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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.

32 Keywords

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

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35

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41

42

43 1. Introduction

44

45 Mangrove forests grow along tropical intertidal coastlines, estuaries, lagoons and they penetrate inland as far as

46 the tide can reach (Walsh 1974). Mangroves are made up of trees that thrive in unusual conditions, such as

47 alternatively waterlogged and drained saline soils (Walsh 1974). Even though mangroves are able to store vast

48 amounts of carbon and mitigate the effect of catastrophic climatic events on the shoreline, there is evidence they

49 could disappear within the next century because of anthropogenic activities (Duke et al. 2007). A 20 to 35%

50 decrease in worldwide mangrove surface areas has already been observed in the last 50 years (Polidoro et al. 2010).

51 A moderate proportion of the world's mangrove forests also are to be greatly affected by seawater level and

52 sediment subsidence (Alongi 2008 for review).

53 Mangrove forests cover about 137 760 km² of sheltered tropical and subtropical coastlines (Giri et al. 2011) and

54 they offer extremely valuable services to both humans and biodiversity as a whole (Nagelkerken et al. 2008). The

55 rate of mangrove primary production equals that of tropical humid evergreen forests, thus making mangroves vital

56 contributors in C sequestration (Alongi 2009). Carbon dynamics, storage and mineralization are hot topics for

57 mangrove research, and some gaps persist in knowledge regarding the role of the benthic compartment in those

58 processes (Lee et al. 2014). Mangroves' soft sediments are colonized by macrofaunal organisms, such as crabs

59 and polychaetes, and many other small invertebrates among which meiofauna is numerically dominant (Alongi

60 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 (Sommerfield 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

91 implies the replacement of species between two assemblages as a result of either environmental forcing, spatial or
92 historical constraints (Legendre et al. 2005). The β -diversity concept can be applied to explore the functional
93 diversity of the community as well, by substituting species with functional traits (Cardoso et al. 2014; Martini et
94 al. 2021). Although there is still no widely acknowledged and validated set of functional traits for marine
95 nematodes, the literature usually refers to life strategy (Bongers 1990; Bongers et al. 1991, 1995), tail shape
96 (Thistle et al. 1995), body cuticle (Pinto et al. 2013; Raes and Vanreusel 2006 ; Semprucci et al. 2014 , Semprucci
97 et al. 2018), body size and shape (Schratzberger et al. 2007; Alves et al. 2014), shape of amphideal fovea
98 (Semprucci et al. 2018) and morphology of the buccal cavity (Wieser, 1953; Moens and Vincx 1997; Hodda 2022).
99 The two approaches have been used for macrofauna diversity in mangroves (Menegotto et al. 2019; Cannicci et
100 al. 2021) and for nematodes in temperate estuaries (Alves et al. 2014; Sroczynska et al. 2021), but they are still
101 unexplored for nematodes in mangroves.

102 Besides, nematodes can provide a complementary tool relevant for conservation purposes as they may serve as a
103 cost-efficient biological indicator of environmental quality status (Moreno et al. 2011). Nematodes show some
104 peculiar physiological adaptations in response to specific stress in extreme environments (e.g. deep sediments),
105 such as highly sulphidic and anoxic conditions, for instance *Halomonhystera disjuncta* ovoviviparous strategy
106 (Van Gaever et al. 2006; Zeppilli et al. 2015b) and Oncholaimidae sulfur droplets (Thiermann et al. 2000). These
107 adaptive characteristics allow researchers to detect distinctive community features in response to different kinds
108 of stressors (Semprucci et al. 2015). In mangroves, nematodes have been used to characterize several
109 anthropogenic contexts in the Indian, Pacific and Atlantic regions (Della Patrona et al. 2016; Capdeville et al.
110 2018; Michelet et al. 2021). Nematodes' potential role as bioindicators has been widely discussed (Semprucci and
111 Balsamo 2014; Semprucci et al. 2015; Zeppilli et al. 2015a; Ridall and Ingels 2021), yet their use in mangroves is
112 still hampered by the lack of data, namely on unexplored areas. A bioindicator should consider the natural
113 variability of the ecosystem and exclude it as a driver of the community to give a straightforward and unequivocal
114 signal of anthropogenic pressure. Hence, characterizing nematode community structure in response to mangrove
115 natural variability first is essential to avoid misinterpretation of the factors responsible for their presence or absence
116 at a given location. The scientific community has been stressing the need of management and conservation
117 strategies for sustainable mangroves, which so far have been realized both locally and globally (see Romanach et
118 al. 2018 for review).

119 Nonetheless, such initiatives sometimes fail to integrate mangrove ecosystem services to their social benefits and
120 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

131 2. Environmental filters acting at different spatial 132 scales

133 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 (Lams 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. Three 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

179 environmental parameters (e.g. salinity, oxygen, organic matter content) essential for the interpretation of
180 nematode data, the exclusion of rare genera (only the dominant ones, i.e. >1% of relative abundance, are
181 considered), analytical methods changing between studies, and the representativeness of local (small scale)
182 datasets when considering the whole heterogeneity of a given mangrove area (see Online Resource 1). To our
183 knowledge, none of these meta-analyses tested the influence of the type of vegetation (mangrove tree species), nor
184 the impact of variable environmental conditions within the same vegetation type, on nematode density, richness
185 and community composition at a global scale.

