

Nematode functional traits and community structure change from river to the terrestrial border in Segara Anakan Mangrove, Indonesia

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Abstract. Maharning AR, Ardli ER, Prabowo RE. 2023. Nematode functional traits and community structure change from river to the terrestrial border in Segara Anakan Mangrove, Indonesia. *Biodiversitas* 24: 2434-2446. We intended to explore the spatial distribution of nematode functional traits and community structure in Segara Anakan Mangrove, Cilacap District, Central Java, Indonesia. Samples were retrieved from 14 stations, extending from the river to the area adjacent to terrestrial forest. We used taxonomic and functional trait identification, covering body shape, length, tail shape, feeding type, and life history as independent traits, and combined traits by collecting traits describing individual nematodes. The principal component analysis suggested that predatory or omnivorous or long-size nematodes mainly inhabited stations adjacent to the terrestrial forest but were unclear for the mid-stations. There were 29 combined traits and 38 genera of nematodes observed. The detrended correspondence analysis revealed that nematode compositional changes from the river to the terrestrial adjacent area were clearer for the combined traits and nematode genera. Seven combined traits and 12 genera inhabited only the particular stations of the study site. The common nematodes were slender, 1-2 mm long, elongated filiform tails, non-selective deposit feeders, and very tolerant to pollutants, which lived in almost all stations (92.86%). The genus relative abundance (>10%) included *Anoplostoma*, *Eubostrichus*, and *Chromadorina*. The results suggest that distance from the river might regulate the habitability of nematodes, in which nematode functional traits play roles.

Keywords: Body length, body shape, feeding type, life history trait, tail type trait

INTRODUCTION

Free-living nematodes are the most numerous and diverse organisms among the meiofaunal groups of marine environments (Pereira et al. 2018; Wafula et al. 2019; Cai et al. 2020). Their abundance in the sedimentary environment reaches more than 60% of the total meiofauna. Chinnadurai and Fernando (2007) reported nematode dominance up to 86-93% in mangroves of India's southeast coast. Similarly, nematode relative abundance reached 63-96% in an estuarine intertidal area of Mondego, Portugal (Alves et al. 2015). Recent studies reported that 92% of the total meiofauna of Bohai Bay (Hua et al. 2021) and 98% in the tidal flat mangrove in Shenzhen, China (Song et al. 2022) were nematodes. Likewise, it was estimated that 20% of known nematode species are marine free-living (Chinnadurai and Fernando 2007).

Nematode high abundance and diversity relate to their adaptation capability to a wide range of habitat types, reflected in their diverse morphology (Mitwally and Fleeger 2016). Their great dominance suggests their essential roles in the ecosystem as an important component of the food web. Nematodes recycle nutrients via their feeding activities, enriching the environment to support the production of other organisms. Their various food sources and trophic position in the food web show their high functional diversity and demonstrate their critical link to the higher-level food web (Semprucci et al. 2016).

As a habitable ecosystem for nematodes, mangroves might provide high microhabitat variability. Mangroves are exposed to continuously fluctuating environmental parameters from tide, rivers, and rainfall, creating diverse microhabitats which affect the community structure and function in mangrove physical space. Moreover, mangrove tree roots and litter enhance habitat diversity by providing various niches for fauna colonization (Pinto et al. 2013). Low oxygen content in mangrove substrate and human interference surrounding the mangrove increase the ecosystem complexity. These mangrove environmental dynamics are challenging for mangrove inhabitants. Nevertheless, they might have adapted to mangrove conditions through the physiological changes reflected in their morphology (Semprucci et al. 2018a). The microhabitat heterogeneity created by various parameters and biotic interactions among mangrove communities might provide habitat suitability for variously adapted nematodes.

Two main approaches, taxonomic and functional group identifications, are common methods to reveal patterns of nematode community structure (Liao et al. 2020; Semprucci et al. 2022). The former, however, may not entirely reveal nematode roles in ecosystem functions. Hence, nematode functional analysis is included to understand nematode contribution to an ecosystem.

Environmental variables have been reported to influence the dominant traits of the nematodes (Singh and Ingole 2016). This analysis requires morpho-functional traits, which represent their adaptation to life in various habitats of mangroves (Semprucci et al. 2018b). Mitwally (2022) showed that predatory nematodes, and conical tail nematodes dominated fine-grained sand habitats with high salinity, highly contaminated, and high acidity in the Abo-Qir Bay of Egypt. In contrast, scavengers, conical or elongate tails nematodes mainly inhabited coarse sediment and low salinity habitat of El-Mex Bay.

Despite nematode abundance and significant contribution to ecosystem functioning, scientific information on free-living nematode community structure in tropical areas is limited (Bhadury et al. 2015), particularly in mangrove ecosystems. A recent meta-analysis of mangrove nematodes included various areas of tropical mangroves (Brustolin et al. 2018), but none from Indonesia. A more recent global analysis of nematode abundance and composition showed that less than one percent of data is from terrestrial areas in Indonesia (Van Den Hoogen et al. 2019). Therefore, to contribute to the current knowledge of nematodes in mangroves, we conducted a nematode study on the naturally growing mangrove area of Segara Anakan, Cilacap District, Central Java, Indonesia. More specifically, we intended to explore the spatial distribution of nematode functional traits and community structure in Kembangkuning Area of Segara Anakan Mangrove.

MATERIALS AND METHODS

Study area

Kembangkuning of Segara Anakan Mangrove covers approximately 136 ha of the 12,850 ha mangrove-lagoon system in Segara Anakan, and relatively have low exposure to illegal cutting (Ardli et al. 2022). The site is located northeast of Nusakambangan Island, and south of Cilacap District, Central Java, Indonesia. To the north is the river Kembangkuning, and to the south is a terrestrial forest (Figure 1). Kembangkuning is distinguished by the natural growth of mangrove forests dominated by *Rhizophora apiculata* and *Aegiceras corniculatum*, which extends from 7° 43' 3.48" S, 108° 56' 57.21" E to 7° 44' 0.37" S, 108° 58' 44.87" E. The site is characterized by a semidiurnal mixed tide with an amplitude between 2.30 and 2.57 m (Handoyo and Suryoputro 2015; Awaludin et al. 2017). It has a humid tropical environment with an average temperature of 27 °C and precipitation of 3,400 mm without seasonal variance. Human activities and industries such as agriculture and oil refineries surrounding the site, most likely affect the mangrove by exposing it to chemicals.

The sediment properties at the study site were described by Maharning et al. (2022). The organic carbon ranged between 9.98 and 18.66%, with total nitrogen from 0.18 to 0.63%. The total phosphorous (P₂O₅) and potassium (K₂O) were 0.03-0.08% and 0.16-0.34%, respectively. The electrical conductivity was from 11.90 to 154.00 mS, and the salinity range was 7-35 ppt. The sediment pH was between 5.80 and 7.44, and water content reached 57.86-77.08%.

