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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

Acknowledgments

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).

61 Although meiofauna plays an important role in litter degradation and acts like a critical link between

62 microorganisms and higher levels of the food web (Gee, 1989), its role in mangrove carbon dynamics and fluxes

63 is not yet quantified (Schratzberger and Ingels 2018 and references therein).

64 Metazoan meiofauna includes 24 of the 35 animal phyla, plus several protist groups as well as the taxon

65 Foraminifera, and it encompasses all benthic metazoans with an upper size limit of 1000 μm and a lower of 20 μm

66 (Giere 2009). Because of its short life cycle, high diversity and density, ubiquitous distribution in soft (sediments)

67 and hard (roots, animal tubes) substrates, and sensitivity to environmental changes, meiofauna has already been

68 used to test the effects of natural and anthropogenic forcings and it proved to be a good indicator for climate change

69 and anthropogenic impacts in shallow waters and deep sea, in tropical, temperate and polar ecosystems (Zeppilli

70 et al. 2015a). Nonetheless, the lack of taxonomic information from poorly explored areas such as mangroves,

71 together with the scarcity of studies integrating environmental monitoring and biological datasets, hinder our

72 understanding on meiofauna dynamics and functioning in such areas and its routine use in impact studies (Zeppilli

73 et al. 2015a). Nematodes could be good candidates for impact studies in mangroves since they represent over 90%

74 of total meiofauna abundance in mangrove sediments, with high densities (up to 5000 ind.10cm^{-2}) allowing the

75 collection of small, yet statistically significant samples (Somerfield and Warwick 2013; Schenk et al. 2020;

76 Venekey et al. 2016; Venekey et al. 2019).

77 The environmental factors structuring nematode diversity in a variety of aquatic ecosystems (e.g. deep sea,

78 intertidal, freshwater) have been investigated for decades, resulting in a common set of drivers (food availability,

79 substrate type, physical disturbance, physico-chemical characteristics as the salinity, grain size, redox potential),

80 which can be differently hierarchized according to the ecosystem and spatial scales (Giere 2009; Vanreusel et al.

81 2010; Venekey et al. 2010; Sahoo et al. 2013; Abdullah and Lee, 2017; Rosli et al. 2018 ; Michelet et al. 2021).

82 Recent research in tropical mangrove forests addressed whether environmental filtering is the most powerful

83 mechanism regulating nematode diversity compared to dispersal-based ones, regardless of the spatial scale

84 (Brustolin et al. 2021). At the landscape scale, habitat selection shapes nematode community and metacommunity

85 organization in mangroves is most likely the result of the interaction between species sorting and patch-dynamics

86 (Brustolin et al. 2021). An effective but poorly explored way to unravel patterns of species sorting (intended as

87 the effect of environmental variables, dispersal and stochasticity on the capacity of a given species to colonize a

88 given habitat) is analyzing the β-diversity of a community by partitioning it in its nestedness (species loss) and

89 turnover (species replacement) components (Baselga, 2010). Nestedness occurs between two assemblages when

90 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

121 exploitation, tourism and all other mangrove-related human activities should be designed considering every

122 component of the mangrove ecosystem (trees, water column and sediments, with their flora and fauna) in order to

123 reverse the dramatic rate of forest loss (Ellison 2008). In this review, the available studies on the biodiversity, the

124 ecology and the adaptations of nematodes to mangrove ecosystems are analyzed in order to understand: i) how

125 mangrove environmental filters are acting on nematode communities in terms of diversity, density and functional

126 traits, and ii) if the ecological mechanisms shaping nematode communities change according to the spatial scale

127 of observation. Then, strategies to improve current knowledge and overcome limitations in mangrove nematode

128 research are discussed. Eventually, the present review suggests further avenues of nematode research in order to

129 legitimize their use as bioindicators, in view of the elaboration of future sustainable management plans.