186 2.2 Local scale drivers

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

201 2.2.1. Vegetation type

202 The effects of mangrove tree species and habitat heterogeneity on nematode distribution have not been considered
203 in most macroecological studies available in literature, but there is evidence of their influence on nematode
204 diversity and density patterns at a smaller scale. The few studies that take into account the presence of the different
205 types of tree as independent in a given forest patch are all situated in the IWP, whereas to our knowledge there is
206 no such study in the ACEP. In Nha Trang Bay (Vietnam) for instance, nematode density progressively increased
207 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 (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 *Cerriops* (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 *Paracomescima* 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 Guiana (Michelet et al. 2021) and Guadeloupe
231 (Boucher and Goubault 1990). In Ratonnes 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

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

274 In the ACEP, we are not able to establish any causal relationship between a particular mangrove tree species and
275 nematode trophic activity. In the referenced literature, the main tree species (*Avicennia*, *Rhizophora* and
276 *Laguncularia*) are reported to occur together, though with a dominance of *Avicennia*. ACEP mangroves host
277 mostly epistrate-feeders (2A) and detritus-feeders (1A) in a minor proportion in French Guiana and Guadeloupe
278 (Michelet et al. 2021; Boucher and Gourbault 1990) and detritus-feeders (1B, 1A) in Brazil (Netto and Gallucci
279 2003; Venekey et al. 2019). As for the IWP, different nematode genera, yet belonging to one specific trophic group
280 colonize sites apart from each other, thus taxonomic diversity is enhanced compared to the functional one. For
281 instance, detritus-feeders (1B and 1A) dominating in Brazil are represented by either *Haliplectus*, *Anoplostoma*
282 and *Terschellingia* (Netto and Gallucci 2003) or *Daptonema*, *Elzalia*, *Hypodontholaimus*, *Neochromadora*,
283 *Dichromadora* and *Thalassomonhystera* (Venekey et al. 2019). The dominance of either 2A or 1B-1A depends on
284 the availability of the respective food sources and oscillations of their relative abundances can be observed in
285 mangroves according to season, canopy cover, amount and origin of organic matter. Epistrate-feeders graze on
286 bacteria, protozoa and microphytobenthos and such food sources are more abundant in the warmest months and
287 where water transparency and canopy cover allow light penetration for photosynthesis (Netto and Gallucci 2003).
288 The dominance of this trophic mode in mangroves has been related to chlorophyll *a* and other pigment parameters
289 (Michelet et al. 2021), though the origin of such chlorophyll is yet to be clarified. To our knowledge, the role of
290 mangrove trees in providing epistrate-feeders food sources has not been quantified. Detritus-feeders rely on the
291 high amount of organic matter which deposits in muddy sediments, but the extent to which nematodes feed directly
292 on mangrove-derived low palatable detritus is yet to be quantified.

293 Trophic group is the most used functional trait in mangroves, but the apparent redundancy of epistrate feeders
294 across spatial scales arises questioning about the sensibility of the trophic group in detecting functional diversity
295 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 (Ólafsson 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 (Ólafsson 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 (Ólafsson 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; Ólafsson et al. 2000; Pandiya rajan et al. 2022) and occasionally
318 *Terschellingia* (Alongi 1988) and *Microlaimus* (Ólafsson et al. 2000).

319 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 Araçá 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*

325 (19%). The authors didn't take into account trophic groups, but the high abundance of selective and non-selective
326 detritus feeders can be due to either a decompositional state of the roots or to the sediment that is trapped by the
327 algae, which consequently stores more organic matter. Gwyther and Fairweather (2002) analyzed the nematode
328 community of real *Avicennia*, mimic (wooden-made) and transplanted pneumatophores. Genera richness on
329 natural pneumatophores was lower (7 species) compared to the other substrates (23 and 8 species respectively)
330 and the only common genera were *Tripyloides*, *Diplolaimella* and *Metachromadora*. The reason for the lower
331 nematode richness in natural and transplanted pneumatophores could be found in the production of toxic
332 secondary metabolites (i.e. phenols) by the roots (Gwyther and Fairweather 2002). Nematode genera richness
333 increased with time during the colonization of the pneumatophores and Chromadoridae was the pioneer family.
334 Epistrate feeders (2A), well represented by Chromadoridae were the most abundant trophic group, followed by
335 detritus feeders. 2A nematodes graze on the vegetal cells of the algae growing on the pneumatophores by piercing
336 and sucking their content. Late stages of colonization were characterized by the presence of Monhysteridae, which
337 can be associated with pneumatophores' decomposition processes, since they feed on bacteria.

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

349 Leaf decay process would not significantly affect nematode community structure over time. For instance, in Puerto
350 Rico's *Rhizophora mangle* forest, the nematode communities were quite nested whatever the decay time, with
351 *Adoncholaimus* and *Dichromadora* being dominant and no significant shift in dominance over time (Torres-Pratts
352 and Schizas 2007). Similarly, *Rhizophora* leaves decay stages only differed for relative abundances of the
353 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.

364 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 m² 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*, *Paracanthochus*,
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 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 Ndaró

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 Ndaró 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 Gullede 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.

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

455

456 3. Conclusions and perspectives

457 At the global scale, the main factor determining nematode richness in mangroves is latitude, with lowest latitudes
458 exhibiting the highest nematode genus richness. Surprisingly, genus richness is not higher in the Indo-Pacific area,
459 where the highest mangrove trees richness is registered. Along this longitudinal gradient, a higher structural
460 complexity of the ecosystem doesn't support a higher nematode richness, but different genus composition.
461 Conversely, at the local scale, a higher structural complexity of the environment supports a higher diversity.
462 Indeed, compared to mangrove-colonized sediments, intertidal bare mud sites generally host a higher density of
463 nematodes, but the same or a lower genus richness. In other words, species loss (nestedness) prevails on species
464 turnover along a land-sea continuum. At this spatial scale, nematode genus composition is mostly influenced by
465 the type of mangrove tree and the surrounding environment rather than the substrate on which the community
466 develops. However, when further reducing the spatial scale, the above mentioned factors may not have the same
467 strength in driving the nematode community: potentially very different microhabitats turned out to host similar
468 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 β -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. β -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.