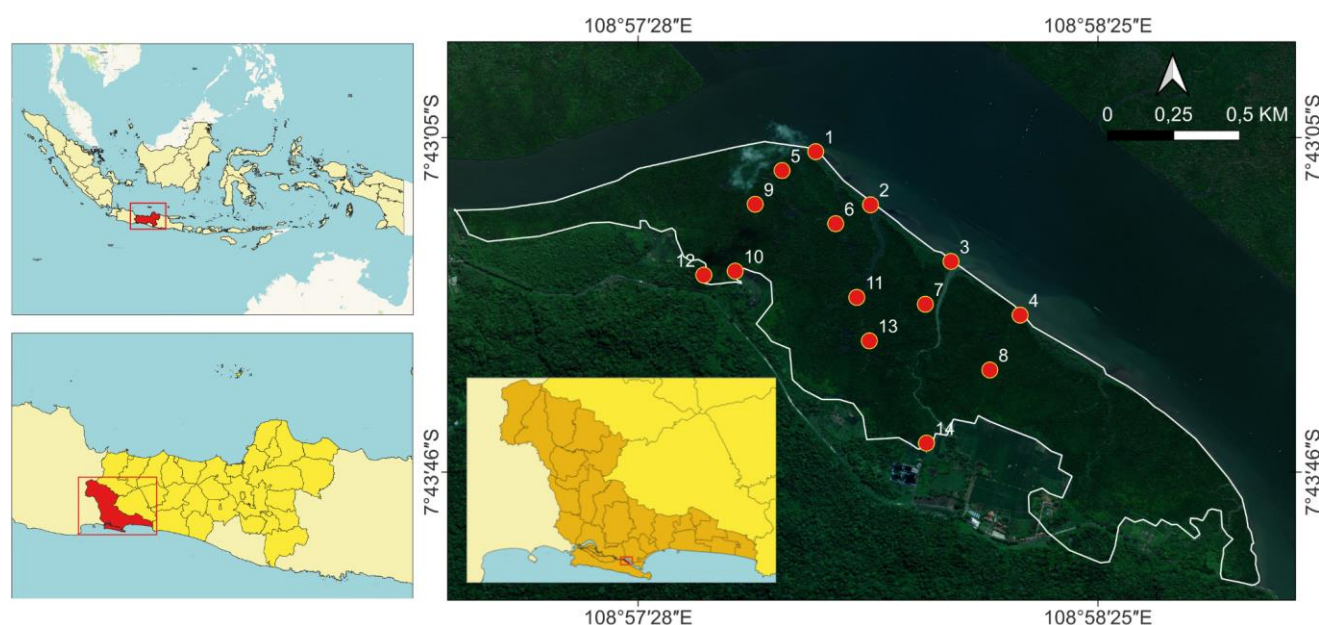


Figure 1. The study site is south of Cilacap District, Central Java, Indonesia, in Nusakambangan Island, Kembangkuning Mangrove Area. There were 14 stations assigned within the area of the site. The outermost stations (S1, S2, S3, S4) were adjacent to the river, whereas the innermost stations (S12, S13, S14) were adjacent to the terrestrial forest. The mid-stations between them included S5, S6, and S7 (closer to the river) and S8, S9, S10, and S11 (closer to the terrestrial forest).

Sampling design and fieldwork

We established 14 sampling stations across the study site, extending from the area adjacent to the river to the area adjacent to a terrestrial forest. Four stations were adjacent to the river (S1, S2, S3, S4), and three were adjacent to a terrestrial ecosystem (S12, S13, S14). Seven other stations were the mid-stations between the river adjacent area and the terrestrial adjacent area. Stations S5, S6, and S7 were mid-stations closer to the river, whereas stations S8, S9, S10, and S11 were mid-stations closer to the terrestrial forest (Figure 1). Each station covered a 1x1 m quadrant where two cored sediment samples of 10 cm depth (surface area of 19.63 cm²) were retrieved from July to August 2021 for further analysis. The samples were packed in plastic containers and transferred for nematode identification.

Nematode Extraction

We followed the Baermann funnel extraction method to retrieve the nematodes from the sample (Forge and Kimpinski 2008). Approximately 20 g of two composite samples from each station's core was submerged in distilled water for 48 hours. The sample was wrapped in tissue paper prior to submersion. The bottom liquid (5 ml) was retrieved from the funnel and then fixed with formaldehyde 4% final solution for identification.

Nematode Identification

We applied nematode taxonomic identification to the genus level following the World Register of Marine Species (WoRMS) Website (Steyaert et al. 2005). We used five morphological characters to determine the morpho-functional traits. The body shape was performed according to Soetaert et al. (2002) and used the nematode length-width ratio: (A) stout < 18, (B) slender 18-27, and (C) long thin > 72. Nematode body length was: (A) < 1 mm, (B) 1-2 mm, (C) 2-4 mm, and (D) > 4 mm (Singh and Ingole 2016). The tails were classified into four groups based on Thistle and Sherman (1985), namely (A) short blunt, (B) elongate filiform, (C) conical, and (D) clavate.

The feeding type classifies nematodes into four groups, according to Weiser (1953): (A) 1A refers to selected deposit feeders with no buccal cavity, (B) 1B includes non-selective deposit feeders with a large unarmed buccal cavity, (C) 2A includes epistrate feeders and a buccal cavity with scraping tooth or teeth, (D) 2B nematodes are predators or omnivores, with a buccal cavity with large jaws.

The nematode life history was based on the colonizer-persister (cp) scale, according to Bongers (1990): (A) cp1 nematodes have a short generation time, a high reproductive rate, are tolerant to pollutants and are capable of forming *dauer larvae*, (B) cp2 nematodes have a short generation time and a relatively high reproduction rate and are very tolerant to pollutants, (C) Nematodes of cp3 have a longer generation time than cp2 and are sensitive to pollutants, (D) cp4 nematodes show a long generation time and are highly sensitive to pollutants, and (E) cp5 nematodes have a long lifespan, low reproductive rate, and

slow movement and are very sensitive to pollutants. The nematode habitat range followed Steyaert et al. (2005).

We adopted Semprucci et al. (2022) method to simplify the combined traits description and analysis. The morpho-functional traits describing each nematode individual were collected. The nematode was then coded using a series of letters assigned for the given traits in a sequence of body shape, length, tail shape, feeding type, and life history. For example, a nematode specimen with a slender body shape, 1-2 mm long, elongated filiform tail, non-selective deposit feeder with a large unarmed buccal cavity, and cp2 scale having a short generation time, a relatively high reproduction rate and are very tolerant to pollutants, was coded as BBBBB.

Data analysis

Measurements of the nematode community across the site were accommodated by multivariate ordination analysis, including Principal Component Analysis (PCA) and Detrended Correspondence Analysis (DCA) using the Canoco v5 software (Šmilauer and Lepš 2014). We applied the PCA to investigate the possible pattern of nematode morpho-functional traits over the study site. The variables for this analysis included the proportion of all five independent traits in each station. Because the response data were not compositional, a linear method was used with four computed axes, but two ordination axes were presented. The data were centered and standardized by traits before analysis. The DCA was to observe nematode distribution and composition based on their combined traits. The compositional response data consisted of 29 combined traits of all stations. The response data had a gradient of 3.0 standard deviation units long; hence we selected a unimodal method. The DCA was also used to examine the nematode community structure based on the 38 genera of all stations to find out their distribution and compositions. The response data were compositional with a gradient of 3.5 standard deviation units long, appropriate for a unimodal method. The data were log-transformed prior to analysis.

RESULTS AND DISCUSSION

The morpho-functional traits

Morpho-functional traits of the nematode community in Kembangkuning Mangrove Area are presented in Table 1, and trait analysis of the PCA is in Figure 1. In general, the slender nematodes (76.99%) were common in all stations, with an increased trend from the stations adjacent to the river (S1-S4) toward those of the terrestrial area border (S12-S14). Most nematodes were 1-2 mm long (56.35%) and frequently had elongated filiform (36.04%) or conical tails (33.33%). Likewise, cp3 nematodes (53.97%) were more common than the other life history categories, whereas all feeding types occurred at similar proportions with slightly high predators or omnivores (26.98%).

The PCA revealed that all morpho-functional traits, except clavate tail, were observed in all stations but with various abundance (total explained variation: 70.88%).

