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Deciphering environmental forcings in the distribution of meiofauna and nematodes in mangroves of the Atlantic-Caribbean-East Pacific and Indo-West Pacific regions

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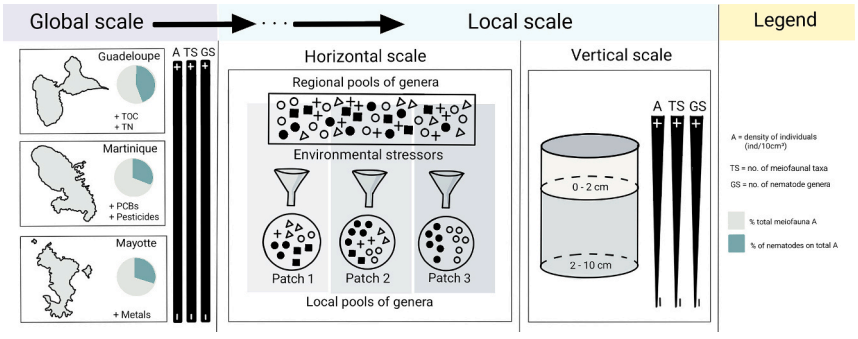
HIGHLIGHTS

- Metals, PCBs, PAHs or pesticides exceed toxicity thresholds on each island.
- Meiofauna and nematode density significantly decreased over depth.
- The nematode community is structured at the scale of the station in all islands.
- Nematode communities form local patches with highly different genus composition.
- Site-specific variability of nematode response to multiple stressors

GRAPHICAL ABSTRACT



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ABSTRACT

Mangroves develop under environmental conditions and anthropogenic pressures whose impact on benthic meiofauna remains poorly understood. It is unclear how meiofauna communities are structured according to local sedimentary conditions. This study was designed to characterize the community structure of meiofauna and nematodes (dominant taxa) and the associated environmental forcings in intertidal mangrove sediments from Mayotte (Indo-West-Pacific), Martinique and Guadeloupe (Caribbean). Sediment cores were sampled at the end

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Perturbations
Guadeloupe
Martinique
Mayotte

of the dry season at low tide on adult mangrove stands with similar immersion time. In each sediment layer, we analyzed redox potential, pH, porewater salinity, grain size, organic matter, metals, organic contaminants, prokaryotes and meiofauna. Our results show that sediments far from cities and agricultural fields trapped site-specific contaminants due to local water transport processes. Some metals, PAHs or pesticides exceeded toxicity thresholds in most of the studied stations, thus being harmful to benthic fauna. The sedimentary environment acts as a filter selecting specific meiofauna communities at station scale only in the Caribbean. In Mayotte, horizontal homogeneity contrasts with vertical heterogeneity of the sedimentary environment and the meiofauna. Nematode genera showed particular distribution patterns horizontally and vertically, suggesting the presence of sediment patches suitable for a restricted pool of genera on each island. Results in the Caribbean are consistent with nested diversity patterns due to environmental filtering. Conversely, horizontal homogeneity at Mayotte would reflect greater dispersal between stations or more spatially homogeneous anthropogenic pressures. The nematode genera present at depth may not be the most specialized, but the most versatile, capable of thriving in different conditions. *Terschellingia* and *Daptonema* showed contrasted responses to environmental forcing, likely due to their versatility, while *Desmodora* showed uniform responses between study areas, except when toxicity thresholds were exceeded. Our results emphasize that a given genus of nematode may respond differently to sedimentary conditions depending on sites.

1. Introduction

Mangrove forests grow in the inter-tropical area, thriving on saline soils that are alternately waterlogged and drained (Walsh, 1974). Salinity, flooding, evapotranspiration, oxygen and nutrient availability vary daily, giving mangroves a high degree of natural variability in space and time (Feller et al., 2010). These forests often border urban centers, industrial sites and agricultural plots, representing a boundary between terrestrial human activities and the open sea (Saenger et al., 1990). Natural environmental variability and human activities have an impact on the development of mangrove trees, surrounding sediments and associated meiofauna (Ólafsson, 1995). Polidoro et al. (2010) estimated that up to 35 % of the historical range of mangroves worldwide have been lost. If this trend continues at its current rate, almost all unprotected mangroves could disappear in the next 100 years (Duke et al., 2007). Relative to their surface area, the greatest losses of mangroves have been recorded in Southeast Asia and the Caribbean (Bunting et al., 2022).

Mangroves in the French Overseas Territories (FOT) represent a core ecosystem for carbon sequestration, coastal protection, water purification and fish biomass production. Due to their scattered distribution (Africa, America and Oceania), the FOT mangroves develop under different environmental conditions and anthropogenic pressures in each ecoregion (Taureau, 2017). The FOTs included in the areas most impacted in Bunting et al. (2022) are Guadeloupe and Martinique in the Caribbean, and Mayotte in the Indo-West Pacific. All three islands have undergone significant urban, industrial and demographic development over the past two decades (Imbert et al., 2000; Jeanson et al., 2014). Their mangroves are subject to direct and diffuse pollution, the impact of which on benthic fauna remains poorly understood. Beyond the loss of surface area, changes in habitat suitability and ecosystem structure and functioning impact benthic biodiversity.

