially important role for sulfur bacteria and 15N-enriched bacteria associated with animal burrows in nematodes diet. Despite the importance of biological interactions in structuring meiofauna and specifically nematode communities, there is an impressive lack of information and studies on them, perhaps because of methodological issues due to the organisms' size. A handful of practical techniques for the investigation of trophic interactions of meiofauna is provided by Majdi et al. 2020.

The structure of biological communities depends on niche-based or dispersal-based processes. For nematodes in mangroves, it has been proposed that the strongest mechanism shaping the community is niche-based, especially species sorting as a consequence of environmental filtering (Brustolin et al. 2021). However, the study of Pinto et al. (2013), who found *a priori* different microhabitats to be colonized by similar nematode communities, seems to support the existence of a degree of local stochasticity, which has been suggested to be potentially relevant at local scale (Gansfort et al. 2020). Local stochasticity implies a low degree of specialization of species and small, rather homogeneous, isolated habitats whose species pool may depend on the dispersal ability of the taxa (Hubbell 2001). At the scale considered, nematodes are not limited by dispersal and the selected microhabitats are *a priori* heterogeneous. Hence, one could argue that (i) the environmental filtering in the selected microhabitats was not strong enough to determine a clear species sorting and (ii), a patch dynamic mechanism was preponderant at local scale. Since patch dynamics usually occur in homogeneous environments, a proper environmental characterization of the microhabitats is unavoidable. The analyzed nematode's functional traits further support the unrevealed potential homogeneity among microhabitats and consequently the hypothesis that different mechanisms could structure the nematode community according to spatial scale.

3. Conclusions and perspectives

At the global scale, the main factor determining nematode richness in mangroves is latitude, with lowest latitudes exhibiting the highest nematode genus richness. Surprisingly, genus richness is not higher in the Indo-Pacific area, where the highest mangrove trees richness is registered. Along this longitudinal gradient, a higher structural complexity of the ecosystem doesn't support a higher nematode richness, but different genus composition. Conversely, at the local scale, a higher structural complexity of the environment supports a higher diversity. Indeed, compared to mangrove-colonized sediments, intertidal bare mud sites generally host a higher density of nematodes, but the same or a lower genus richness. In other words, species loss (nestedness) prevails on species turnover along a land-sea continuum. At this spatial scale, nematode genus composition is mostly influenced by the type of mangrove tree and the surrounding environment rather than the substrate on which the community develops. However, when further reducing the spatial scale, the above mentioned factors may not have the same strength in driving the nematode community: potentially very different microhabitats turned out to host similar nematode communities. Hence, the mechanisms shaping the nematode community could be different according to the spatial scale taken into account, shifting from niche-based to dispersal-based patterns, or to a combination of both.

Trophic group, the most commonly used functional group, showed some degree of redundancy across mangroves worldwide. Epistrate and detritus feeders dominate the ecosystem, without any significant variation among sites but rather fluctuations of the relative importance of each of the two groups. Trophic diversity doesn't mirror taxonomic diversity, indeed taxonomically distinct communities exhibit similar functionality in locations either far apart or near to each other. The efficiency of other seldom used traits (for instance life strategy, cuticle type, buccal morphology and tail shape) in detecting spatial patterns hasn't been assessed in mangroves yet. We promote further testing of different functional traits in order to quantify functional diversity and understand the underlying ecosystem dynamics generating it in space and time.

The classical approach in ecological studies on nematodes is based on a detailed taxonomic identification at genus or species level, which is discussed according to the local environmental filters. Such an approach fuels useful basic knowledge on nematode diversity, but it allows limited exploration of community dynamics, functional interactions and the underlying ecological mechanisms. Recent and cutting-edge ways of analyzing nematode diversity, which broaden the current perspectives should be promoted; they include:

1. analyzing ß-diversity, thus considering the turnover and nestedness components of the diversity of the nematode assemblage in relation to environmental parameters, in order to test how abiotic variables affect replacement and loss of species. ß-diversity offers several advantages when it comes to the analysis of community composition, namely it quantifies the variation of the whole assemblage (taking into account rare species as well) and it reflects the underlying processes determining such diversity (Baselga 2010). Applying this approach while accounting for spatial effects, can allow building a hierarchy of environmental variables responsible for species sorting at different spatial scales (Menegotto et al. 2019).
2. testing Functional Traits Based Approaches (FTBAs), which recently gained popularity because they enable predictions about ecological dynamics in a rapidly changing world (Kremer et al. 2017). FTBAs focus on individual properties of organisms (traits) rather than on the taxonomic identity of the species itself, whose main aim is to relate community structure to ecosystem functioning and services (Martini et al. 2021). Instead of species identification, the nematode dataset can be built on the so-called "response traits", i.e. mostly the morphological and physiological features that influence the colonizing ability of nematodes for a given environment.