130

2. Environmental filters acting at different spatial scales

2.1 Global scale drivers

134 Mangrove forests are mainly found in river deltas, lagoons and estuarine zones throughout the coastlines of tropical

135 regions between 30°N and 30°S (Robertson and Alongi 1992). Because of the Earth's plate separation, two

136 biogeographic areas of distribution are distinguished nowadays, the Atlantic-Caribbean-East Pacific (ACEP) and

137 the Indo-West Pacific (IWP) (Alongi 2016). IWP hosts the greatest tree diversity (36 species), whereas in ACEP

138 there are 15 species, of which 2 were introduced by man (Day et al 2013). These two areas only share 3 common

139 genera of mangrove trees (*Acrostichum*, *Rhizophora* and *Avicennia*)   (Ellison et al. 1999). According to a typical

140 zonation pattern for IWP area, the low intertidal zone is colonized by *Aegiceras*, *Avicennia* and *Sonneratia*, the

141 mid-intertidal by *Bruguiera* and *Rhizophora*, and the high intertidal by *Heritiera* and *Xylocarpus* (Robertson and

142 Alongi 1992). Along estuaries, mangroves species differ mainly according to salinity conditions (Bunt et al. 1982).

143 In the ACEP, mangrove forests are quite homogeneous in structure: *Laguncularia* and/or *Avicennia* dominate

144 pioneer seafront and riverine forests, whereas *Rhizophora* appears in a minor proportion in mature coastal and

145 riverine mangroves (Fromard et al. 1998). *Avicennia* tolerates wide salinity ranges and its propagules efficiently

146 settle in mudcracks, thus it can grow in areas with high porewater salinities and evaporation and it can colonize

147 unstable mudbanks (Marchand et al. 2004; Fiot and Gratiot 2006). *Rhizophora* is less tolerant to salinity variation

148 and its seedlings cannot colonize unstable coastal sediments (Lambs et al. 2008). Consequently, in Brazil and

149 French Guiana, weak salinity variations characterize the estuaries for several km inland and mangroves are

150 dominated by *Avicennia*, which often forms monospecific forests, followed by *Rhizophora*. However, mangrove

151 tree zonation patterns are not universal and they cannot be generalized from local observations (Bunt and

152 Williams, 1981). Therefore, mangrove ecologists extensively use a functional classification of mangrove forests,

153 which includes overwash, fringe, riverine, basin, scrub and hammock mangroves (Lugo and Snedaker 1974).

154 In order to understand the drivers of nematode richness and community composition, two macroecological studies

155 tested the influence of latitude, biogeographical region and presence of mangrove trees using data from all over

156 the world. According to Fonseca and Netto (2015), who compared estuaries at different latitudes and regions, the

157 presence or the absence of mangroves does not significantly affect nematode genus richness. Considering

158 exclusively mangroves, Brustolin et al. (2018) stated that mangrove tree richness cannot explain nematode genus

159 richness. Indeed, nematode genus richness increases towards the Equator but not from the ACEP to the IWP, while

160 mangrove trees richness is much higher in the Indo-Pacific area (Brustolin et al. 2018). While the presence itself

161 of mangrove trees doesn't increase nematode richness, it influences community composition, which changes

162 gradually towards higher latitudes by decreasing turnover (Fonseca and Netto 2015). In other words, nematode

163 assemblages at higher latitudes are poorer in number of genera and their composition can be a subset of lower

164 latitudes assemblages. Moreover, the increasing turnover from ACEP to IWP means that two nematode

165 communities from those two regions will have a highly different genera composition despite having the same

166 genera richness. T hree geographical areas were determined according to community composition (first North

167 America and Europe, then Africa, India and East Asia, and lastly South America and Australia), inside which

168 mangrove nematodes were consistently characterized by the genera *Parodontophora*, *Desmodora*, *Trissonchulus*

169 and *Terschellingia* (Fonseca and Netto 2015).

170 Despite the differences in the analytical methods, both Fonseca and Netto (2015) and Brustolin et al. (2018)

171 highlighted latitude as the most significant factor structuring nematode richness and community composition in

172 estuaries (with or without mangroves) and in mangrove ecosystems (Fig 1). They hypothesized that patterns of

173 nematode distribution might be related to temperature gradients, which suggest the roles of regional environmental

174 and climatic factors in structuring nematode richness at large scales, as also observed for the terrestrial nematodes

175 (Song et al. 2017). Biogeographical region didn't affect genus richness, but it influenced nematode genus

176 composition (Fonseca and Netto 2015) (Fig 1).