Meiofaunal organisms (32–1000 μm), comprising metazoans and protists, are abundant in mangrove sediments because they have a short life cycle and exhibit high diversity and density, ubiquitous distribution in soft (sediments) and hard (roots) substrates, and strong adaptations to environmental changes (see Spedicato et al., 2023 for review). While meiofaunal density may increase or decrease due to contamination, community composition is subject to taxon loss, providing a good proxy of the effect of anthropogenic pressures in mangroves (Della Patrona et al., 2016; Capdeville et al., 2018). The spatial distribution of taxa is determined by a cause-and-effect relationship with environmental variations (Boucher and Gourbault, 1990). Among metazoan meiofauna, nematodes account for up to 90 % of total abundance and can be found down to 15 cm depth, due to sediment oxygenation and food availability (e.g., carbon content, carbon/nitrogen (C/N) ratio) in the rhizosphere network (Dye, 1983; Sahoo et al., 2013; Ghosh and Mandal, 2019). In mangroves, environmental filtering has been identified as the main mechanism structuring nematode diversity, with species loss associated with environmental gradients (Brustolin et al., 2021). These gradients act on both the horizontal and vertical dimensions, generating patches with different nematode communities. However, how these patches are structured and evolve according to environmental forcing remains unclear. In particular, the link between horizontal and vertical (at depth) distributions of nematodes is still under debate. Some authors hypothesize that only specialized nematodes colonize the deepest sediments, while others believe that it depends on the pool of genera living at the surface and their ability to migrate to depth (Vieira and Fonseca, 2013 and references therein). In mangroves, the type of natural or anthropogenic factors that determine the horizontal and vertical patterns of nematode diversity at small spatial scales are not clearly identified or are still controversial (Spedicato et al., 2023).

The aim of this study was to define the horizontal and vertical distributions of meiofauna, and in particular nematodes, in mangrove sediments from Mayotte, Guadeloupe and Martinique, and to identify the environmental forcings responsible for these distributions. We hypothesize that i) mangrove sediments around urban centers and agricultural land are more severely affected by contamination than mangrove sediments far from anthropogenic activities, ii) each station-specific nematode community is determined by an equally specific environmental filtering process, and iii) some nematode genera react in the same way on all islands.

To test our hypotheses, we used an integrated approach to characterize the environmental parameters and sample the meiofauna of mangrove sediments in Mayotte, Martinique and Guadeloupe, i.e. three islands belonging to two different biogeographical regions, which are subject to anthropogenic pressures specific to each of them, and for which information on the distribution of meiofauna is scarce.

2. Material and methods

2.1. Study areas

The present study was conducted in Mayotte (October 2018) in the Indo-West Pacific, and in Martinique (June 2018) and Guadeloupe (June 2019) in the Caribbean (Fig. 1). All field sampling was carried out at the end of the dry season and at low tide. Station selection depended on their distance from urban centers and agricultural land, as well as their accessibility, which explains why only certain mangrove areas on each island were finally selected. In order to have comparable ecological conditions at all stations, only sampling points distanced from channels, crab burrows and tree trunks within adult mangrove stands, and with similar immersion time were chosen (data not shown).

2.1.1. Mayotte

Mayotte island (Fig. 1b) is located approximately 13°S and 45°E in

the north of Mozambique Channel, between Madagascar and continental Africa. Mayotte has a tropical climate with a hot rainy monsoon season (November to April), and a cooler, dry trade wind season (May to November). The whole island is surrounded by an almost continuous ring of coral reef barrier (Herteman et al., 2011). The tidal regime is semi-diurnal and the mean spring tidal range is about 3.2 m (Jeanson et al., 2014).

Samples were collected at five stations from October 5 to 8, 2018 (Fig. 1e): DP (−12°50′15.64N 45°11′31.41E), DS (−12°50′41.61N 45°11′41.36E), MP (−12°55′25.06N 45°9′10.41E), MS (−12°55′19.04N 45°9′10.11E) and ZI (−12°47′7.65N 45°5′48.41E). DP and DS, located respectively 500 m north and 140 m south of the village of Dembeni (east coast), both receive freshwater from the Dembeni river, which rises in the Bénara mountains. Contrary to DP, DS is located at the mouth of small urban sewages without wastewater treatment. In addition, regular logging by local residents has enhanced the decline of the DS forest since 1950 (Jeanson et al., 2014). MP and MS are both located 400 m from the village of Malamani on the west coast (Chirongui Bay). MS was subject during 10 years to discharges pretreated domestic wastewater by an *in situ* experimental system, aiming to monitor the impacts on the mangrove ecosystem (Herteman et al., 2011; Capdeville et al., 2018). MP, being the control site, was not directly affected. We observed a high mortality of mangrove trees (40 %; data not shown) at MS. ZI is crossed by the Mrowalé river, which flows nearby Tsingoni town (west coast). The mangrove swamps of the five stations in Mayotte were mainly dominated by *Rhizophora* and *Bruguiera* trees; they are all tidally inundated 4.3 h per day on average (Capdeville et al., 2018).