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

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

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

516

517 References

- 518 Abdullah M, Lee S (2017) Structure of mangrove meiofaunal assemblages associated with local sediment
519 conditions in subtropical eastern Australia. *Estuar Coast Shelf Sci* 198:438-449.
520 <https://doi.org/10.1016/j.ecss.2016.10.039>
- 521 Aller RC, Aller JY (1992) Meiofauna and solute transport in marine muds. *Limnol Oceanogr* 37:1018–1033.
522 <https://doi.org/10.4319/lo.1992.37.5.1018>
- 523 Alongi D (1987a) Inter-estuary variation and intertidal zonation of free-living nematode communities in
524 tropical mangrove systems. *Mar Ecol Prog Ser* 40:103–114. <https://doi.org/10.3354/meps040103>
- 525 Alongi DM (1987b) The influence of mangrove-derived tannins on intertidal meiobenthos in tropical
526 estuaries. *Oecologia* 71:537–540. <https://doi.org/10.1007/BF00379293>

- 527 Alongi DM (1988) Microbial-meiofaunal interrelationships in some tropical intertidal sediments. *J Mar Res*
528 46:349–365. <https://doi.org/10.1357/002224088785113630>
- 529 Alongi DM (2009) *The energetics of mangrove forests*. Springer, Dordrecht
- 530 Alongi DM (1989) Ecology of tropical soft-bottom benthos : a review with emphasis on emerging concepts.
531 *Rev Biol Trop* 37 (1):86–100
- 532 Alongi DM (2008) Mangrove forests: Resilience, protection from tsunamis, and responses to global climate
533 change. *Estuar Coast Shelf Sci* 76:1–13. <https://doi.org/10.1016/j.ecss.2007.08.024>
- 534 Alongi DM (2016) Mangroves. In: *Encyclopedia of Estuaries*. pp 393–404
- 535 Alves AS, Veríssimo H, Costa MJ, Marques JC (2014) Taxonomic resolution and Biological Traits Analysis
536 (BTA) approaches in estuarine free-living nematodes. *Estuar Coast Shelf Sci* 138:69–78.
537 <https://doi.org/10.1016/j.ecss.2013.12.014>
- 538 Baldrighi E, Dovgal I, Zeppilli D, et al (2020) The cost for biodiversity: Records of ciliate-nematode
539 epibiosis with the description of three new suctorian species. *Diversity* 12:1–25.
540 <https://doi.org/10.3390/d12060224>
- 541 Baselga A (2010) Partitioning the turnover and nestedness components of beta diversity. *Macroecological*
542 *methods* 19:134–143. <https://doi.org/10.1111/j.1466-8238.2009.00490.x>
- 543 Bongers T (1990) The maturity index: an ecological measure of environmental disturbance based on
544 nematode species composition. *Oecologia* 83:14–19. <https://doi.org/10.1007/BF00324627>
- 545 Bongers T, Alkemade R, Yeates GW (1991) Interpretation of disturbance-induced maturity decrease in
546 marine nematode assemblages by means of the Maturity Index. *Mar Ecol Prog Ser* 76:135–142.
547 <https://doi.org/10.3354/meps076135>
- 548 Bongers T, Goede RGM, Korthals GW, Yeates GW (1995) Proposed changes to c-p classification for
549 nematodes. *Russ J Nematol* 3:61–62
- 550 Boucher G, Gourbault N (1990) Sublittoral meiofauna and diversity of nematode assemblages of
551 Guadeloupe island (French west Indies). *Bull Mar Sci* 47:448–463
- 552 Brustolin MC, Nagelkerken I, Fonseca G (2018) Large-scale distribution patterns of mangrove nematodes:
553 A global meta-analysis. *Ecol Evol* 8:4734–4742. <https://doi.org/10.1002/ece3.3982>
- 554 Brustolin MC, Fonseca G, Gallucci F (2021) Habitat Attributes Dictate the Roles of Dispersal and
555 Environmental Filtering on Metacommunity Assembly at Coastal Soft-Bottom Ecosystems Habitat
556 Attributes Dictate the Roles of Dispersal and Environmental Filtering on Metacommunity Assembly
557 at Coastal So. *Estuaries and Coasts*. <https://doi.org/10.1007/s12237-021-00976-5>
- 558 Bunt JS, Williams WT (1981) Vegetational Relationships in the Mangroves of Tropical Australia. *Mar Ecol*
559 4:349–359
- 560 Bunt JS, Williams WT, Clay HJ (1982) River Water Salinity and the Distribution of Mangrove Species
561 Along Several Rivers in North Queensland. *Aust J Bot* 30:401–412
- 562 Cai L, Fu S, Zhou X, et al (2020) Benthic meiofauna with emphasis on nematode assemblage response to
563 environmental variation in the intertidal zone of the Danshuei River estuary, northwest Taiwan. *Ecol*
564 *Res* 35:857–870. <https://doi.org/10.1111/1440-1703.12159>
- 565 Cannicci S, Yip S, Bravo H, Cantera-kintz JR (2021) A functional analysis reveals extremely low
566 redundancy in global mangrove invertebrate fauna. 118:1–8. <https://doi.org/10.1073/pnas.2016913118>