177 However, as the previous authors noted, such meta-analyses at global scale suffer from other limitations, namely

178 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

208 eventually bare mud (avg 435 ind.10 cm^{-2}). In addition, the various genera exhibited similar relative abundances

209 in the *Rhizophora* site, while dominances were observed in the other biotopes (Mokievsky et al. 2011). Similar

210 patterns were shown elsewhere in Vietnam (Can Gio mangrove), with increasing density from the *Rhizophora* site

211 (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})

212 sites, while the mixed *Avicennia-Rhizophora* sites exhibited the lowest nematode density (968 ± 151.7 ind.10 cm^{-2}

213 ^{2}) (Xuan et al. 2007). In the Pichavaram estuary (India), *Avicennia*-dominated stations showed the highest

214 nematode density (890 ind.10 cm^{-2}) compared to *Rhizophora* (257 ind.10 cm^{-2}), and genus composition was

215 different (Chinnadurai and Fernando 2007). In the Matla estuary (India), *Sonneratia* occupied the lowest intertidal

216 and sustained the highest nematode density (3100 ± 62 ind.10 cm^{-2}) and richness (17 genera). The *Avicennia* station

217 was second in density (1735 ± 52 ind.10 cm^{-2}) and richness (14 genera), whereas the *Aegiceras*, *Bruguiera* and

218 *Rhizophora* stations exhibited much lower density and diversity (Ghosh and Mandal 2019). By contrast, in Gazi

219 Bay (Kenya), the highest nematode density (4500 ind.10 cm^{-2}) was found in *Bruguiera* stands, followed by

220 *Rhizophora* and then *Avicennia*, *Sonneratia* and *Ceriops* (lowest density: 1700 ind.10 cm^{-2}) (Vanhove et al. 1992).

221 In Australia, nematode density is not consistently higher at low intertidal *Avicennia* stations, for instance in

222 Terranora and Tallebudgera creek there is a decrease in density at mid-intertidal *Rhizophora* stations and an

223 increase at high intertidal *Aegiceras* stations (Abdullah and Lee 2017). Thus, this land-sea gradient in nematode

224 density and diversity, common among different areas in the Indo-Pacific, cannot be generalized. Bare mud

225 nematode communities are nested to *Avicennia* ones overall, while the turnover increases between *Avicennia* and

226 *Rhizophora* communities, except for some dominant genera such as *Paracomesoma* and *Terschellingia* (Xuan et

227 al. 2007; Mokievsky et al. 2011; Cai et al. 2020).

228 To our knowledge, such relationships between the occurrence of a specific mangrove tree and nematode

229 diversity have not been studied (or shown) for the ACEP. Most of the research on this area is located in Brazil

230 (Netto and Gallucci 2003; Venekey et al. 2019), French Guaiana (Michelet et al. 2021) and Guadeloupe

231 (Boucher and Gourbault 1990). In Ratones estuary (Santa Catarina, Brazil), nematode density and richness

232 decrease and increase inconsistently along the land-sea continuum. Along the Piratuba Reserve coast (Brazil),

233 nematode density and richness were consistently higher in non-vegetated intertidal bare muds rather than in

234 mangroves and the overall diversity was lower compared to other Brazilian locations (Pinto et al. 2013; Netto

235 and Gallucci 2003, Venekey et al. 2019). In the Cayenne estuary (French Guiana) the diversity pattern is more

236 straightforward, since both nematode density and richness increase inland (Michelet et al. 2021). No land-

237 sea transect was realized so far in Guadeloupe, but diversity seems to be generally lower compared to the

238 mentioned studies (Boucher and Gourbault 1990).Such trends in nematode diversity along the land-sea

239 continuums we cited are most likely explained by the physico-chemical gradients specific of every land-sea

240 transect (Fig. 1). For instance, *Avicennia marina* sediments have a higher ratio of silt and clay particles, and clay

241 is known for storing carbon which can be more or less readily available for microbial degradation (Yang et al.

242 2021). Nematodes may profit from this carbon desorption both directly by feeding on the dissolved organic matter

243 released and indirectly by grazing on the growing bacteria population. Granulometry is known to affect size and

244 composition of the nematode community. Indeed, nematode body shape and consequent locomotion strategy relate

245 to grain size (and oxygen availability) since a long and slender body allows effective movements between particles

246 and displacement between sediment layers. Moreover, an increased ratio of body surface to body diameter supports

247 intensive transepidermal oxygen uptake, useful in harsh conditions (Giere 2009). Nematode diversity can also be

248 shaped by sediment chemistry, which can be altered by the presence of decaying vegetal material, such as wood

249 and leaves and the consequent production of secondary metabolites, such as tannins, which are toxic for meiofauna

250 (Alongi 1987b). Compared to *Avicennia*, the leaves of *Rhizophora*, *Bruguiera* and *Ceriops* release a higher amount

251 of tannins during their decay process. Furthermore, the dissolved organic matter they produce is more refractory

252 compared to *Avicennia* leaves, meaning that it is not readily consumed by nematodes (Gee and Somerfield 1997).