Predatory or omnivorous (2B) nematodes or long-size nematodes (2–4 mm and > 4 mm) mostly inhabited stations adjacent to the terrestrial forest (S12–S14). However, these traits were less pronounced in the mid-stations (S8–S11) next to it. In these stations, clavate-tailed nematodes (S10) or conical tails, small nematodes (< 1 mm), or pollutant-sensitive nematodes (cp4) were more frequent. No specific morpho-functional types characterized the mid areas (S5–S7) or area adjacent to the river (S1–S4). All traits were available, but each area had a different relative abundance (Figure 2A).

Based on axis-1 (56.83% explained variation), determined primarily by nematode life history, feeding habit, body shape, and tail shape, changes in nematode morpho-functional traits most likely were influenced by their habitat proximity to the river. The trait changes in the nematode community were subtle across the study site, shown by the close or overlapping stations in the analysis (Figure 2B). The analysis appeared to separate the study site into five groups of nematodes, each with a similar composition of the morpho-functional traits. A station in the adjacent river area (S1) showed a similar trait pattern of the nematode community as a mid-station area (S6), in

which all traits occurred in a similar proportion between them. Then, the trait pattern changed in another station group covering the adjacent river area and mid area (S2, S4, S7, S9, and S10) being S10 the most different trait within the group, followed by changes in S5, S11, S13, and S14 (mid area and terrestrial forest adjacent area). The last three stations appeared to harbor two different patterns of morpho-functional traits in nematode assemblage, S3 (river adjacent area), and a group of S8 and S12 (mid area and terrestrial forest adjacent area). These results suggest that three major groups of nematodes characterize the study site. They were a nematode group that lived in the river adjacent area, those in the forest adjacent area, and a group of the mid area with similar trait patterns to nematodes of river adjacent or terrestrial adjacent area.

Nonetheless, the analysis was based on independent traits, each of which might belong to the same or different nematode individuals. Therefore, we combined all morpho-functional traits describing each individual nematode into combined traits to compare them to their genera, and understand the trait and genus distribution across the study site. There were 29 combined traits of nematodes observed from the study site.

Table 1. The morpho-functional trait proportion of all nematode specimens categorized into body shape, body length, tail shape, feeding types, and life history

	S1-S4	S5-S7	S8-S11	S12-S14	Total
Body shape (%)					
Stout	4.76	1.59	3.97	4.76	15.08
Slender	17.45	11.91	23.02	24.61	76.99
Long thin	2.38	0.79	3.17	1.59	7.93
Body length (%)					
< 1 mm	3.97	2.38	5.56	3.17	15.08
1 - 2 mm	14.29	9.52	17.46	15.08	56.35
2 - 4 mm	6.35	2.38	6.35	11.11	26.19
> 4 mm	0.00	0.00	0.79	1.59	2.38
Tail shape (%)					
Short blunt	7.21	4.51	9.01	7.21	27.93
Elongated filiform	9.91	7.21	10.81	9.91	36.84
Conical	7.21	2.70	10.81	12.61	33.33
Clavate	0.00	0.00	0.90	0.00	0.90
Feeding type (%)					
1A	7.14	1.59	8.73	6.35	23.81
1B	4.76	4.76	7.15	7.14	23.81
2A	5.56	3.17	7.94	8.73	25.40
2B	7.14	4.76	6.35	8.73	26.98
Life history (%)					
cp2	9.52	5.56	11.90	11.11	38.09
cp3	13.49	7.94	14.29	18.25	53.97
cp4	1.59	0.79	3.97	1.59	7.94

Notes: S1–S4: Stations adjacent to the river, S5–S7: Stations located in the mid area but closer to the river, S8–S11: Stations located in the mid area but closer to the terrestrial forest, S12–S14: Stations adjacent to the terrestrial forest, 1A: Selected deposit feeders, no buccal cavity, 1B: Non-selective deposit feeders, large unarmed buccal cavity, 2A: Epistrate feeders, buccal cavity with scraping tooth or teeth, 2B: Predator or omnivore, buccal cavity with large jaws, cp: Colonizer–persister scale

The DCA based on 29 combined traits showed various responses of nematodes to the mangrove areas (total explained variation: 26.98%) (Figure 3). It revealed nematodes with one specific trait combination (BBBCC), in the area adjacent to the river (S3) (Table 2). Mid-stations in the area next to it had no specific combined traits (S5-S7), which were consistent with the previous independent trait analysis. The long size (2-4 mm) predatory or omnivorous nematodes that were common in area adjacent to terrestrial forest (S12-S14) (Figure 2A) were also demonstrated in the combined-trait analysis with three characteristics combined traits. They were BCBCC, BCBCB, and BCCCB (S12) (Figure 3A, Table 2). The area closer to the terrestrial forest (S8-S11) was characterized by nematodes with three different combined traits (AABDC in S8, BBBCB in S9, and CCDAD in S10). The most common combined traits in the Kembangkuning Mangrove were BBBB, which inhabited 92.86% of the total stations. The other two combined traits were AACDC and BBBD, which each occupied 64.29% of the total stations (Table 2).

The analysis also demonstrated a consistent but clearer pattern of nematode combined traits across the study site, compared to independent traits. The combined traits composition in the terrestrial adjacent area differed from those in the river adjacent area, except for one station adjacent to the terrestrial forest (S14) (Figure 3B). Based on axis-1 (18.31% explained variation), the analysis showed six groups of nematodes, each with different composition of combined traits. The combined trait

composition in the river adjacent area (S1) was followed by similar composition in the terrestrial adjacent area (S14). The third group consisted of S3, and S9 (area adjacent to the river, and mid area). The next was a station group of mid area (S5, S8, and S10) followed by a group of adjacent river area (S2, S4) and stations of mid area (S6, S7, and S11). The last group was the area adjacent to the terrestrial forest (S12, S13).

The community structure

There were 69 morphologically different nematodes observed in the study site. Most (92.10%) were classified into 38 genera; the rest were identified to their family level. Overall, 19 families of nematodes were found in the study site. Across the study site, most of the nematodes (24 genera) were in low abundance, between 0.12 and 1.82%, and accounted for 18.77% of the community. In contrast, the relative abundance for 14 other genera was between 2.08 and 17.53%, contributing to 81.23% of the total nematode community (Table 3). Three genera showed a high relative abundance, *Anoplostoma* (17.53%), *Eubotrichus* (10.36%), and *Chromadorina* (11.09%). The first two genera were common in all stations, but the last genus was limited only to the mid-stations (S5-S7 and S8-S11). When comparing the community between the area, the results showed increasing trend of nematode relative abundance from the stations in river adjacent area of S1-S4 (11.30%) toward the stations adjacent to terrestrial forest of S12-S14 (36.27%) (Figure 4A).