- 567 Capdeville C, Abdallah K, Buffan-Dubau E, et al (2018) Limited impact of several years of pretreated
568 wastewater discharge on fauna and vegetation in a mangrove ecosystem. *Mar Pollut Bull* 129:379–
569 391. <https://doi.org/10.1016/j.marpolbul.2018.02.035>
- 570 Cardoso P, Carvalho C, Fortelius M (2014) Partitioning taxon, phylogenetic and functional beta diversity
571 into replacement and richness difference components. *41:749–761*. <https://doi.org/10.1111/jbi.12239>
- 572 Chinnadurai G, Fernando OJ (2007) Meiofauna of mangroves of the southeast coast of India with special
573 reference to the free-living marine nematode assemblage. *Estuar Coast Shelf Sci* 72:329–336.
574 <https://doi.org/10.1016/j.ecss.2006.11.004>
- 575 Cleary DFR, Smalla K, Mendonça-Hagler LCS, Gomes NCM (2012) Assessment of variation in bacterial
576 composition among microhabitats in a mangrove environment using DGGE fingerprints and barcoded
577 pyrosequencing. *PLoS One* 7:1–8. <https://doi.org/10.1371/journal.pone.0029380>
- 578 Coull BC, Greenwood JG, Fielder DR, Coull BA (1995) Subtropical Australian juvenile fish eat meiofauna:
579 experiments with winter whiting *Sillago maculata* and observations on other species. *Mar Ecol Prog*
580 *Ser* 125:13–19. <https://doi.org/10.3354/meps125013>
- 581 D’Hondt AS, Stock W, Blommaert L, et al (2018) Nematodes stimulate biomass accumulation in a
582 multispecies diatom biofilm. *Mar Environ Res* 140:78–89.
583 <https://doi.org/10.1016/j.marenvres.2018.06.005>
- 584 Day JW, Hall CAS, Kemp WM, Yanez-Arancibia A (2013) *Estuarine ecology*, Second. Wiley-Blackwell
- 585 de Man JG (1886) *Anatomische Untersuchungen über freilebende Nordsee-Nematoden*. Leipzig (Verlag von
586 Paul Froberg)
- 587 de Man JG (1889) *Espèces et genres nouveaux de Nématodes libres de la mer du Nord et de la Manche*.
588 *Mémoires Société Zool Fr* 2:1–10
- 589 Demopoulos AWJ, Fry B, Smith CR (2007) Food web structure in exotic and native mangroves: A Hawaii-
590 Puerto Rico comparison. *Oecologia* 153:675–686. <https://doi.org/10.1007/s00442-007-0751-x>
- 591 Dittel AI, Epifanio CE, Cifuentes LA, Kirchman DL (1997) Carbon and nitrogen sources for shrimp
592 postlarvae fed natural diets from a tropical mangrove system. *Estuar Coast Shelf Sci* 45:629–637.
593 <https://doi.org/10.1006/ecss.1996.0228>
- 594 Della Patrona L, Marchand C, Hubas C, et al (2016) Meiofauna distribution in a mangrove forest exposed
595 to shrimp farm effluents (New Caledonia). *Mar Environ Res* 119:100–113.
596 <https://doi.org/10.1016/j.marenvres.2016.05.028>
- 597 Dufrière M, Legendre P (1997) Species assemblages and indicator species: The need for a flexible
598 asymmetrical approach. *Ecol Monogr* 67:345–366. <https://doi.org/10.2307/2963459>
- 599 Duke, N.C., Maynecke JO (2007) A World Without Mangroves? *Science* 317(5834):41–43.
600 <https://doi.org/10.1126/science.317.5834.41b>
- 601 Dye A, Lasiak T (1986) Microbenthos, meiobenthos and fiddler crabs: trophic interactions in a tropical
602 mangrove sediment. *Mar Ecol Prog Ser* 32:259–264. <https://doi.org/10.3354/meps032259>
- 603 Ellison AM (2008) Managing mangroves with benthic biodiversity in mind: Moving beyond roving banditry.
604 *J Sea Res* 59:2–15. <https://doi.org/10.1016/j.seares.2007.05.003>

- 605 Ellison AM, Farnsworth EJ, Merkt RE (1999) Origins of mangrove ecosystems and the mangrove
606 biodiversity anomaly. *Glob Ecol Biogeogr* 8:95–115. <https://doi.org/10.1046/j.1466->
607 822X.1999.00126.x
- 608 Faust MA, Gulledge RA (1996) Associations of microalgae and meiofauna in floating detritus at a mangrove
609 island, Twin Cays, Belize. *J Exp Mar Bio Ecol* 197:159–175. <https://doi.org/10.1016/0022->
610 0981(95)00159-X
- 611 Fiot J, Gratiot N (2006) Structural effects of tidal exposures on mudflats along the French Guiana coast. *Mar*
612 *Geol* 228:25–37. <https://doi.org/10.1016/j.margeo.2005.12.009>
- 613 Fonseca G, Netto SA (2015) Macroecological Patterns of Estuarine Nematodes. *Estuaries and Coasts*
614 38:612–619. <https://doi.org/10.1007/s12237-014-9844-z>
- 615 Fromard F, Puig H, Mougou E, et al (1998) Structure, above-ground biomass and dynamics of mangrove
616 ecosystems: New data from French Guiana. *Oecologia* 115:39–53.
617 <https://doi.org/10.1007/s004420050489>
- 618 Gallucci F, Christofolletti RA, Fonseca G, Dias GM (2020) The effects of habitat heterogeneity at distinct
619 spatial scales on hard-bottom-associated communities. *Diversity* 12:1–13.
620 <https://doi.org/10.3390/d12010039>
- 621 Gansfort B, Fontaneto D, Zhai M (2020) Meiofauna as a model to test paradigms of ecological
622 metacommunity theory. *Hydrobiologia* 847:2645–2663. <https://doi.org/10.1007/s10750-020-04185-2>
- 623 Gee JM (1989) An ecological and economic review of meiofauna as food for fish. *Zool J Linn Soc* 96:243–
624 261. <https://doi.org/10.1111/j.1096-3642.1989.tb02259.x>
- 625 Gee JM, Somerfield PJ (1997) Do mangrove diversity and leaf litter decay promote meiofaunal diversity? *J*
626 *Exp Mar Biol Ecol* 218:13–33. [https://doi.org/10.1016/S0022-0981\(97\)00065-8](https://doi.org/10.1016/S0022-0981(97)00065-8)
- 627 Gerdes G, Krumbein WE, Reineck HE (1985) The depositional record of sandy, varicolored tidal flats (
628 Mellum Island, southern North Sea). *J Sediment Petrol* 55:265–278.
629 <https://doi.org/10.1306/212F8698-2B24-11D7-8648000102C1865D>
- 630 Ghosh M, Mandal S (2019) Does vertical distribution of meiobenthic community structure differ among
631 various mangrove habitats of Sundarban Estuarine System? *Reg Stud Mar Sci* 31:100778.
632 <https://doi.org/10.1016/j.rsma.2019.100778>
- 633 Giere O (2009) *Meiobenthology: The microscopic motile fauna of aquatic sediments*, 2nd edn. Springer,
634 Berlin, Heidelberg <https://doi.org/10.1007/978-3-540-68661-3>
- 635 Giri C, Ochieng E, Tieszen LL, et al (2011) Status and distribution of mangrove forests of the world using
636 earth observation satellite data. *Glob Ecol Biogeogr* 20:154–159. <https://doi.org/10.1111/j.1466->
637 8238.2010.00584.x
- 638 Gwyther J (2003) Nematode assemblages from *Avicennia marina* leaf litter in a temperate mangrove forest
639 in south-eastern Australia. *Mar Biol* 142:289–297. <https://doi.org/10.1007/s00227-002-0944-0>
- 640 Gwyther J, Fairweather PG (2002) Colonisation by epibionts and meiofauna of real and mimic
641 pneumatophores in a cool temperate mangrove habitat. *Mar Ecol Prog Ser* 229:137–149.
642 <https://doi.org/10.3354/meps229137>
- 643 Hodda M (2022) Phylum Nematoda: feeding habits for all valid genera using a new, universal scheme
644 encompassing the entire phylum, with descriptions of morphological characteristics of the stoma, a
645 key, and discussion of the evidence for trophic relationships. *Zootaxa* 5114:318–451.
646 <https://doi.org/10.11646/zootaxa.5114.1.3>