253 Site-specific environmental conditions may be responsible for the high structural and functional turnover in

254 nematode genera composition between *Avicennia* and *Rhizophora* communities, which indeed share few common

255 genera (Fig. 2). *Avicennia* supports similar relative abundances of epistrate feeders (2A) (Wieser 1953), such as

256 *Dorylaimopsis*, *Hopperia*, *Ptycholaimellus*, *Desmodora* and *Monoposthia*, and detritus feeders (1A, 1B), such as

257 *Terschellingia*, and *Sabatieria*. *Rhizophora* is characterized by detritus feeders (1A, 1B), such as *Daptonema*,

258 *Theristus*, *Sabatieria*, and *Terschellingia,* and omnivores/predators (2B), such as *Metachromadora* and *Viscosia*

259 (Chinnadurai and Fernando 2007; Ghosh and Mandal 2019).   Different types of vegetation in a given area can

260 result in the dominance of different trophic groups, for instance at Matla (India), Rhizophora forest patches are

261 mostly colonized by detritus feeders (1A, 1B) and Avicennia by epistrate feeders (2A), despite belonging to the

262 same mangrove forest (Ghosh and Mandal 2019) (Fig. 2).   The same type of vegetation in two geographically

263 distinct areas can host the same dominant trophic group. *Avicennia* sites in Zanzibar, in Vietnam and in India are

264 all dominated by group 2A (and secondarily 1B), with the genera *Spirinia*, *Microlaimus* and *Desmodora* (Ólafsson,

265 1995), *Chromadorella*, *Ptycholaimellus* and *Tripyloides* (Mokievsky et al. 2011), and *Desmodora*, *Monoposthia*

266 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

296 more specific traits combinations (mouth morphology for instance), but having more significant results this way i

297 s unlikely, because of the relatedness of those traits (Schratzberger et al. 2007). Different functional traits should

298 be tested in a consistent way in order to enhance their liability and efficiency in detecting spatial patterns. So far,

299 nematode functional redundancy in mangroves has not been tested.

300 According to the aforementioned literature, the decrease in nematode density and diversity is more or less

301 consistent with the presence of *Rhizophora* trees. One could argue that this trend might be simply due to the tidal

302 regime that contributes in driving the zonation of mangroves and benthic fauna and flora. Lower intertidal stations

303 may be more suitable for nematodes than higher intertidal zones because of longer inundation time and subsequent

304 higher turnover of dissolved oxygen and food availability in sediment porewater. Indeed, along the northeast coast

305 of Australia and in Unguja Island (Zanzibar), regardless of the location and the different environmental settings,

306 the low-intertidal sites are consistently the most densely populated by nematodes (Alongi 1987a; Ólafsson 1995).

307 At the opposite, nematode assemblages colonizing high-intertidal sites, such as Muwanda (Zanzibar), which are

308 only inundated during spring tide, show no relevant variation after a single inundation event (Ó lafsson et al. 2000).

309 Muwanda is characterized by hypersalinity due to the evaporation of water after tidal inundation. The nematode

310 assemblage at this site remains stable in density and diversity regardless of the tide, which suggests adaptive

311 metabolism to hypersaline conditions (Ó lafsson et al. 2000). Nematodes showed successive changes from dry to

312 wet season rather than from one tide to another, most likely because tidal inundations didn't affect salinity as much

313 as rainfall did on a much longer time span (Ó lafsson et al. 2000). In response to high salinity variation (from 0.3

314 to 6%), marine nematodes up-regulate genes for damage control, osmolytes and collagen production and they

315 reduce neural signaling adopting a quiescent behavior (Xie et al. 2021). So far, *Daptonema*, *Sabatieria*,

316 *Dichromadora* and *Oncholaimus* have been found in association to hypersaline conditions in different localities

317 (Red Sea, India, Zanzibar) (Gerdes et al. 1985; Ó lafsson et al. 2000; Pandiya rajan et al. 2022) and occasionally

318 *Terschellingia* (Alongi 1988) and *Microlaimus* (Ó lafsson et al. 2000).