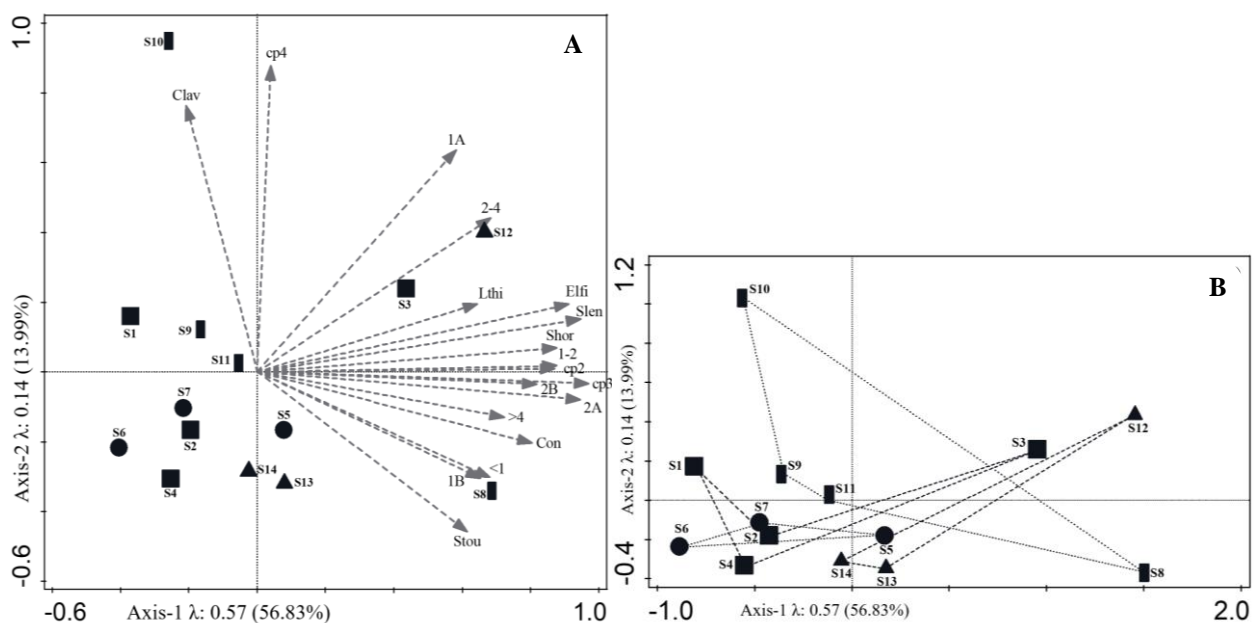
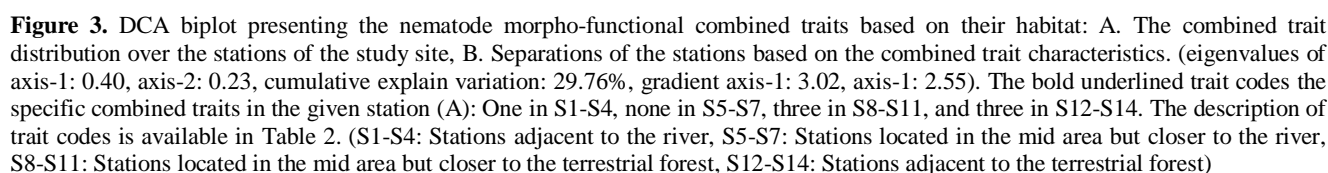


Figure 2. PCA biplot illustrating the nematode morpho-functional traits in relation to their habitat: A. Morpho-functional trait distribution across the stations of the study site, B. Separations of the stations based on morpho-functional trait characterized the station. (eigenvalues of axis-1: 0.57, axis-2: 0.14, cumulative explain variation: 70.82%, S1-S4: Stations adjacent to the river, S5-S7: Stations located in the mid area but closer to the river, S8-S11: Stations located in the mid area but closer to the terrestrial forest, S12-S14: stations adjacent to the terrestrial forest, Stou: Stout, Slen: Slender, Long: Long-thin, <1: < 1 mm, 1-2: 1-2 mm, 2-4: 2-4 mm, >4: > 4 mm, Shob: Short Blunt, Elfi: Elongated Filiform, Coni: Conical, Clav: Clavate, 1A: Selective deposit feeders, 1b: Non-selective deposit feeders, 2a: Epistrate feeders, 2b: Predators or omnivores, cp2: Colonizer-persister scale 2, cp3: Colonizer-persister scale 3, cp4: Colonizer-persister scale 3)



Area	Code	Body shape	Body length	Tail shape	Feeding type	Life history	Station cover (%)
Specific combined traits to the stations							
S1-S4	BBBCC	Slender	1-2 mm	Elongated filiform	Epistrate feeder	cp3	7.14
S8-S11	AABDC	Stout	<1 mm	Elongated filiform	Predator omnivore	cp3	7.14
	BBBCB	Slender	1-2 mm	Elongated filiform	Epistrate feeder	cp2	7.14
S12-S14	CCDAD	Long thin	2-4 mm	Clavate	Selective deposit feeder	cp4	7.14
	BCBCC	Slender	2-4 mm	Elongated filiform	Epistrate feeder	cp3	7.14
	BCBCB	Slender	2-4 mm	Elongated filiform	Epistrate feeder	cp2	7.14
	BCCCB	Slender	2-4 mm	Conical	Epistrate feeder	cp2	7.14
Common combined trait to more than one stations							
	AACDC	Stout	<1 mm	Conical	Predator omnivore	cp3	64.29
	ABBCC	Stout	1-2 mm	Elongated filiform	Epistrate feeder	cp3	21.43
	BAAAB	Slender	<1 mm	Short blunt	Selective deposit feeder	cp2	28.57
	BABCB	Slender	<1 mm	Elongated filiform	Epistrate feeder	cp2	21.43
	BACCC	Slender	<1 mm	Conical	Epistrate feeder	cp3	14.29
	BBAAC	Slender	1-2 mm	Short blunt	Selective deposit feeder	cp3	28.51
	BBACC	Slender	1-2 mm	Short blunt	Epistrate feeder	cp3	21.43
	BBADC	Slender	1-2 mm	Short blunt	Predator omnivore	cp3	21.43
	BBBBB	Slender	1-2 mm	Elongated filiform	Non-selective deposit feeder	cp2	92.86
	BBBDC	Slender	1-2 mm	Elongated filiform	Predator omnivore	cp3	64.29
	BBBDD	Slender	1-2 mm	Elongated filiform	Predator omnivore	cp4	21.43
	BBCAB	Slender	1-2 mm	Conical	Selective deposit feeder	cp2	35.71
	BBCBB	Slender	1-2 mm	Conical	Non-selective deposit feeder	cp2	28.57
	BBCDC	Slender	1-2 mm	Conical	Predator omnivore	cp3	28.57
	BCBAC	Slender	2-4 mm	Elongated filiform	Selective deposit feeder	cp3	28.57
	BCBAD	Slender	2-4 mm	Elongated filiform	Selective deposit feeder	cp4	21.43
	BCCAB	Slender	2-4 mm	Conical	Selective deposit feeder	cp2	14.29
	BCCBB	Slender	2-4 mm	Conical	Non-selective deposit feeder	cp2	14.29
	BCCCC	Slender	2-4 mm	Conical	Epistrate feeder	cp3	42.86
	BDAAC	Slender	>4 mm	Short blunt	Selective deposit feeder	cp3	14.29
	CCACC	Long thin	2-4 mm	Short blunt	Epistrate feeder	cp3	21.43
	CCBCC	Long thin	2-4 mm	Elongated filiform	Epistrate feeder	cp3	42.86

Note: S1-S4: Stations adjacent to the river, S5-S7: Stations located in the mid area closer to the river, S8-S11: Stations located in the mid area closer to the terrestrial forest, S12-S14: Stations located adjacent to the terrestrial forest, cp: Colonizer-persister scale

The DCA (total explained variation: 25.02%) of nematode distribution and composition in each station are presented in Figure 5. The genus compositions in the mid area (S5-S7 and S8-S11) appeared to differ from those in stations of the terrestrial adjacent area (S12-S14) and most of the stations in the river adjacent area (S1-S4) (Figure 5B). The DCA analysis also provided two data summaries of diversity measurements, genus richness (S) and diversity index (H) for each area. The area adjacent to the river (S1-S4) was a habitat for 22 genera (H: 2.72), dominated by *Anoplostoma* (23.75%), and two particular genera that only live in this area, *Pomponema* (S3) and *Nannolaimus* (S4). The next area covering S5-S7 was characterized by the presence of *Trissonchulus* (S5), and dominance of *Anoplostoma* (24.45%), low genus richness (S: 15), and lower diversity compared to that of S1-S4 (H: 2.38). The S8-S11 stations located in the mid-area closer to the terrestrial forest were home to 28 genera with a diversity value of H: 2.41. *Chromadorina* (37.93%) dominated this

area, whereas *Adoncholaimus* (S8), *Dorylamiopsis* (S9), and *Oxystomina* (S10) were the specific inhabitants. The area adjacent to the terrestrial forest (S12-S14) was rich with *Halichoanulaimus* (23.89%), and specified with the presence of *Anticyathus* and *Paralinhomoeus* (S13), *Chromadora*, *Dichromadora*, *Longicyatholaimus*, and *Paracanthionchus* (S12). The 21 other nematode genera also inhabited the area of S12-S14 (S: 27), with a diversity value of H: 2.67 (Figures 4 and 5A, Table 3).