2.1.2. Guadeloupe and Martinique

Guadeloupe (16°N, −61°E) and Martinique (14°N, −61°E) are part of the Lesser Antilles archipelago, located in the Caribbean Sea (Fig. 1a). Their tropical climate is characterized by a dry season (from February to June) and a rainy cyclonic season (from July to January). The tidal range is <0.5 m for both islands. The mangrove swamps targeted in this study were all dominated by *Rhizophora* and *Avicennia* trees (Taureau, 2017).

Five stations were sampled in Guadeloupe between June 17 and 20, 2019 (Fig. 1c): Fajou (FA; 16°21′3.24N–61°35′26.16E), Babin (BA; 16°20′19.68N–61°31′45.84E), Intermédiaire (IN; 16°16′39.036N–61°32′55.68E), Décharge (DE; 16°15′33.84N–61°32′48.84E) and Goyave (GO; 16°8′16.44N–61°34′27.48E). FA (an isolated island north of Basse Terre) and BA are respectively located in the northern and southern part of a protected area, Le Grand Cul de Sac Marin, in the Parc National de la Guadeloupe (PNG). IN and DE are located along the Rivière Salée, an inlet running between Grande Terre and Basse Terre, and close to the Gabarre landfill site, Raizet airport and urbanized areas belonging to the most urbanized zone of Guadeloupe (Pointe-à-Pitre). A high mortality of mangrove trees (35 %) was specifically observed at DE during the fieldwork (data not shown). GO is the only station on Grande Terre and the only one to receive freshwater directly from inland areas where high concentrations of chlordecone have historically been measured (Coat et al., 2011). GO faces the influence of the open sea and its west-to-east waves. It is located near housing, a harbor, and an agricultural watershed. Most of these stations are impacted by pyrolytic pollution (Ramdine et al., 2012).

Four stations were sampled in Martinique between June 25 and 28, 2018 (Fig. 1d): Baie du Trésor (S4; 14°46′0.07N–60°52′56.24E), Pointe Marin (S5; 14°26′48.767N–60°52′39.12E), Pointe Merle (S6; 14°33′40.62N–61°0′37.05E) and Cohé du Lamentin (S7; 14°36′12.93N–61°1′14.13E). S4 is located on the east coast, in the protected Caravelle nature reserve (a natural zone of ecological interest for fauna and flora), far from any urban center. S5 is located on the edge of Marin Bay, home to the island's largest marina and close to the Belfond wastewater treatment plant. S6 and S7 are situated in the Bay of Fort-de-France (main city), which is known to be the most polluted area on the island, with industries, refineries and wastewater dump sites (Mille et al., 2006). S6, close to agricultural land, receives freshwater from the southern part of the island (Caleçon, La Manche and Rivière Salée rivers). S7 is bordered by La Lézarde and Longvillier rivers, which rise to the northwest in the mountains. This alluvial mangrove is surrounded by agri-food and chemical industries, refineries and wastewater dumps, and lies close to the island's main airport. Pesticides (chlordecone) and metals (arsenic) have had a major impact on Martinique's littoral (Dromard et al., 2022). Fiard et al. (2024) recently showed the influence of agricultural by-products on the microbial compartment of mangroves.

2.2. Field sampling

For each station, three sediment cores (10 cm internal diameter, 20 cm height) were manually collected at the peak of the low tides, making

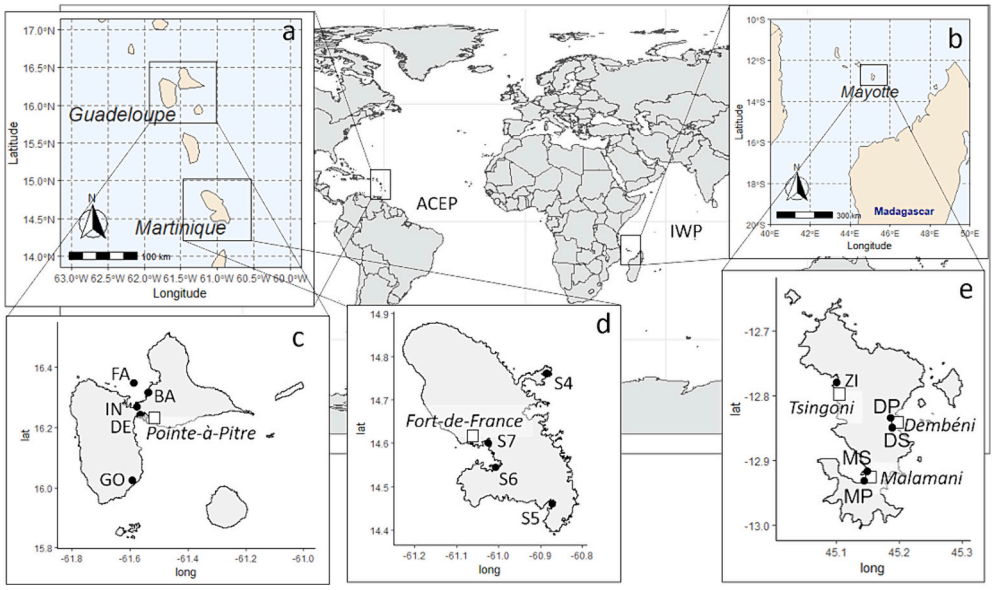

Fig. 1. Location of the three study areas and 14 stations sampled in 2018 and 2019 in the two main biogeographical regions of mangrove distribution: the Atlantic-Caribbean East Pacific (ACEP) and the Indo-West Pacific (IWP). (a, c) Guadeloupe; (a, d) Martinique; (b, e) Mayotte. See Section 2.1 for the name and description of sampling stations.