3. integrating nematodes, microbes, protozoans and macrofauna, which mutually interact through top-down and bottom-up mechanisms (Schratzberger and Ingels 2018), to elucidate direct and indirect dependency of the different biotic components of the benthos (Baldrighi et al. 2020). This multi-scale approach can identify “core communities” constituted by covarying assemblages strongly driven by shifts in ecosystem properties (Murdock et al. 2021).
4. and exploring metacommunity dynamics, which is a powerful approach to reveal the mechanisms structuring biological communities (either environmental-based or dispersal-based) at different spatial scales (Holyoak et al. 2005; Presley et al. 2010).

Future research on nematodes in mangroves should focus on filling the data gaps existing in less explored areas of the world in order to allow testing for ecological hypotheses at different spatial scales. Moreover, the comparison of the existing literature on nematode diversity suffers from the lack of a common methodological framework (both practical and analytical), and from the unavailability of raw data, which can impede the integration of some publications in global meta-analysis. Hence, we encourage worldwide nematologists to reach a methodological compromise.

Understanding how nematode and more generally benthic infauna diversity is shaped in mangrove forests at different spatial scales is of vital importance when evaluating the potential repercussions of mangroves degradation on biodiversity. Conservation strategies should be designed consequently in order to protect species reservoirs that fuel dispersal, colonization and connectivity patterns of nematode and infauna communities.

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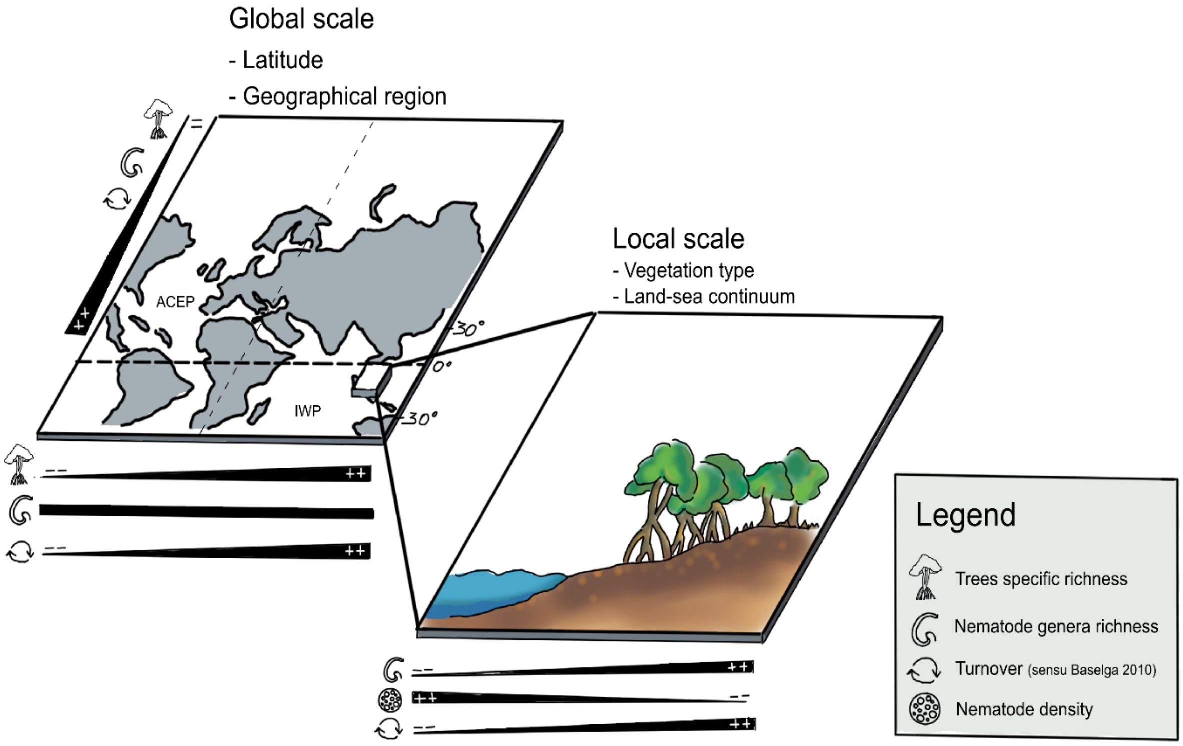
Fig. 1 Patterns of mangrove trees and nematode diversity at global and local scale, together with the respective driving forces. The increase or decrease of a given variable is given by ++ or -- on black bars. At the global scale, tree richness is higher towards the Equator and in the Indo-West Pacific (IWP), while nematode richness increases with latitude but remains constant across geographical regions. The turnover is responsible for differences in community composition, according to both the latitude and geographical regions. At the local scale, nematode genera richness and turnover increase landward, whereas density increases seaward. Vegetation type is likely responsible for differences in nematode community composition along the land-sea continuum, since it affects sediment chemistry