Based on the nematode genus morphology, we described their combined traits and observed that some genera had similar combined traits. There were 15 genera coded by six combined traits. They were *Paraspaerolaimus* and *Synonchiella* (AACDC), *Nannolaimus* and *Ptycholaimellus* (ABBCC), *Spirinia* and *Trissonchulus* (BBACC), *Halichoanulaimus* and *Sphaerolaimus* (BBBDC), *Chromadora*, *Eubotridhus*, and *Pseudochromadora* (BCCCC), *Anoplostoma*, *Paralinhomoeus*, *Sabatiera*, and *Theristus* (BBBBB).

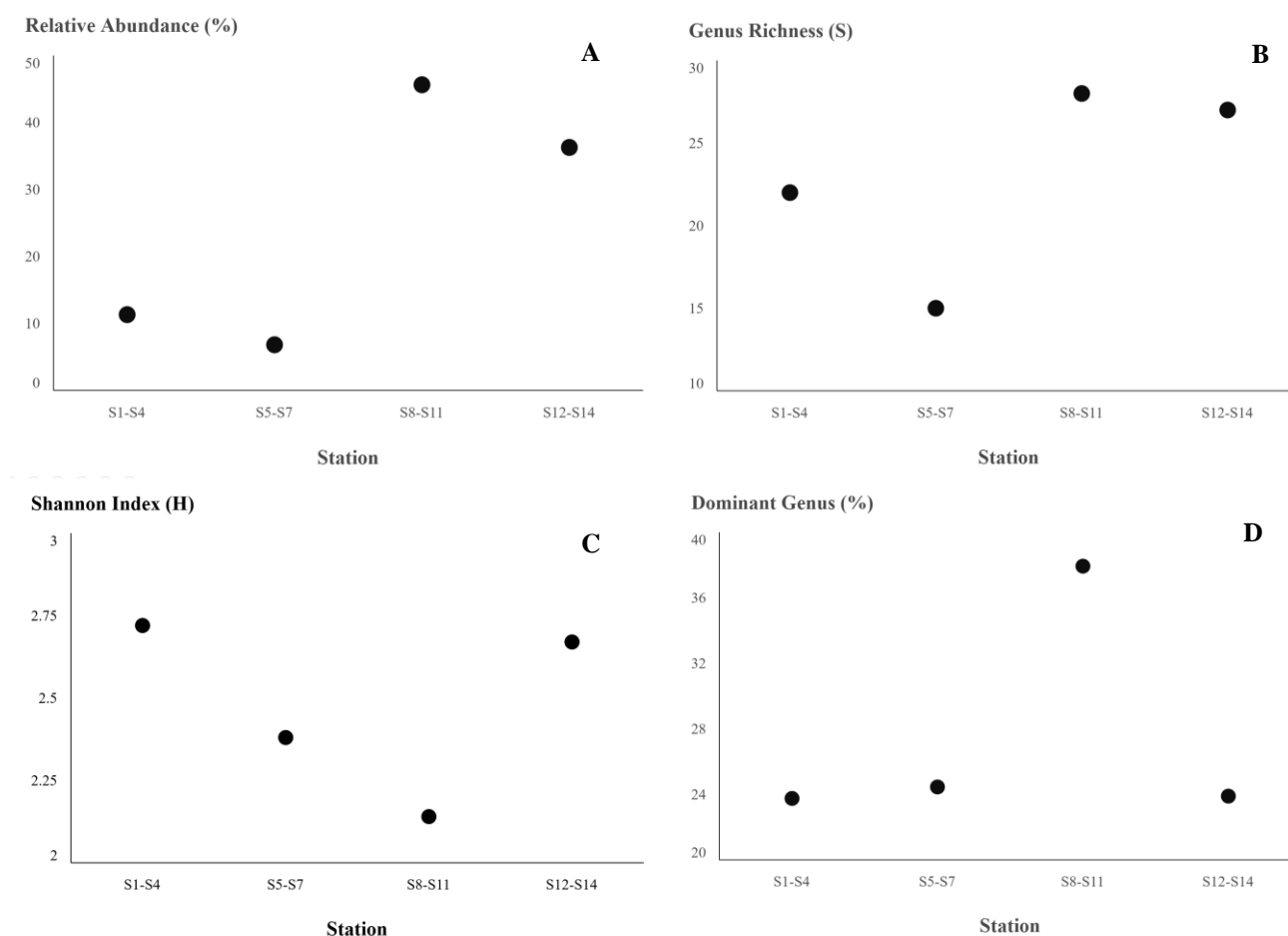


Figure 4. A. The nematode relative abundance, B. Genus richness, C. Shannon diversity index, and D. the dominant genus across the study site showing increasing trend in the relative abundance and genus richness but not in diversity and genus dominance from stations in the river adjacent area (S1-S4) to terrestrial adjacent area (S12-S14)

Table 3. The relative abundance of nematode genera and their corresponding trait codes inhabited Kembangkuning Mangrove Area of Segara Anakan, Indonesia