the sampling stations easily accessible by walking from land. The cores were about 2 m apart from each other. Without quantifying it, we observed a high density of small roots in Caribbean mangrove sediments throughout the sedimentary column, whereas in Mayotte, sediment texture was more homogeneous.

Each core was cut into 2 horizontal sediment slices: 0–2 cm (H100) and 2–10 cm (H200), according to the protocol established by Michelet et al. (2021) and Fiard et al. (2022). Redox potential (Eh), pH and temperature were measured directly in the cores for each sediment layer using a multi-parameter system coupled to soil specific probes WTW Multi 3420. Instrument precision was 0.01 mV (Eh) and 0.001 pH, the latter calibrated with NIST Buffers. Redox potential was not measured in Mayotte due to an instrument malfunction.

Within each sediment layer, sub-sampling was carried out with syringe-cores of known diameter (1.5 cm) and height, preserving sample vertical structure. Seven subsamples were collected for i) porewater salinity, ii) grain size, iii) total organic carbon (TOC) and nitrogen (TN) contents, and sediment-associated organic matter isotopic composition, iv) metal contents, v) organic compound contents, vi) microbial analyses (prokaryotic and archaeal abundance, and microbial biomass), and vii) meiofauna. This sub-sampling was triplicated as three cores were taken at each station. A total of 3 samples for each environmental and infaunal parameter were taken from each sediment layer at each station.

Pore-water salinity was directly measured using a refractometer (1 ppt; practical salinity scale) after extracting a drop of filtered pore water from the sediment (Michaud et al., 2022). Subsamples for grain size analysis were kept in the fridge (4 °C), whereas sediments for biogeochemistry and prokaryotic analyses were immediately frozen (−80 °C). The meiofauna samples were fixed in diluted 4 % formaldehyde buffered with sodium bicarbonate and stored cold until analysis.

2.3. Biogeochemical analyses

Granulometry, total organic carbon (TOC) and total nitrogen (TN) were analyzed following Michelet et al. (2021) and Fiard et al. (2022). Sediments were freeze-dried (24 h), crushed to powder and homogenized for bulk sediment analyses. For sediment granulometry, the sediment powder was sieved to 2 mm to remove plant detritus before being analyzed using a laser beam diffraction analyzer (Partica LA-950V2; Horiba Instruments, Inc.).

TOC and TN were analyzed by combustion at 930 °C using an elementary analyzer (Flash-2000; Thermo Fisher Scientific Inc., Milan, Italy). The inorganic fraction was obtained from acidified (HCl, 1 N) aliquots and the organic fraction from the difference between both fractions. The molar TOC:TN ratio was calculated and used as a proxy of the refractory versus labile nature of the organic matter.

The isotope analysis was performed using a vario MICRO cube (Elementar, Germany) elemental combustion system coupled to a precision (Elementar, United Kingdom) isotope ratio mass spectrometer. Isotope ratios were expressed using the widespread δ notation (Coplen 2010). IAEA (International Atomic Energy Agency, Vienna, Austria) certified reference sucrose (IAEA-C-6; $\delta^{13}C = -10.8 \pm 0.5$ ‰; mean ± SD) and ammonium sulfate (IAEA-N-1; $\delta^{15}N = 0.4 \pm 0.2$ ‰; mean ± SD) were used as primary analytical standards. Sulfanilic acid (Sigma-Aldrich; $\delta^{13}C = -25.6 \pm 0.4$ ‰; $\delta^{15}N = -0.13 \pm 0.4$ ‰; means ± SD) was used as a secondary analytical standard. Secondary and internal lab standards (seabass muscle) were interspersed with samples (one replicate of each standard every 15 analyses). Standard deviations on multi-batch replicate measurements were 0.2 ‰ for $\delta^{13}C$ and 0.3 ‰ for $\delta^{15}N$.

The size of the bacterial and archaeal population was estimated by quantifying the copy numbers of the 16S rRNA genes by qPCR using protocols presented in detail in Fiard et al. (2022). The total DNA extracts quantified by fluorometric dosage with a Quantifluor dsDNA system kit (Promega) were used as a proxy for microbial biomass.

The bioavailable fraction (<63 μm) of 14 out of the 15 trace metals considered in this study (see Tables A.1 to A.3) was quantified by a High-Resolution Inductively Coupled Plasma – Mass Spectrometer (HR-ICP/MS, Element 2 Finnigan; Besson et al., 2020). Mercury (Hg) concentrations were quantified by cold vapor atomic absorption spectrometry (CV-AAS, Leco Ama 254) with a low-level optical cell.