- 647 Holyoak M, Leibold MA, Holt RD (2005) *Metacommunities: Spatial Dynamics and Ecological*
648 *Communities*. The University of Chicago Press, Chicago
- 649 Hsieh HL (1995) Spatial and temporal patterns of polychaete communities in a subtropical mangrove
650 swamp: influences of sediment and microhabitat. *Mar Ecol Prog Ser* 127:157–167
- 651 Hubas C, Sachidhanandam C, Rybarczyk H, et al (2010) Bacterivorous nematodes stimulate microbial
652 growth and exopolymer production in marine sediment microcosms. *Mar Ecol Prog Ser* 419:85–94.
653 <https://doi.org/10.3354/meps08851>
- 654 Hubbell SP (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University
655 Press, Princeton
- 656 Kon K, Kurokura H, Tongnunui P (2011) Influence of a microhabitat on the structuring of the benthic
657 macrofaunal community in a mangrove forest. *Hydrobiologia* 671:205–216.
658 <https://doi.org/10.1007/s10750-011-0718-0>
- 659 Kremer CT, Williams AK, Finiguerra M, et al (2017) Realizing the potential of trait-based aquatic ecology :
660 New tools and collaborative approaches. *Limnol Oceanogr* 62:253–271.
661 <https://doi.org/10.1002/lno.10392>
- 662 Kristensen E, Penha-Lopes G, Delefosse M, et al (2012) What is bioturbation? the need for a precise
663 definition for fauna in aquatic sciences. *Mar Ecol Prog Ser* 446:285–302.
664 <https://doi.org/10.3354/meps09506>
- 665 Lambs L, Muller E, Fromard F (2008) Mangrove trees growing in a very saline condition but not using
666 seawater. *Rapid Commun Mass Spectrom* 22:2835–2843. <https://doi.org/10.1002/rcm.3676>
- 667 Lee SY, Primavera JH, Dahdouh-Guebas F, et al (2014) Ecological role and services of tropical mangrove
668 ecosystems: A reassessment. *Glob Ecol Biogeogr* 23:726–743. <https://doi.org/10.1111/geb.12155>
- 669 Legendre P, Borcard D, Peres-Neto PR (2005) Analyzing beta diversity: partitioning the spatial variation of
670 community composition data. *Ecological Monogr* 75(4):435–450.
671 <https://doi.org/https://doi.org/10.1890/05-0549>
- 672 Lugo AE, Snedaker SC (1974) The Ecology of Mangroves. *Annu Rev Ecol Syst* 5:39–64.
673 <https://doi.org/10.1146/annurev.es.05.110174.000351>
- 674 Marchand C, Baltzer F, Lallier-Vergès E, Albéric P (2004) Pore-water chemistry in mangrove sediments:
675 Relationship with species composition and developmental stages (French Guiana). *Mar Geol* 208:361–
676 381. <https://doi.org/10.1016/j.margeo.2004.04.015>
- 677 Martini S, Larras F, Boyé A, et al (2021) Functional trait-based approaches as a common framework for
678 aquatic ecologists. *Limnol Oceanogr* 66:965–994. <https://doi.org/10.1002/lno.11655>
- 679 Menegotto A, Dambros CS, Netto SA (2019) The scale-dependent effect of environmental filters on species
680 turnover and nestedness in an estuarine benthic community. *Ecology* 100:1–9.
681 <https://doi.org/10.1002/ecy.2721> Michaud E, Aschenbroich A, Gauthier O, et al (2022) The
682 Codevelopment of Mangroves and Infaunal Community Diversity in Response to the Natural
683 Dynamics of Mud Deposition in French Guiana. *Sustain* 14:. <https://doi.org/10.3390/su14052829>
- 684 Michelet C, Zeppilli D, Hubas C, et al (2021) First assessment of the benthic meiofauna sensitivity to low
685 human-impacted mangroves in French Guiana. *Forests* 12:. <https://doi.org/10.3390/f12030338>
- 686 Moens T, Vincx M (1997) Observations on the feeding ecology of estuarine nematodes. *J mar biol Ass UK*
687 77:211–227. <https://doi.org/10.1080/02541858.1980.11447695>