Genus	Body shape	Body length (mm)	Tail shape	FT	LH Cp	Habitat range	S1-S4 (%)	S5-S7 (%)	S8-S11 (%)	S12-S14 (%)	All stations (%)
<i>Anoplostoma</i> *	B. slender	B. 1.75	B. elongated filiform	B. 1B	B. 2	mbf	23.75	24.45	7.10	14.82	17.53
<i>Eubostriechus</i> *	B. slender	B. 2.04	C. conical	C. 2A	C. 3	m	6.08	10.53	14.90	12.84	11.09
<i>Chromadorina</i>	B. slender	A. 0.44	C. conical	C. 2A	C. 3	mbf	0.00	3.51	37.93	0.00	10.36
<i>Synonchiella</i> *	A. stout	A. 0.84	C. conical	D. 2B	C. 3	m	13.38	11.65	1.35	6.16	8.13
<i>Halichoanulaimus</i> *	B. slender	B. 1.04	B. elongated filiform	D. 2B	C. 3	m	1.99	3.14	1.21	23.89	7.56
<i>Theristus</i> *	B. slender	B. 1.72	B. elongated filiform	B. 1B	B. 2	mbft	2.05	16.81	4.06	4.94	6.96
<i>Cobbia</i> *	C. long thin	C. 2.33	B. elongated filiform	C. 2A	C. 3	mb	4.83	3.14	2.58	3.31	3.47
<i>Sabatieria</i> *	B. slender	B. 1.89	B. elongated filiform	B. 1B	B. 2	mb	1.39	3.59	3.26	3.31	2.89
<i>Syringolaimus</i>	B. slender	B. 1.88	B. elongated filiform	D. 2B	D. 4	mb	5.96	3.14	0.61	0.00	2.43
<i>Sphaerolaimus</i> *	B. slender	B. 1.01	B. elongated filiform	D. 2B	C. 3	mb	1.99	3.59	1.23	2.21	2.25
<i>Leptonemella</i>	C. long thin	C. 2.16	A. short blunt	C. 2A	C. 3	m	5.96	0.00	1.66	1.10	2.18
<i>Viscosia</i> *	B. slender	B. 1.92	C. conical	D. 2B	C. 3	mbf	3.97	3.14	0.55	1.05	2.18
<i>Ascolaimus</i>	B. slender	B. 1.94	C. conical	B. 1B	B. 2	m	0.00	3.14	1.35	4.01	2.12
<i>Terschellingia</i> *	B. slender	C. 2.10	B. elongated filiform	A. 1A	C. 3	mbf	1.99	3.51	0.61	2.21	2.08
<i>Thalassomonhystera</i>	B. slender	A. 0.91	A. short blunt	A. 1A	B. 2	mbf	1.99	3.51	1.78	0.00	1.82
<i>Leptolaimus</i>	B. slender	B. 1.43	C. conical	A. 1A	B. 2	mb	3.33	0.00	2.51	1.05	1.72
<i>Microlaimus</i>	B. slender	A. 0.73	B. elongated filiform	C. 2A	B. 2	mbf	3.97	0.00	0.68	1.05	1.42
<i>Parasphaerolaimus</i>	A. stout	A. 0.69	C. conical	D. 2B	C. 3	mb	2.79	0.00	1.35	1.05	1.30
<i>Deontolaimus</i>	B. slender	B. 1.58	A. short blunt	A. 1A	C. 3	mb	0.00	0.00	1.58	3.59	1.29
<i>Pseudochromadora</i>	B. slender	C. 2.62	C. conical	C. 2A	C. 3	mbf	0.00	0.00	4.06	1.10	1.29
<i>Ptycholaimellus</i>	A. stout	B. 1.10	B. elongated filiform	C. 2A	C. 3	mb	0.00	0.00	3.39	1.10	1.12
<i>Pomponema</i>	B. slender	B. 1.97	B. elongated filiform	C. 2A	C. 3	mb	**3.97	0.00	0.00	0.00	0.99
<i>Halalaimus</i>	B. slender	C. 2.03	B. elongated filiform	A. 1A	D. 4	mbft	2.69	0.00	0.48	0.52	0.92
<i>Metalinhomoeus</i>	B. slender	C. 2.08	C. conical	B. 1B	B. 2	m	1.99	0.00	0.00	1.57	0.89
<i>Pseudolella</i>	B. slender	C. 2.38	C. conical	A. 1A	B. 2	mbf	1.99	0.00	1.35	0.00	0.84
<i>Trissonchulus</i>	B. slender	B. 1.33	A. short blunt	C. 2A	C. 3	mbt	0.00	**3.14	0.00	0.00	0.78
<i>Dolicholaimus</i>	B. slender	B. 1.74	A. short blunt	D. 2B	C. 3	m	0.00	0.00	1.96	1.10	0.77
<i>Spirinia</i>	B. slender	B. 1.86	A. short blunt	C. 2A	C. 3	m	1.99	0.00	0.68	0.00	0.67
<i>Chromadora</i>	B. slender	C. 2.38	C. conical	C. 2A	C. 3	mbft	0.00	0.00	0.00	**2.21	0.55
<i>Nannolaimus</i>	A. stout	B. 1.53	B. elongated filiform	C. 2A	C. 3	m	**1.99	0.00	0.00	0.00	0.50
<i>Anticyathus</i>	B. slender	D. 4.71	A. short blunt	A. 1A	C. 3	m	0.00	0.00	0.00	**1.80	0.45
<i>Paracanthochus</i>	B. slender	C. 2.29	C. conical	C. 2A	B. 2	mb	0.00	0.00	0.00	**1.10	0.28
<i>Longicyatholaimus</i>	B. slender	C. 3.06	B. elongated filiform	C. 2A	C. 3	m	0.00	0.00	0.00	**1.10	0.28
<i>Dichromadora</i>	B. slender	C. 2.74	B. elongated filiform	C. 2A	B. 2	mbf	0.00	0.00	0.00	**1.10	0.28
<i>Paralinhomoeus</i>	B. slender	B. 1.32	B. elongated filiform	B. 1B	B. 2	m	0.00	0.00	0.00	**0.69	0.17
<i>Adoncholaimus</i>	A. stout	A. 0.62	B. elongated filiform	D. 2B	C. 3	mbf	0.00	0.00	**0.68	0.00	0.17
<i>Dorylamiopsis</i>	B. slender	B. 1.69	B. elongated filiform	C. 2A	B. 2	mb	0.00	0.00	**0.61	0.00	0.15
<i>Oxystomina</i>	C. long thin	C. 2.72	D. clavate	A. 1A	D. 4	mbf	0.00	0.00	**0.48	0.00	0.12

Note: *Common genus inhabited all stations, **Genus specific to the given station in the area, FT: Feeding Type, LH: Life History, S1-S4: Stations adjacent to the river, S5-S7: Stations located in the mid area closer to the river, S8-S11: Stations located in the mid area closer to the terrestrial forest, S12-S14: Stations located adjacent to the terrestrial forest, 1A: Selected deposit feeders, no buccal cavity, 1B: Non-selective deposit feeders, large unarmed buccal cavity, 2A: Epistrate feeders, buccal cavity with scraping tooth or teeth, 2B: Predator or omnivore, buccal cavity with large jaws, cp: Colonizer–persister scale, m: Marine, b: Brackish, f: Freshwater, t: Terrestrial