Fig. 2 Map summarizing the distribution of nematode taxonomic and functional diversity according to mangrove tree species in the “Africa, India and East Asia” geographical region (from Ó lafsson et al. 1995; Mokievsky et al. 2011; Ghosh and Mandal, 2019). Dominant nematode communities in *Avicennia* spp. areas are represented in squares and dominant ones in *Rhizophora* spp. in circles. Local taxonomic and functional community changes occurred according to tree species. Different nematode genera, yet all belonging to 2A group, dominated *Avicennia*-colonized IWP sites. Conversely, *Rhizophora*-colonized sites showed taxonomical and functional diversification between the areas



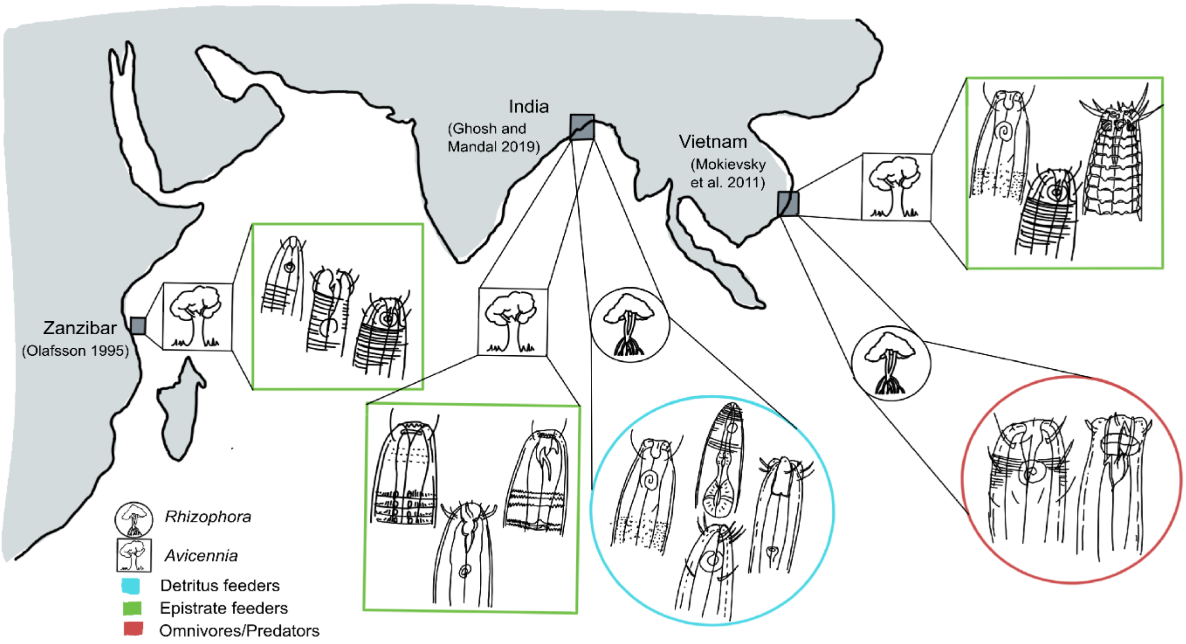


Figure 1 and Figure 2 have been realized with Concepts app (TopHatch 2022) and Inkscape (Inkscape Project 2020).

Statements & Declarations

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Competing Interest

The authors have no relevant financial or non-financial interests to disclose.

Author Contributions

Adriana Spedicato designed the paper, performed the literature search and drafted the manuscript. Emma Michaud contributed in shaping the structure of the manuscript and in revising the content. Gérard Thouzeau revised the manuscript in both content and form. Daniela Zeppilli contributed to the revision.