- 688 Moens T, Dos Santos GAP, Thompson F, et al (2005) Do nematode mucus secretions affect bacterial
689 growth? *Aquat Microb Ecol* 40:77–83. <https://doi.org/10.3354/ame040077>
- 690 Mokievsky VO, Tchesunov A V., Udalov AA, Toan ND (2011) Quantitative distribution of meiobenthos
691 and the structure of the free-living nematode community of the mangrove intertidal zone in Nha Trang
692 bay (Vietnam) in the South China Sea. *Russ J Mar Biol* 37:272–283.
693 <https://doi.org/10.1134/S1063074011040109>
- 694 Moreno M, Semprucci F, Vezzulli L, et al (2011) The use of nematodes in assessing ecological quality status
695 in the Mediterranean coastal ecosystems. *Ecol Indic* 11:328–336.
696 <https://doi.org/10.1016/j.ecolind.2010.05.011>
- 697 Murdock SA, Tunnicliffe V, Boschen-Rose RE, Juniper SK (2021) Emergent “core communities” of
698 microbes, meiofauna and macrofauna at hydrothermal vents. *ISME Commun* 1, 27
699 <https://doi.org/10.1038/s43705-021-00031-1>
- 700 Nagelkerken I, Blaber SJM, Bouillon S, et al (2008) The habitat function of mangroves for terrestrial and
701 marine fauna: A review. *Aquat Bot* 89:155–185. <https://doi.org/10.1016/j.aquabot.2007.12.007>
- 702 Netto SA, Gallucci F (2003) Meiofauna and macrofauna communities in a mangrove from the Island of
703 Santa Catarina, South Brazil. *Hydrobiologia* 505:159–170.
704 <https://doi.org/10.1023/B:HYDR.0000007304.22992.b2>
- 705 Ólafsson E, Carlström S, Ndaro SG (2000) Meiobenthos of hypersaline tropical mangrove sediment in
706 relation to spring tide inundation. *Hydrobiologia* 426:57–64
- 707 Ólafsson E (1995) Meiobenthos in mangrove areas in eastern Africa with emphasis on assemblage structure
708 of free-living marine nematodes. *Hydrobiologia* 312:47–57. <https://doi.org/10.1007/BF00018886>
- 709 Ólafsson E, Ndaro SGM (1997) Impact of the mangrove crabs *Uca annulipes* and *Dotilla fenestrata* on
710 meiobenthos. *Mar Ecol Prog Ser* 158:225–231. <https://doi.org/10.3354/meps158225>
- 711 Pandiya rajan RS, Gera A, Ramu K, et al (2022) Influence of salinity on the meiofaunal distribution in a
712 hypersaline lake along the southeast coast of India. *Environ Monit Assess* 194:199
713 <https://doi.org/10.1007/s10661-022-09829-5>
- 714 Pinto TK, Austen MCV, Warwick RM, et al (2013) Nematode diversity in different microhabitats in a
715 mangrove region. *Mar Ecol* 34:257–268. <https://doi.org/10.1111/maec.12011>
- 716 Polidoro BA, Carpenter KE, Collins L, et al (2010) The loss of species: Mangrove extinction risk and
717 geographic areas of global concern. *PLoS One* 5:e10095.
718 <https://doi.org/10.1371/journal.pone.0010095>
- 719 Presley SJ, Higgins CL, Willig MR (2010) A comprehensive framework for the evaluation of
720 metacommunity structure. *Oikos* 119:908–917. <https://doi.org/10.1111/j.1600-0706.2010.18544.x>
- 721 Raes M, Vanreusel A (2006) Microhabitat type determines the composition of nematode communities
722 associated with sediment-clogged cold-water coral framework in the Porcupine Seabight (NE
723 Atlantic). *Deep Res Part I Oceanogr Res Pap* 53:1880–1894. <https://doi.org/10.1016/j.dsr.2006.08.012>
- 724 Ridall A, Ingels J (2021) Suitability of Free-Living Marine Nematodes as Bioindicators: Status and Future
725 Considerations. *Front Mar Sci* 8:1–16. <https://doi.org/10.3389/fmars.2021.685327>
- 726 Robertson AI, Alongi DM (1992) *Tropical Mangrove Ecosystems*. American Geophysical Union,
727 Washington DC
- 728 Romañach SS, DeAngelis DL, Koh HL, et al (2018) Conservation and restoration of mangroves: Global
729 status, perspectives, and prognosis. *Ocean Coast Manag* 154:72–82.
730 <https://doi.org/10.1016/j.ocecoaman.2018.01.009>

- 731 Rosli N, Leduc D, Rowden AA, Probert PK (2018) Review of recent trends in ecological studies of deep-
732 sea meiofauna, with focus on patterns and processes at small to regional spatial scales. *Mar Biodivers*
733 48:13–34. <https://doi.org/10.1007/s12526-017-0801-5>
- 734 Ross PM (2006) Macrofaunal loss and microhabitat destruction: The impact of trampling in a temperate
735 mangrove forest, NSW Australia. *Wetl Ecol Manag* 14:167–184. <https://doi.org/10.1007/s11273-005-7552-y>
736
- 737 Sahoo G, Suchiang SR, Ansari ZA, Blair P (2013) Meiofauna-Mangrove interaction: a pilot study from a
738 tropical mangrove habitat. *Cah Biol Mar* 54:349–358
- 739 Schratzberger M, Ingels J (2018) Meiofauna matters: The roles of meiofauna in benthic ecosystems. *J Exp*
740 *Mar Bio Ecol* 502:12–25. <https://doi.org/10.1016/j.jembe.2017.01.007>
- 741 Schratzberger M, Warr K, Rogers SI (2007) Functional diversity of nematode communities in the
742 southwestern North Sea. *Mar Environ Res* 63:368–389.
743 <https://doi.org/10.1016/j.marenvres.2006.10.006>
- 744 Schrijvers J, Fermon H, Vincx M (1996) Resource competition between macrobenthic epifauna and infauna
745 in a Kenyan *Avicennia marina* mangrove forest. *Mar Ecol Prog Ser* 136:123–135.
746 <https://doi.org/10.3354/meps136123>
- 747 Schrijvers J, Okondo J, Steyaert M, Vincx M (1995) Influence of epibenthos on meiobenthos of the *Cerriops*
748 tagal mangrove sediment at Gazi Bay, Kenya. *Mar Ecol Prog Ser* 128:247–259.
749 <https://doi.org/10.3354/meps128247>
- 750 Schenk J, Höss S, Brinke M, et al (2020) Dataset supporting the use of nematodes as bioindicators of polluted
751 sediments. *Data Br* 32:106087. <https://doi.org/10.1016/j.dib.2020.106087>
- 752 Semprucci F, Balsamo M (2014) New records and distribution of marine free-living nematodes in the
753 Maldivian Archipelago New records and distribution of marine free-living nematodes. *Proc Biol Soc*
754 *Washingt* 127:35–46. <https://doi.org/10.2988/0006-324X-127.1.35>
- 755 Semprucci F, Losi V, Moreno M (2015) A review of Italian research on free-living marine nematodes and
756 the future perspectives on their use as Ecological Indicators (EcoInds). *Mediterr Mar Sci* 16:452–465.
757 <https://doi.org/10.12681/mms.1072>
- 758 Somerfield PJ, Warwick RM (2013) Meiofauna Techniques. In: *Methods for the Study of Marine Benthos*.
759 pp 253–284
- 760 Song D, Pan K, Tariq A, et al (2017) Large-scale patterns of distribution and diversity of terrestrial
761 nematodes. *Appl Soil Ecol* 114:161–169. <https://doi.org/10.1016/j.apsoil.2017.02.013>
- 762 Sroczyńska K, Chainho P, Vieira S, Adão H (2021) What makes a better indicator? Taxonomic vs functional
763 response of nematodes to estuarine gradient. *Ecol Indic* 121:.
764 <https://doi.org/10.1016/j.ecolind.2020.107113>
- 765 Thiermann F, Vismann B, Giere O (2000) Sulfide tolerance of the marine nematode *Oncholaimus*
766 *campyloceroides* - A result of internal sulfur formation? *Mar Ecol Prog Ser* 193:251–259.
767 <https://doi.org/10.3354/meps193251>
- 768 Thistle D, Lamshead PJD, Sherman KM (1995) Nematode tail-shape groups respond to environmental
769 differences in the deep sea. *Vie Milieu* 45:107–115
- 770 Tietjen JH, Alongi DM (1990) Population growth and effects of nematodes on nutrient regeneration and
771 bacteria associated with mangrove detritus from northeastern Queensland (Australia). *Mar Ecol Prog*
772 *Ser* 68:169–179. <https://doi.org/10.3354/meps068169>