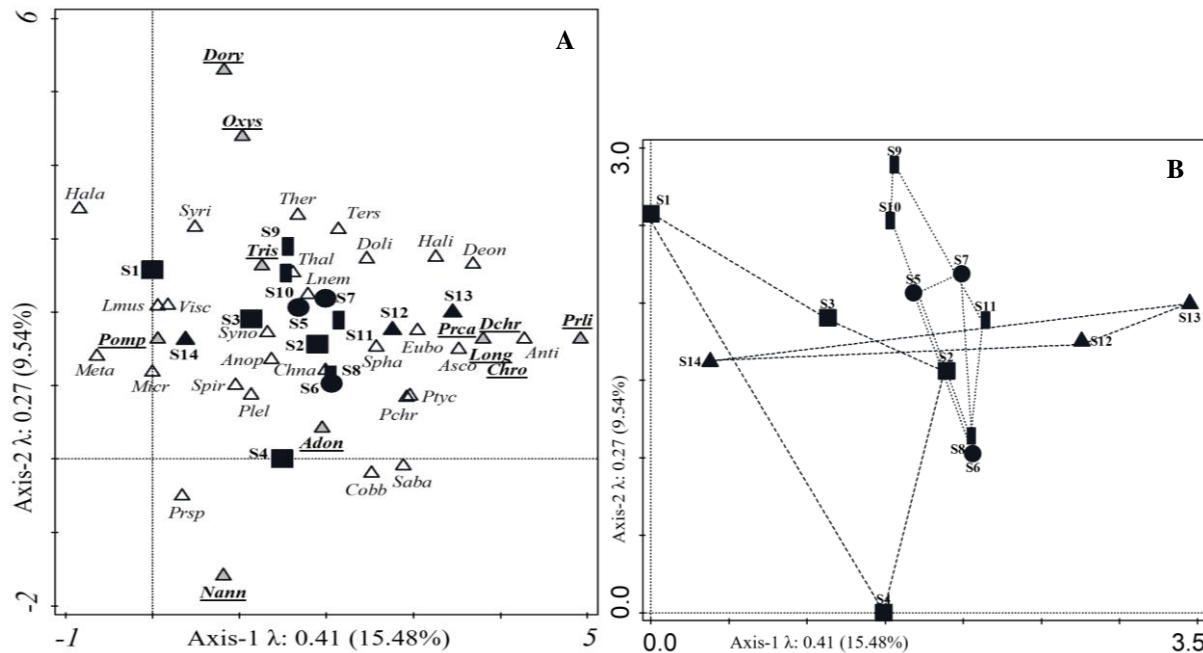


Figure 5. DCA biplot illustrating the nematode distribution and composition in each station group: (A) the genus distribution in relation to the station they live in, (B) nematode composition in each station based on nematode relative abundance and genus richness. The genera specified in each area were in bold, underlined characters. (eigenvalues of axis-1: 0.41, axis-2: 0.27, total explain variation: 25.02%, S1-S4: Stations adjacent to the river, S5-S7: Stations located in the mid area but closer to the river, S8-S11: Stations located in the mid area but closer to terrestrial forest, S12-S14: Stations adjacent to the terrestrial forest, *Adon*: *Adoncholaimus*, *Anop*: *Anoplostoma*, *Anti*: *Anticyathus*, *Asco*: *Ascolaimus*, *Chna*: *Chromadorina*, *Chro*: *Chromadora*, *Cobb*: *Cobbia*, *Dchr*: *Dichromadora*, *Deon*: *Deontolaimus*, *Doli*: *Dolicholaimus*, *Dory*: *Dorylamiopsis*, *Eubo*: *Eubostriechus*, *Hala*: *Halalaimus*, *Hali*: *Halichoanulaimus*, *Lmus*: *Leptolaimus*, *Lnem*: *Leptonemella*, *Long*: *Longicyatholaimus*, *Meta*: *Metalinhomoeus*, *Micr*: *Microlaimus*, *Nann*: *Nannolaimus*, *Oxys*: *Oxystomina*, *Pchr*: *Pseudochromadora*, *Plell*: *Pseudolella*, *Pomp*: *Pomponema*, *Prca*: *Parachanthochus*, *Prli*: *Paralinhomoeus*, *Prsp*: *Paraspaerolaimus*, *Ptyc*: *Ptycholaimellus*, *Saba*: *Sabatieria*, *Spha*: *Sphaerolaimus*, *Spir*: *Spirinia*, *Syno*: *Synonchiella*, *Syri*: *Syringolaimus*, *Ters*: *Terschellingia*, *Thal*: *Thalassomonhystera*, *Ther*: *Theristus*, *Tris*: *Trissonchulus*, *Visc*: *Viscosia*).

Discussion

Our exploration reveals the details of free-living nematodes from a mangrove area in Indonesia. Three approaches we used to analyze our nematode data, namely independent morpho-functional traits, combined morpho-functional traits describing the individual nematodes, and nematode genera, suggested various nematode compositions over the study site. The last two approaches generally revealed nematode traits and genus composition that characterized river adjacent area (S1-S4) and terrestrial adjacent area (S12-S14). However, the nematode community of the mid area (S5-S7 and S8-S11) was unclear when the independent morpho-functional trait was applied. High variability of the traits occurred within the mid area, as demonstrated by the wide distribution of the mid stations in the biplot diagram (Figure 2).

However, the nematode composition based on the combined traits was less varied in the mid area (Figure 3). At the same mid area, the nematode genera showed distinct genus composition (Figure 4). These findings suggest that distance from the river might determine the habitability of nematodes, in which nematode morpho-functional traits play roles. Similarly, the three divided areas in Kembangkuning Mangrove support the difference genus composition and abundance of nematodes.

The nematode morpho-functional traits

Body shape is an essential feature for nematodes, reflecting the ability to move and feed, susceptibility to predation, and response to chemical stress (Ghosh and Mandal 2021). Nematodes with slender bodies dominated the community of our study site (Table 1). The result is in agreement with Singh and Ingole (2016) who investigated that slender nematodes dominate silty-sandy sediment or clay-silty sediment of the Arabian Sea. Similarly, Ghosh and Mandal (2021) observed slender bodies as the most typical shape of nematodes in the muddy sediment of the Sundarbans Estuarine System, India. In our study, the sediment of all stations was muddy. However, the nematode proportions with a slender body and body length tended to increase toward stations adjacent to the terrestrial forest, which most possibly relates to their adaptability to low oxygen habitat. Ghosh and Mandal (2021) suggested that an elongated body, such as the slender shape of nematodes, is an adaptive characteristic in hypoxic muddy sediment to increase oxygen uptake.

The muddy sediment of our study site also harbors nematodes with two common tail shapes: elongated filiform and conical (Table 1). This finding is consistent with Singh and Ingole (2016), who reported frequent occurrences of conical-tailed nematodes in muddy

sediment. A high silt and clay content in sediment strongly correlates to nematodes with elongated and filiform tails (Aswathy et al. 2017). We did not analyze the sediment textures of Kembangkuning Mangrove, but muddy sediment most likely contains a significant proportion of clay and silt (Hunt and Jones 2019). These tail shapes suggest adaptation that allows the nematodes to forage for food in narrow spaces between the sediment particles (Ghosh and Mandal 2021). Nematodes with clavate tails were rare and observed only at a mid-station closer to the terrestrial forest. In our study, these nematodes have long, thin body shapes, living as selective deposit feeders (1A) with a rather long generation time (cp4) (Table 2). Clavate-tailed nematodes frequently inhabit stressful ecosystems (Semprucci et al. 2022). However, cp4 is usually a predator or omnivore that actively searches for prey and is sensitive to pollutants (Ferris et al. 2001). Approximately 50% of clavate-tailed nematodes were observed in a study in the Arabian Sea (Singh and Ingole 2016), which is typical of a sandy substrate. Therefore, their presence in one of the stations is most likely temporary due to the drifting tide (Ptatscheck and Traunspurger 2020).

Nematode life history reflects direct functional roles in the ecosystem, although it is a less accessible trait (Ferris 2010). It also indicates the environmental conditions in which they live (Gabriela and Pastor 2020; Mueller et al. 2020; Sahraeian et al. 2020; Ridall and Ingels 2021). In our study, most nematodes were in the cp3 category, including epistrate feeders, predators, or omnivores with various body shapes (Tables 1 and 2). Nematodes of cp3 have a relatively long generation time and are relatively sensitive to pollutants (Bongers 1990), which might suggest that the area was less polluted. This condition is further supported by the absence of cp1, in which its presence is indicative of pollutant and organic matter decomposition products.