Organic contaminants (Polycyclic aromatic hydrocarbons (PAHs), Polychlorinated biphenyls (PCBs), Polybrominated diphenyl ethers (PBDEs), pesticides, phthalates and phenols) were measured with a GC–MS/MS. For PAH, PCB and pesticides, naphthalene D8, biphenyl D10, phenanthrene D10, pyrened10, chrysene D12, benzo(*a*)pyrene D12, benzo(*g*,*h*,*i*)perylene D12 were used as standards. For the plastic additives (phthalates and PBDE), di (2-ethylhexyl) phthalate D4 and BDE 77 were used as standards, respectively. All standards were obtained from LGC Standard (Wesel, Germany) and Interchim (Montluçon, France).

Measured contaminant concentrations were compared with the values given in NOAA's Sediment Quality Guidelines (Buchman, 2008), to assess whether they exceeded official hazard thresholds for estuarine and marine sediments.

2.4. Meiofauna analyses

All samples were sieved on 32 μm and 1 mm mesh to retain the full size spectrum of meiofauna (Giere, 2009). Meiofauna was extracted from the sediment by means of Ludox centrifugation according to Heip et al. (1974), stained with rose bengal and fixed in 4 % formalin. The animals were counted and identified at phylum level under a stereomicroscope (Stemi 508, Leica Microsystems GmbH, Wetzlar, Germany). In marine and terrestrial biodiversity studies, nematodes are generally identified by randomly selecting 100 individuals per sample (Bianchelli et al., 2013; Semprucci et al., 2018; Liang et al., 2020). Thus, nematodes were mounted on permanent slides following the formalin-ethanol-glycerol technique (Seinhorst, 1959) and 100 randomly selected specimens per sample were identified at genus level with a Leica DM2500 LED microscope according to Platt et al. (1985, 1988), the pictorial key of Warwick et al. (1998), Schmidt-Rhaesa (2014), and the NeMys Online World Database of Nematodes (NeMys eds., 2023). When <100 specimens were found in a sample, all nematodes were identified. The total abundance of a given taxon in a sample was calculated from the proportion of that taxon in the 100 specimens identified and the total number of nematodes counted in the sample.

The number of meiofaunal taxa (TS), the number of nematode genera (GS), the density (number of individuals per 10 cm^3) and the composition of meiofauna and nematode communities were analyzed. Raw abundances were transformed into density per 10cm^3 to make all layers comparable with each other and with the literature.

2.5. Statistical analyses

As the islands showed strong differences in their respective sedimentary environment (Fig. 2), we conducted the statistical analyses separately. Variables or samples with missing data were excluded from the analyses (see Table A.6).

First, an environmental characterization of the three study areas was carried out using a Hierarchical Clustering on Principal Components (HCPC) (Husson et al., 2010), which performs agglomerative hierarchical clustering on Principal Components Analysis (PCA). PCA, which identifies orthogonal dimensions (i.e. components) extracting the main structures from the data, can be seen as a denoising procedure. The number of dimensions explaining most of the variability (95 %) is used to calculate a hierarchical tree, which is cut to identify clusters. A heatmap was used to visualize the significant variables for each cluster. The R package "FactoMineR" (Lê et al., 2008) was used to compute the analyses.

In order to estimate the effect of sample size on meiofauna and nematode diversity, rarefaction curves were plotted with the R package "iNEXT" (Hsieh et al., 2024) for each island. The sample size for