2.2 .2. Substrate type

320 Although mangrove sediments may offer the greatest colonizable surface for nematodes, the latter can develop on

321 fallen and rotting mangrove leaves and on pneumatophores as well. Gallucci et al. (2020) tested the influence of

322 either the kind of biological substrate or its position in different environments on the nematode assemblage of

323 Araçà Bay (Brazil). Pneumatophores of *Laguncularia racemosa*, colonized by the macroalgae *Bostrychia* sp.

324 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).

354 The taxonomical difference between the nematode communities of the two aforementioned studies was mirrored

355 by a functional one: omnivores-predators (2B) dominated in Torres- Pratts and Schizas (2007), whereas epistrate

356 (2A) and non selective deposit feeders (1B) prevailed in Gee and Somerfield (1997).

357 It has been suggested that nematode assemblages might be more influenced by the microbial communities

358 developing on the various vegetal substrates (i.e. leaves and roots) than by the substrate itself (Gwyther 2003).

359 Indeed, Alongi (1988) found *Terschellingia longicaudata* to be positively correlated with bacterial growth rates

360 and inversely with bacterial densities. *Oncholaimus brachycercus* (2B group) was positively correlated with

361 flagellates and the overall epistrate-feeders with chlorophyll *a* (Alongi 1988). To our knowledge, there is no study

362 integrating microbes, meiofauna and macrofauna in mangroves, thus the trophic dynamics between the biotic

363 components of the benthos are yet to be clarified.

2.2 .3. Microhabitats

365 Eventually, the literature agrees on the pitfalls of examining nematode diversity at large scale because of the lack

366 of information and the difficulties in integrating studies using different methodologies (Fonseca and Netto 2015;

367 Brustolin et al. 2018). On the other hand, the former studies highlighted the importance of considering medium

368 and small scale patterns, in order to depict the whole local heterogeneity of the environment. The word

369 "microhabitat" is often used in mangrove studies to refer to any small scale combination of physical and/or

370 chemical feature of the sediment, which constitute a niche for macrofauna, meiofauna and bacteria (Hsieh 1995;

371 Netto and Gallucci 2003; Ross 2006; Cleary et al. 2012; Kon et al. 2011). Netto and Gallucci (2003) refer to

372 microhabitat as the micro conditions generated by the presence of mangrove detritus in the sediment, which is

373 more palatable for meiofauna than for macrofauna. Pinto et al. (2013) tested the hypothesis that nematode

374 assemblages varied significantly among mangrove microhabitats in a 3000 m^2 area in Northeastern Brazil

375 (Pernambuco). The authors compared four intertidal patches of different sediment granulometry (i.e. sandy mud,

376 mud flat, cyanobacterial mat, and mud associated with *Rhizophora mangle*), four epibenthic habitats all including

377 roots closely associated with microbenthic algae and/or sponges and/or sediments, and one single subtidal site in

378 a stream composed of sandy sediments only. The various microhabitats showed significantly different nematode

379 assemblages, with only 5 genera out of 73 common to all sites: *Anoplostoma*, *Desmodora*, *Paracanthonchus*,

380 *Terschellingia* and *Viscosia*. Nonetheless, the genera *Daptonema*, *Gomphionema* and *Linhomoeus* were dominant

381 in both the sediments associated with microalgae-covered roots and near to *Rhizophora mangle*. Likewise,

382 *Sabatieria*, *Spirinia* and *Terschellingia* were highly specific to both sandy mud and sediments associated with

383 sponge-covered roots. Thus, the presence of sediments on either epibenthic substrate is more important than the

384 substrate itself in defining the nematode community composition (Pinto et al. 2013). Nematode functional traits

385 didn't mirror the taxonomical dissimilarities between microhabitat couples in the latter study: indeed, the grouping

386 could have been different if based on cuticle type or feeding guilds. For instance, the above-cited pairs of

387 microhabitats showed low dissimilarity concerning cuticle types and they contained more than 50% of deposit

388 feeders. It was hard to to identify a specific trophic group as characteristic of a given microhabitat, whereas the

389 type of cuticle ornamentation was related to specific microhabitats, for instance punctuated cuticle was the

390 dominant type at the mudflat, whereas the rows of dots pattern was the most common at the sponge and the rows

391 of structures at the pneumatophores covered by algae microhabitats.