- 773 Torres-Pratts H, Schizas N V. (2007) Meiofaunal colonization of decaying leaves of the red mangrove
774 *Rhizophora mangle*, in Southwestern Puerto Rico. *Caribb J Sci* 43:127–137.
775 <https://doi.org/10.18475/cjos.v43i1.a12>
- 776 Traunspurger W, Bergtold M, Goedkoop W (1997) The effects of nematodes on bacterial activity and
777 abundance in a freshwater sediment. *Oecologia* 112:118–122. <https://doi.org/10.1007/s004420050291>
- 778 Van Gaever S, Moodley L, De Beer D, Vanreusel A (2006) Meiobenthos at the arctic Håkon Mosby Mud
779 Volcano, with a parental-caring nematode thriving in sulphide-rich sediments. *Mar Ecol Prog Ser*
780 321:143–155. <https://doi.org/10.3354/meps321143>
- 781 Vanhove S, Vincx M, Van Gansbeke D, et al (1992) The meiobenthos of five mangrove vegetation types in
782 Gazi Bay, Kenya. *Hydrobiologia* 247:99–108. <https://doi.org/10.1007/BF00008208>
- 783 Vanreusel A, de Groote A, Gollner S, Bright M (2010) Ecology and biogeography of free-living nematodes
784 associated with chemosynthetic environments in the deep sea: A review. *PLoS One* 5:e12449.
785 <https://doi.org/10.1371/journal.pone.0012449>
- 786 Venekey V, de Melo TPG (2016) Nematodes as indicators of shrimp farm impact on an amazonian estuary
787 (Curuçá, Pará, Brazil). *Brazilian J Oceanogr* 64:75–88. [https://doi.org/10.1590/S1679-
788 87592016108206401](https://doi.org/10.1590/S1679-87592016108206401)
- 789 Venekey V, Fonseca-Genevois VG, Santos PJP (2010) Biodiversity of free-living marine nematodes on the
790 coast of Brazil: A review. *Zootaxa* 66:39–66. <https://doi.org/10.11646/zootaxa.2568.1>
- 791 Venekey V, Melo TPG, Rosa Filho JS (2019) Effects of seasonal fluctuation of amazon river discharge on
792 the spatial and temporal changes of meiofauna and nematodes in the amazonian coast. *Estuar Coast
793 Shelf Sci* 227:106330. <https://doi.org/10.1016/j.ecss.2019.106330>
- 794 Walsh GE (1974) Mangroves: a review. In: *Ecology of Halophytes*. Academic Press, INC., pp 51–174
- 795 Wieser W (1953) Die Beziehung zwischen Mundhöhlengestalt, Ernährungsweise und Vorkommen bei
796 freilebenden marinen Nematoden. *Ark Zool* 4(2): 439-484
- 797 Wu X, Vanreusel A, Hauquier F, Moens T (2019) Environmental drivers of nematode abundance and genus
798 composition at two spatial scales on an estuarine intertidal flat. *Hydrobiologia* 846:193–214.
799 <https://doi.org/10.1007/s10750-019-04064-5>Xie Y, Zhang P, Zhang L (2021) Genome-Wide
800 Transcriptional Responses of Marine Nematode *Litoditis marina* to Hyposaline and Hypersaline
801 Stresses. *Front Physiol* 12:1–15. <https://doi.org/10.3389/fphys.2021.672099>
- 802 Xuan QN, Vanreusel A, Thanh NV, Smol N (2007) Biodiversity of meiofauna in the intertidal Khe Nhan
803 Mudflat, Can Gio mangrove forest, Vietnam with special emphasis on free living nematodes. *Ocean
804 Sci J* 42:135–152. <https://doi.org/10.1007/BF03020918>
- 805 Yang JQ, Zhang X, Bourg IC, Stone HA (2021) 4D imaging reveals mechanisms of clay-carbon protection
806 and release. *Nat Commun* 12:. <https://doi.org/10.1038/s41467-020-20798-6>
- 807 Zeppilli D, Leduc D, Fontanier C, et al (2018) Characteristics of meiofauna in extreme marine ecosystems:
808 a review. *Mar Biodivers* 48:35–71. <https://doi.org/10.1007/s12526-017-0815-z>
- 809 Zeppilli D, Sarrazin J, Leduc D, et al (2015a) Is the meiofauna a good indicator for climate change and
810 anthropogenic impacts? *Mar Biodivers* 45:505–535. <https://doi.org/10.1007/s12526-015-0359-z>
- 811 Zeppilli D, Vanreusel A, Pradillon F, et al (2015b) Rapid colonisation by nematodes on organic and
812 inorganic substrata deployed at the deep-sea Lucky Strike hydrothermal vent field (Mid-Atlantic
813 Ridge). *Mar Biodivers* 45:489–504. <https://doi.org/10.1007/s12526-015-0348-2>
- 814