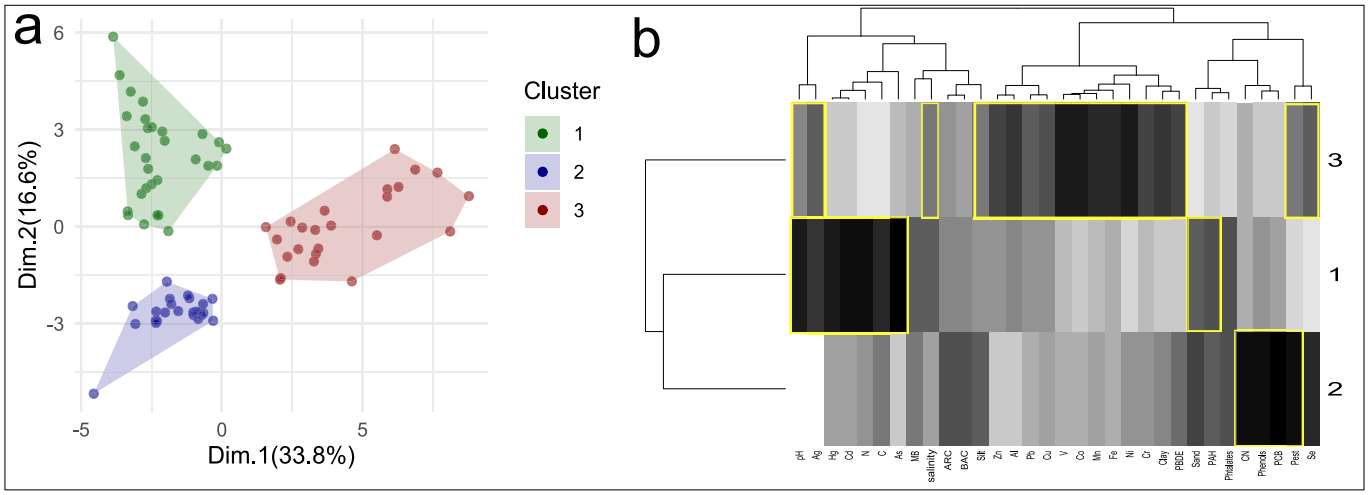

Fig. 2. Hierarchical Clustering on Principal Components (HCPC) performed on the environmental variables of the three islands (a). Three replicate sediment cores per station (A, B, C) and two sediment horizons per replicate (H100: 0–2 cm; H200: 2–10 cm) were sampled. The samples (dots) are grouped into three clusters corresponding to Guadeloupe (1), Martinique (2) and Mayotte (3). The heatmap (b) shows the variables defining each cluster. The shading is based on centered and scaled means per station, and yellow rectangles include only the significant variables ($p < 0.05$) for each cluster. (b) C = TOC; N = TN; CN = TOC:TN ratio; BAC = bacterial abundance; ARC = archaeal abundance; MB = microbial biomass.

rarefaction was set at the size of the smallest sample for meiofauna and nematodes. Confidence intervals at 0.95 were plotted for each curve and a richness extrapolation was calculated on the basis of a doubled number of individuals per station.

The distribution of meiofauna can be structured on the scale of small sediment patches, with little difference on a larger spatial scale (Blanchard, 1990). To assess the effect of the horizontal and vertical dimensions on the presence of meiofauna and nematodes, we performed a PERMANOVA (PERMutation ANalysis Of VAriance, 999 repetitions) on total density (ind/10cm^3), number of meiofaunal taxa (TS), number of nematode genera (GS) and community composition (presence-absence) of meiofauna and nematodes. Bray-Curtis dissimilarity was applied to density, TS and GS, and the Jaccard index to community composition data. The "strata" argument of the function "adonis2" was used to constrain permutations within groups based on the nested nature of the factors used in the analysis. When the effect of the "island" factor was tested on the response variable, permutations were constrained in stations. When the "station" option was tested, blocks of replicates were included in the "strata" argument. To test the effect of depth ("horizon" factor), permutations were limited to blocks of stations. Prior to analysis, we checked the multivariate dispersion. Pairwise comparisons were performed with the function "pairwise.adonis" (Martinez Arbizu and Monteux, https://github.com/pmartinezarbizu/pairwiseAdonis).

To determine how the environment was associated with nematode community composition, we performed a redundancy analysis (RDA) using a Hellinger-transformed matrix of genus abundances (response variables) and a matrix of centered environmental variables as predictor variables. A first model was run including all variables, then, to cope with collinearity, a forward selection (fixed threshold of $p < 0.05$) was chosen to retain only the strongest environmental predictors and compute a second parsimonious model (Borcard et al., 2018). The influence of sediment depth was controlled by including it as a factor in the model (Legendre and Legendre, 2012). The significance of the model as a whole, of each axis and of each term was tested using a permutation test (999 repetitions). To determine the relative contribution of each genus to the inertia explained by the selected variables and by the depth factor, we calculated the genus contribution to beta-diversity (SCBD) with the "inertcomp" function based on the RDA results, which provides values whose sum is equal to 1 (Legendre and De Cáceres, 2013). The multivariate analyses were performed using the R package "vegan" (Oksanen et al., 2022).

All statistical analyses were computed in R (R Development Core Team), version 4.3.1.

3. Results

3.1. Environmental characterization of the study areas

Environmental settings were first compared between the stations of all islands, i.e. taking into account all samples from the three islands. Hierarchical Clustering on Principal Components (HCPC) carried out on all environmental variables (mean values in Appendix Tables A.1 to A.3) separated the three islands (Fig. 2a). The first two components of the PCA explained 50.4 % of the variance between the islands. Mayotte sediments (cluster 3 in Fig. 2a) were defined by clay % ($p < 0.001$), metal enrichment ($p < 0.001$ for Ni, Co, V, Mn, Fe, Al, Cr, Zn, Pb, Cu, Se and Ag), PBDE, pesticides ($p < 0.001$ for all), silt %, pH, salinity ($p < 0.01$ for both, Fig. 2b). Martinique (cluster 2) was defined by PCBs, TOC:TN ratio ($p < 0.001$ for both), pesticides ($p < 0.01$) and phenols ($p < 0.05$). Guadeloupe (cluster 1) sediments were defined by high TOC and TN content, pH, Hg, As, Cd, Hg, Ag ($p < 0.001$ for all), sand % and PAHs ($p < 0.05$) (Fig. 2b). As different sedimentary environments characterize the three islands, the following analyses were carried out island by island.