392 Pinto et al. (2013) applied IndVal analysis (Dufrêne & Legendre 1997) to quantify the specificity of nematode

393 genera to environmental settings. IndVal coefficient combines the relative abundance of a genus and its relative

394 frequency of occurrence in a group of replicates. This index revealed a tight connection between nematode

395 assemblages and mangrove microhabitats. Except for cyanobacterial mat and stream microhabitats, which were

396 characterized by only one genus (respectively *Cobbia* and *Eurystomina*), the other ones exhibited three or four

397 "faithful" genera. *Actinonema*, *Comesa*, *Anoplostoma* and *Pontonema* were specific to the mudflat, whereas

398 *Acanthonchus*, *Araeolaimus*, *Chromadorita* and *Prochromadora* were typical of sediments associated with

399 sponge-covered roots. Sediments associated with algae-covered roots were characterized by *Thalassomonhystera*,

400 *Oncholaimus* and *Microlaimus*. The similarity in community composition between *a priori* different microhabitats

401 led the authors to suggest that the spatial distribution of nematode genera was structured on a larger scale than

402 initially thought. However, interpretation of qualitative data on nematode communities should be cautious when

403 no environmental parameter has been measured. Ideally, microhabitats should be defined according to an accurate

404 screening of environmental conditions prior to sampling the fauna in order to determine causal relationships

405 between nematode composition and environmental forcing.

406 At the microhabitat scale, biological interactions between macrofauna, meiofauna, microbes and microalgae

407 contribute in shaping the diversity of the nematode communities (Alongi 1988; Gee 1989; Hubas et al. 2010;

408 D'Hondt et al. 2018; Wu et al. 2019). In mangroves, where food is generally not a limiting factor, one could

409 hypothesize that predation is more important than competition in population regulation. However, experiments

410 with crabs found evidence for the importance of both predation of crabs on meiofauna and competition for

411 resources depending on the species of crab and the environmental settings of the study area (Ólafsson and Ndaro

412 1997; Schrijvers et al. 1997; Abdullah and Lee 2016). The soldier crab Mictyris longicarpus exerts a trophic top-

413 down control on nematodes (Abdullah and Lee 2016), whereas other crabs (Uca spp., Dotilla fenestrata, Sesarma

414 meinerti, Metopograpsus thukuhar) have rather a competitive or disturbance-related interaction with nematodes

415 (Dye and Lasiak 1986; Schrijvers et al. 1995; Schrijvers et al. 1997), or no effect at all (Ólafsson and Ndaro 1997).

416 Nematodes, and more generally meiofauna, are prey for fishes (Gee 1989; Coull et al. 1995) and crustaceans (Dittel

417 et al. 1997) and especially for juveniles and larvae, but there is no evidence of this in mangroves to our knowledge.

418 Competition effect can be confused with disturbance, as it has been the case with gastropods of the genera

419 Terebralia and Cerithidea (Schrijvers et al. 1997; Carlén and Ólafsson 2002). Bioturbation is the main source of

420 sediment disturbance in mangroves and it is mainly ascribed to crabs and to mesofauna (Aschenbroich et al. 2016,

421 2017), but to our knowledge its effect on nematodes has not been assessed yet. Nematodes could benefit from the

422 micro-niches generated by the sediment reworking and the solute displacement, which take place as a consequence

423 of bioturbation activity (Kristensen et al. 2012). The interaction between nematodes, microbes and microalgae can

424 be direct (grazing), symbiotic and/or indirect, for instance nematodes can stimulate bacterial production thanks to

425 the dispersal of mucus and the activation of geochemical fluxes through bioturbation (Aller and Aller 1992;

426 Traunspurger 1997; Moens et al. 2005; D'Hondt et al. 2018). To our knowledge, the nematodes-microbes-

427 microalgae interaction in mangroves has been investigated only in a correlative way, meaning that the effects they

428 have on each other are only documented as a correlated increase or decrease in abundance (Alongi 1988; Tietjen

429 and Alongi 1990; Faust and Gulledge 1996; Michelet et al. 2020). No direct ingestion rate, enrichment experiment,

430 microscope observation supported by molecular analysis to actually understand such interaction have been

431 performed in mangrove sediments yet. The effect of nematode grazing is not structuring for bacterial communities

432 because of their rapid turnover rates and if available, nematodes seem to prefer microalgae, microphytobenthos

433 and detritus (Giere 2009 and references therein). Those food sources being abundant in mangroves, one could

434 speculate that the interaction nematodes-bacteria could be of an indirect and/or symbiotic origin, but there is no

435 evidence to support this yet. On the other hand, Demopoulos et al. 2007 suggest a potentially important role for

436 sulfur bacteria and 15N-enriched bacteria associated with animal burrows in nematodes diet. Despite the

437 importance of biological interactions in structuring meiofauna and specifically nematode communities, there is an

438 impressive lack of information and studies on them, perhaps because of methodological issues due to the

439 organisms' size. A handful of practical techniques for the investigation of trophic interactions of meiofauna is

440 provided by Majdi et al. 2020.