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 Ólafsson 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

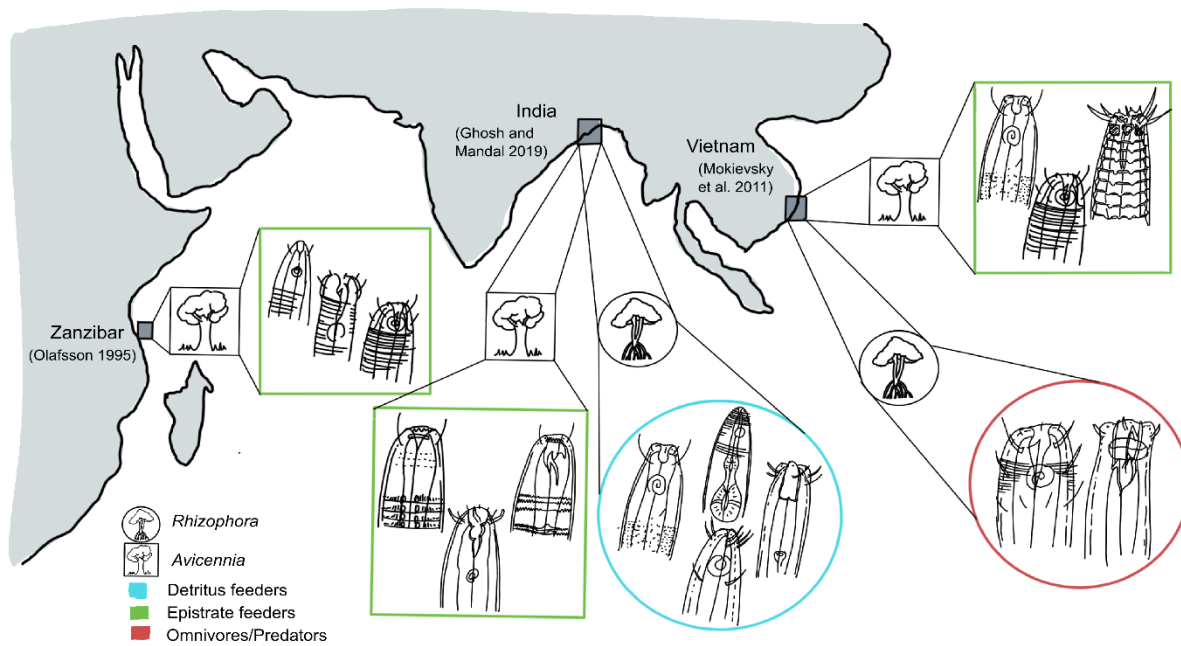
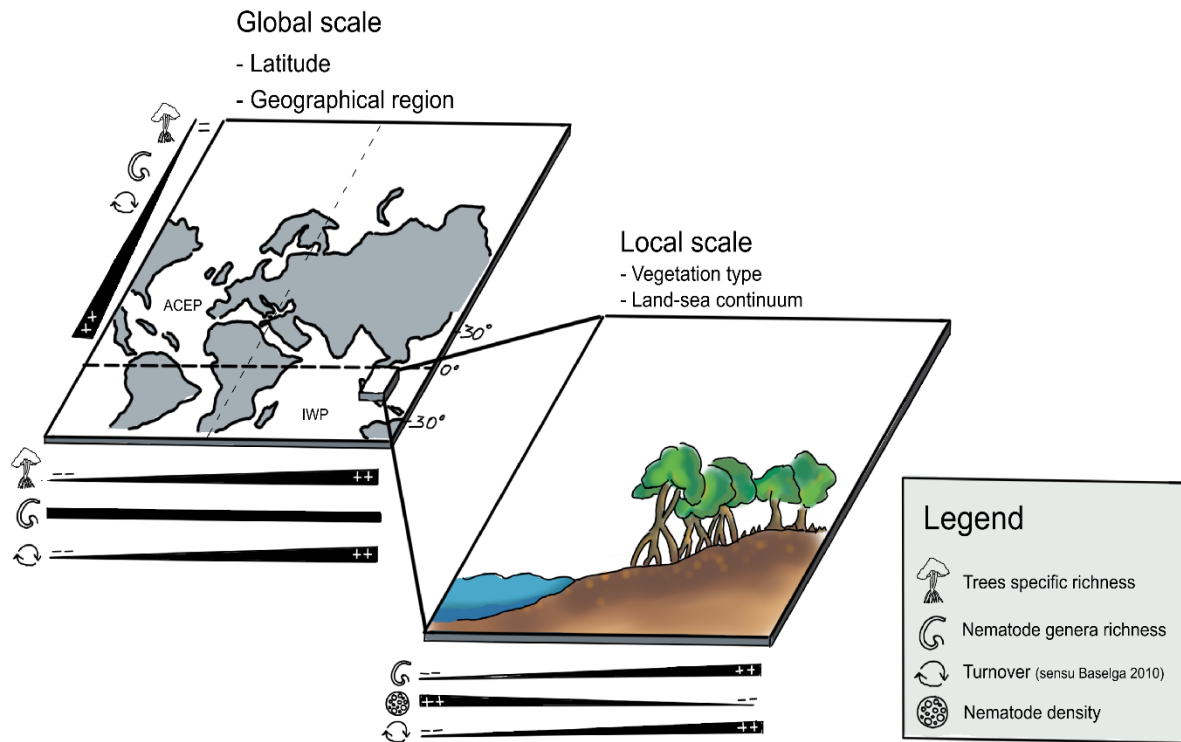


Figure 1 and Figure 2 have been realized with Concepts app (TopHatch 2022) and Inkscape (Inkscape Project 2020).

Statements & Declarations

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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.