The nematode combined traits and community structure

The nematode combined traits (29, Table 2) in Kembangkuning Mangrove Area were lower than those reported in the Mediterranean Sea, reaching 47 combined traits (Semprucci et al. 2022). The generic richness (38 genera, Table 3) is in agreement with that of the tropical mangroves on the Indian south coast, with 36 genera of free-living nematodes (Chinnadurai and Fernando 2007), but lower than those from mangrove forests and plantations in south China Coast that reported 50 – 67 nematode genera (Fu et al. 2021). Approximately 42% of the nematode genera in our study were also found in Indian mangroves of similar dominant trees (Chinnadurai and Fernando 2007). Recently, 43 free-living nematode genera were retrieved from small samples and are documented to live in the soft-bottom habitat on Sao Miguel Island, Portugal, in the Atlantic Ocean (Navarrete et al. 2020). Three of them, *Adoncholaimus*, *Halalaimus*, and *Theristus*, were also observed in Kembangkuning Mangroves. The result, however, are 24 to 36% less than the nematode genera from two mangrove areas in South China (Fu et al. 2021). The climate differences might account for variances in the nematode genus richness, but the above-ground mangrove diversity is also responsible. Two mangrove

species dominate our study site, compared to six dominant mangrove trees in their site. With a higher diversity of mangrove trees, litter production is more diverse, which provides a high available niche variation to support diverse microorganisms as nutrient sources for the nematodes (Heděšec et al. 2023). Thus, our study begins to disclose the belowground richness of the Segara Anakan Mangrove and gain insight into the nematode community association with their habitat. Although our sampling covered a small part of the entire Segara Anakan Mangrove system, our study provides scientific evidence to contribute to the limited knowledge and data on mangrove nematodes from Indonesia.

The results show an interesting community pattern of the nematodes from the river to the terrestrial border (Figures 3 and 4). In general, gradual trait changes appeared to relate to the distance of the stations from the river. Some specific nematode genera inhabited only a particular station across the study site. This pattern was consistent with changes in the nematode combined traits. *Pomponema*, the slender nematodes, 1–2 mm long, with elongated filiform tails, epistrate feeders, and relatively sensitive to pollutants, corresponds to BBBCC, and lived in stations adjacent to the river. *Nannolaimus* (ABBCC) was observed only in adjacent river area. *Adoncholaimus* (AABDC), *Dorylomiopsis* (BBBCB), *Oxystomia* (CCDAD), and *Trissonchulus* (BBACC) characterized the mid-stations. Six genera corresponded to six different combined traits specified stations adjacent to the terrestrial ecosystem, including *Dichromadora* (BCBCB), *Chromadora* (BCCCC), *Parachanthochus* (BCCCB), *Longicyatholaimus* (BCBCC), *Anticyathus* (BDAAC), and *Paralinhomoeus* (BBBBB) (Table 3). However, some combined traits did not always correspond to one nematode genus. For instance, *Paraspaerolaimus* and *Synonchiella* corresponded to the same combination of AACDC (Table 3). These results indicate that the selection of morpho-functional traits in our study is less sensitive. Nematode amphid and cuticle types serve more sensitive traits related to the nematode genus than the body shape when the trait combination of an individual nematode is to apply. Nonetheless, our study supports the suggestion that changes in functional combined traits indicate changes in nematode genus composition and might be a simple alternative method to illustrate nematode communities in a given area (Semprucci et al. 2022).

In our study, we observed that all stout nematodes (<1 mm long) had elongated filiform or conical tails, lived primarily as epistrate feeders (2A) predators or omnivores (2B), had relatively long generation times and were relatively sensitive to disturbances (cp3). Five nematode genera matched these combined traits: *Adoncholaimus*, *Nannolaimus*, *Paraspaerolaimus*, *Ptycholaimellus*, and *Synonchiella*. They more frequently inhabited areas of river adjacent (4.54%) or mid-stations (4.61%) than terrestrial adjacent area (2.08%). The long-thin nematodes (2–3 mm) were mainly epistrate feeders (2A) that were relatively sensitive (cp3) or sensitive to disturbance (cp4) and reproduced relatively slowly. They preferred to live in an area adjacent to the river (10.34%). Their tails were either

elongated, short-round, or clavate, characterizing the nematode genera of *Cobbia*, *Leptonemella*, and *Oxystomina*. Biological trait combinations based on morphological characteristics might further suggest the adaptation of the nematodes to their environment. Human activities, such as oil refinery and agriculture surrounding Kembangkuning Mangrove, might affect the mangrove with the chemical drifting into the area.

Furthermore, there were ten common genera of nematodes (26.32%) with seven combined traits that live in all stations of the study site, suggesting their high tolerance to the variability of environmental parameters across the study site (Table 3). They were *Anoplostoma* (BBBBB), *Cobbia* (CCBCC), *Eubostrichus* (BBCCC), *Halichoanulaimus* (BBBDC), *Sabatiera* (BBBBB), *Spaerolaimus* (BBBDC), *Synonchiella* (AACDC), *Terschellingia* (BCBAC), *Theristus* (BBBBB), and *Viscosia* (BBCDC). Their relative abundance reached 64.14%, with most having high habitat range from marine, brackish, to freshwater, and few restricted to marine. Some other genera at our site may have adapted to high salinity and live strictly in marine environmental conditions, such as *Nannolaimus*, *Metalinhomoeus*, and *Paralinhomoeus*. Maharning et al. (2022) reported that the salinity in Kembangkuning Mangrove reached 35 ppt.

Our data suggest an increasing trend of nematode abundance from the river to the terrestrial border (Figure 4A). This trend was consistent with increased slender nematodes, body length (Table 1), and genus richness (Figure 4B). It is possibly due to the organic carbon content in the study site. Maharning et al. (2022) reported that the Kembangkuning Mangrove had a wide range of organic carbon, and the organic carbon content was the greatest in the border area of the terrestrial ecosystem. In our study, this area corresponds to stations adjacent to terrestrial forests (S11-S14). Liu et al. (2019) reported that organic carbon characterized the nematode distribution. Ghosh and Mandal (2021) also examined that nematode distribution significantly correlated with organic matter. Organic carbon implies detritus availability in the habitat and the capacity to produce and store organic matter (Matsui et al. 2015). Organic matter in the habitat is an essential resource for bacteria and fungi. It enriches the growth of diatoms and protozoa (Marella et al. 2021), which serve as nematode nutrient sources.

Nematode body size affects its energy requirement (Luan et al. 2020). In a terrestrial ecosystem of ungrazed soil, Andriuzzi and Wall (2018) reported that large-size nematodes prefer a habitat with high organic matter, providing sufficient basal resources as required by their large body size. This observation is likely to be true of our mangrove site as well. Organic carbon represents available organic matter that creates habitat heterogeneity due to various stages of decomposition, thus increasing available niches. Large body sizes might enable the nematodes to escape into the muddy sediment, protecting them from predators. Scientific evidence shows that larger body-size species are more sensitive to disturbances and are the first to be lost in disturbed habitats (Andriuzzi and Wall 2018; Majdi et al. 2019). Our results show that large nematodes

mainly inhabit stations away from the river, whereas smaller nematodes occupy all stations. This result may indicate habitat disturbance in the stations next to the river, where chemical pollutants might drift into the area. The substances may originate from human activities such as agriculture, but this requires further investigation.

In conclusion, our study shows the local free-living nematode diversity from a mangrove ecosystem. Distance from the river determines the relative abundance of nematode inhabitants with specific traits and genus compositions. The nematode morpho-functional trait provides a general idea of the specific traits in two farthest areas, adjacent river area and terrestrial adjacent area. Large nematodes, or those relatively sensitive to pollutants, were more abundant in terrestrial adjacent area than in river adjacent area. The combined traits correspond to the changes in genus composition but are not as obvious; hence, selecting sensitive morpho-functional traits is necessary to simplify the nematode community observation related to environmental variability. Nematode community structure indicates genus diversity that generally responded quite specifically to the habitat variations in the mangrove represented by area proximity to the river. Nevertheless, we suggest that further exploration and examination of mangrove nematodes on the extended and varied substrates of mangrove areas in Indonesia are necessary to understand their relationships and temporal dynamics. Nematode sensitive responses to environmental changes can also be adapted to monitor mangrove quality status, particularly in Segara Anakan, where early data are now available.

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