15

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

469 the spatial scale taken into account, shifting from niche-based to dispersal-based patterns, or to a combination of
470 both.

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

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

484 1. analyzing ß-diversity, thus considering the turnover and nestedness components of the diversity of the
485 nematode assemblage in relation to environmental parameters, in order to test how abiotic variables affect
486 replacement and loss of species. ß-diversity offers several advantages when it comes to the analysis of
487 community composition, namely it quantifies the variation of the whole assemblage (taking into account
488 rare species as well) and it reflects the underlying processes determining such diversity (Baselga 2010).
489 Applying this approach while accounting for spatial effects, can allow building a hierarchy of
490 environmental variables responsible for species sorting at different spatial scales (Menegotto et al. 2019).

491 2. testing Functional Traits Based Approaches (FTBAs), which recently gained popularity because they
492 enable predictions about ecological dynamics in a rapidly changing world (Kremer et al. 2017). FTBAs
493 focus on individual properties of organisms (traits) rather than on the taxonomic identity of the species
494 itself, whose main aim is to relate community structure to ecosystem functioning and services (Martini et
495 al. 2021). Instead of species identification, the nematode dataset can be built on the so-called "response
496 traits", i.e. mostly the morphological and physiological features that influence the colonizing ability of
497 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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815 **Fig. 1** Patterns of mangrove trees and nematode diversity at global and local scale, together with the respective

816 driving forces. The increase or decrease of a given variable is given by ++ or -- on black bars. At the global scale,

817 tree richness is higher towards the Equator and in the Indo-West Pacific (IWP), while nematode richness increases

818 with latitude but remains constant across geographical regions. The turnover is responsible for differences in

819 community composition, according to both the latitude and geographical regions. At the local scale, nematode

820 genera richness and turnover increase landward, whereas density increases seaward. Vegetation type is likely

821 responsible for differences in nematode community composition along the land-sea continuum, since it affects

822 sediment chemistry

823

824 **Fig. 2** Map summarizing the distribution of nematode taxonomic and functional diversity according to mangrove

825 tree species in the "Africa, India and East Asia" geographical region (from Ó lafsson et al. 1995; Mokievsky et al.

826 2011; Ghosh and Mandal, 2019). Dominant nematode communities in *Avicennia* spp. areas are represented in

827 squares and dominant ones in *Rhizophora* spp. in circles. Local taxonomic and functional community changes

828 occurred according to tree species. Different nematode genera, yet all belonging to 2A group, dominated