In Mayotte, the first two components of the PCA explained 53 % of the variance between stations, which were grouped into 3 clusters by the hierarchical tree (Fig. 3a). Station MS itself is a cluster, defined by silt %, Se, salinity, Hg ($p < 0.001$ for all), TN ($p < 0.01$) and phthalates ($p < 0.05$, Fig. 3d). HCPC showed horizontal homogeneity between MP and DS-H200, which were grouped together and defined by sand %, TOC, low TOC:TN, Cd ($p < 0.01$ for all) and Ag ($p < 0.05$) (Fig. 3d). ZI and DS-H100 also showed similar sediment conditions, with cluster 3 defined by metal enrichment ($p < 0.001$ for Zn, Pb, Fe, V, Cr and Co; $p < 0.01$ for Mn, $p < 0.05$ for Ni), pH ($p < 0.001$) and the highest microbial biomass ($p < 0.01$). Station DS was vertically heterogeneous, with surface and deep samples grouped into two different clusters, while sediment layers were grouped together at MS, MP and ZI (Fig. 3d).

In Martinique, the HCPC based on the first two dimensions of the PCA (50.4 % of the variance) identified four clusters (Fig. 3b). The analysis associated S6 and S7 (Fig. 3b), based on TOC, TN, pesticides ($p < 0.001$ for all), TOC:TN, Al, Hg, PBDEs, salinity ($p < 0.01$ for all), V and sand % ($p < 0.05$) (Fig. 3e). One superficial sample of S6 formed a cluster