829 *Avicennia*-colonized IWP sites. Conversely, *Rhizophora*-colonized sites showed taxonomical and functional
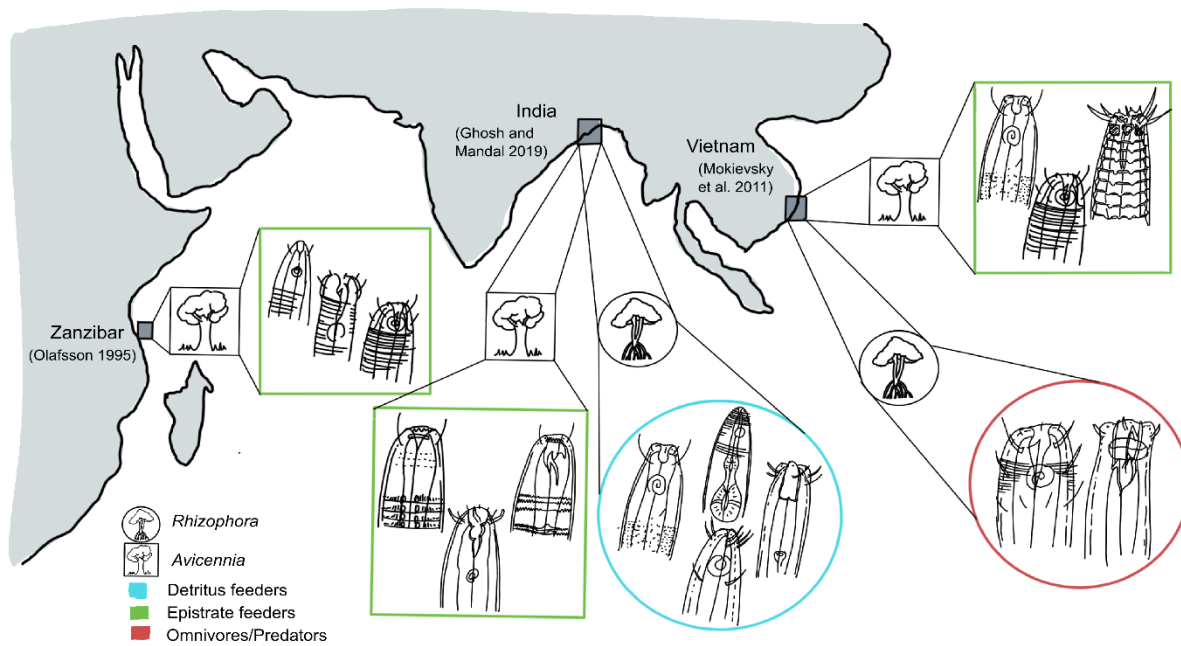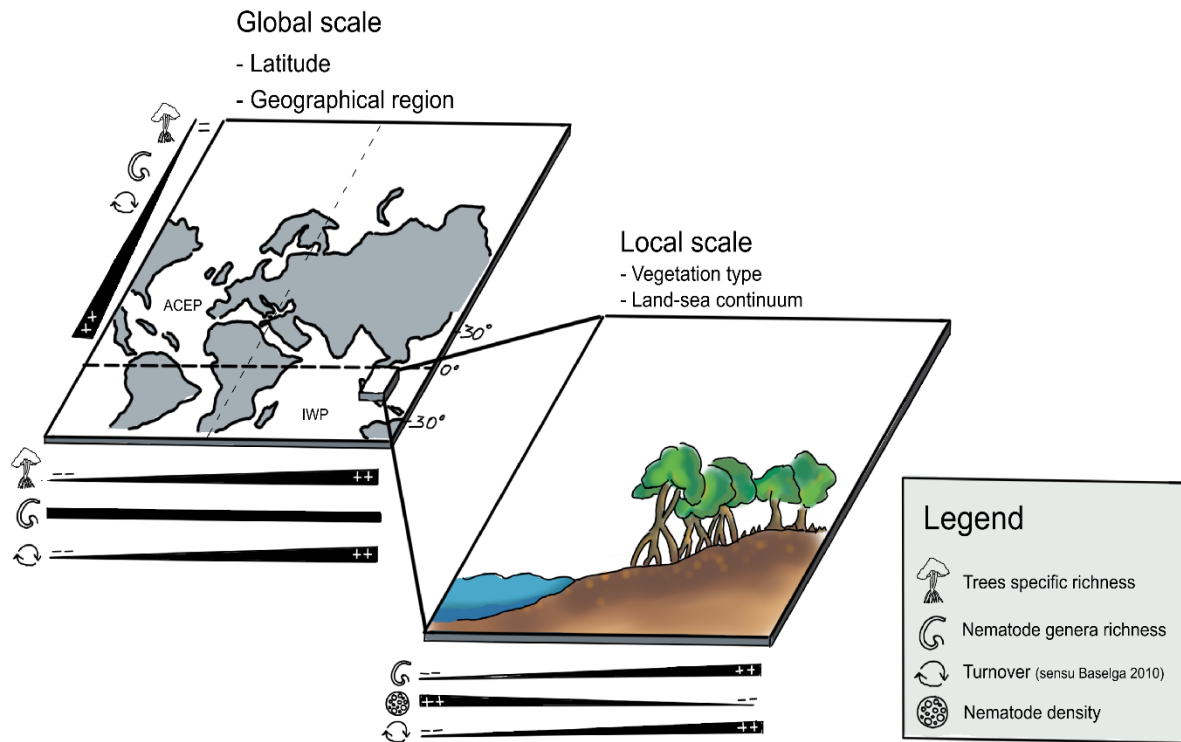
830 diversification between the areas

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

Statements & Declarations

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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.