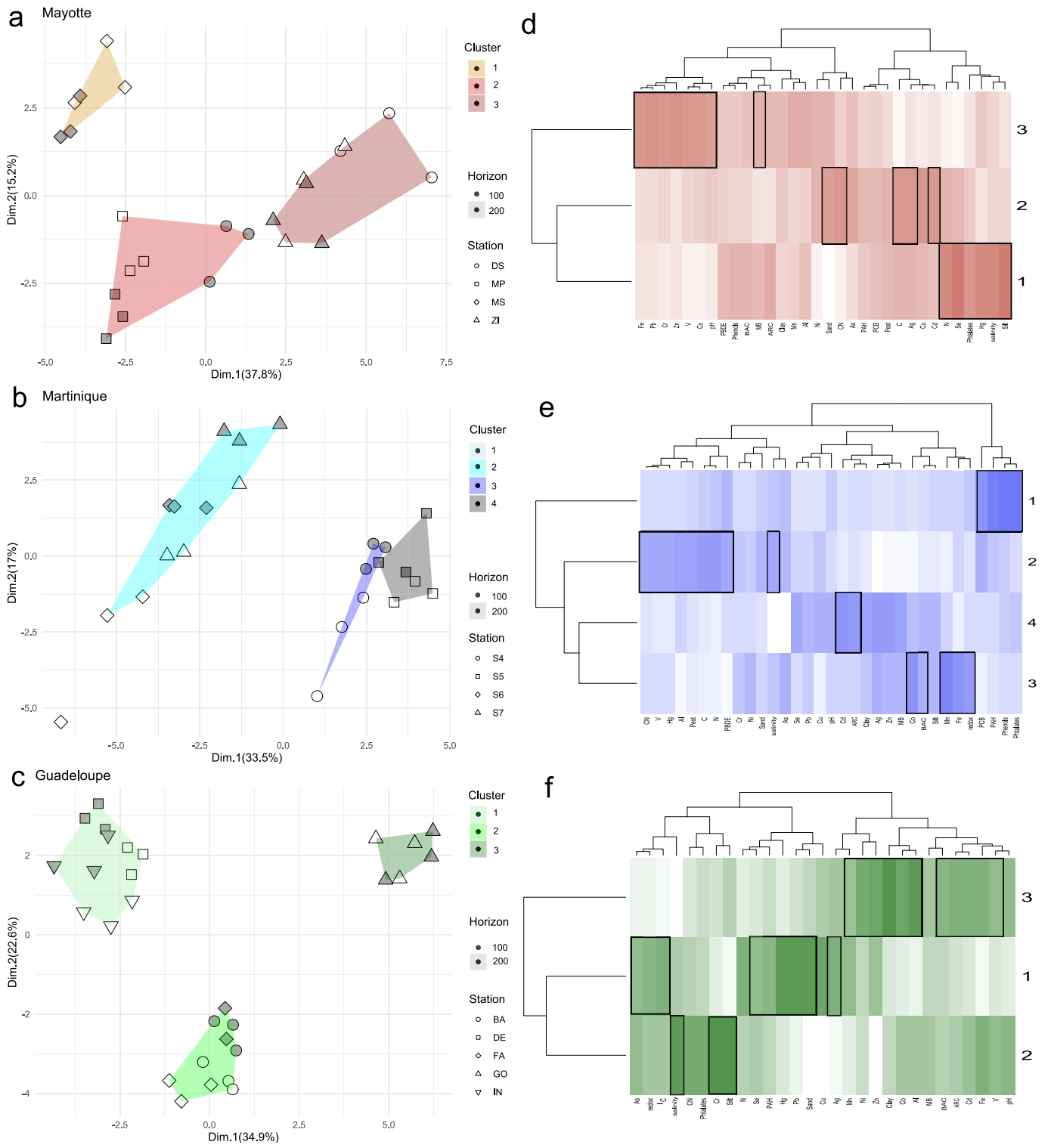

Fig. 3. Hierarchical Clustering on Principal Components (HCPC) performed on the environmental variables of Mayotte (a), Martinique (b) and Guadeloupe (c). Three replicate sediment cores per station (A, B, C) and two sediment horizons per replicate (H100: 0–2 cm; H200: 2–10 cm) were sampled. The variables defining each cluster are shown in the heatmaps (d, e and f); the shading is based on centered and scaled means per station, and black rectangles include the significant ones ($p < 0.05$). C = TOC; N = TN; CN = TOC:TN ratio; BAC = bacterial abundance; ARC = archaeal abundance; MB = microbial biomass.

on its own, due to phenols, phthalates, PAHs and PCBs ($p < 0.001$ for all). Station S5 was defined by Cd, Zn ($p < 0.001$ for both), archaeal abundance, microbial biomass, Ag and pH ($p < 0.05$). S4 sediments were characterized by highest redox potential, Mn, Fe, Co ($p < 0.001$ for all) and bacterial abundance ($p < 0.05$). All the sedimentary horizons belonged to the cluster of their respective station, showing homogeneity on the vertical (Fig. 3b).

In Guadeloupe, the PCA explained 57.5 % of the variance and the hierarchical tree separated three clusters (Fig. 3c): stations IN and DE (1), stations FA and BA (2), and station GO (3). The similarities between IN and DE were ascribed to sand % ($p < 0.001$), high redox potential ($p < 0.01$), high TOC content, PAHs, Pb, Hg ($p < 0.001$ for all), Ag, Se and

As ($p < 0.01$ for all) (Fig. 3f). FA and BA had similar silt % ($p < 0.001$), high salinity ($p < 0.01$) and high Cr concentrations ($p < 0.001$). GO differed from all other stations in terms of clay % ($p < 0.001$), archaeal and bacterial abundances ($p < 0.01$ for both), and concentrations of Al, Co, Zn, Fe ($p < 0.001$ for all), Cd, Ni ($p < 0.01$ for both), V and Mn ($p < 0.05$ for both). Vertically, the stations were homogeneous in terms of sedimentary characteristics, with both horizons grouped together in their respective stations (Fig. 3c).

3.2. Isotopic signature of sediments

Average isotopic values for each station are shown in Tables A.1 to A.3. Mean $\delta^{13}C$ values in Mayotte were −28.5 ‰ in H100 and −28.4 ‰ in H200, and mean $\delta^{15}N$ value was 1.7 ‰ for both sediment layers (Fig. A.1). In Guadeloupe, $\delta^{13}C$ mean values were −27.2 ‰ for the surface layer and −26.9 ‰ for the deep layer, whereas $\delta^{15}N$ mean values were 2.4 ‰ and 2.3 ‰, for the surface and deep layers, respectively. Mean $\delta^{13}C$ values in Martinique were intermediate between the other two islands, both at the surface (−28 ‰) and in depth (−27.6 ‰), whereas mean $\delta^{15}N$ value was the lowest (0.3 ‰ in both sediment layers). There was an 'island effect' on isotopic composition, due to ^{13}C depletion in Mayotte ($p_{adj} = 0.015$, $F = 48$), compared with Guadeloupe (Fig. A.1). Even though differences were not significant between stations, IN and DE (Guadeloupe) and S5 (Martinique) showed ^{15}N enrichment compared with the other stations on each island.

3.3. Meiofauna distribution

Meiofauna density in Mayotte ranged from 354 ± 214 to 1967 ± 293 ind.10 cm^{-3}, versus 65 ± 68 to 829 ± 514 ind.10 cm^{-3} in Martinique and 193 ± 157 to 3803 ± 1481 ind.10 cm^{-3} in Guadeloupe (Fig. 4; Table A.4). The total number of meiofaunal taxa (TS) was 13 in Mayotte, 8 in Martinique and 14 in Guadeloupe. PERMANOVA showed no significant differences in density and TS between stations on each island (Table 1). Vertically, however, density and TS showed significant differences on each of the islands (PERMANOVAs, $P = 0.001$; Table 1).

The rarefaction curves (Fig. B.1) show that the numbers of individuals counted and identified in each station (sample size) are sufficient to estimate TS (i.e., values close to the maximum expected number of meiofaunal taxa at each station), except for GO and, to a lesser extent, BA and IN (Guadeloupe). Different sample sizes between stations makes it difficult to compare TS values between stations, since for the same sample size (i.e., the smallest for each island), most curves do not show an asymptotic value. Nevertheless, the true TS is probably lower at stations GO and FA, compared with other stations in Guadeloupe, and at station S7 in Martinique, while Mayotte stands out for a real TS value that is probably higher at station MP than at the other stations.

The composition of the total meiofauna community (presence-absence) was significantly different between stations in Martinique and Guadeloupe (PERMANOVA, $P = 0.028$ and 0.025; $p < 0.045$), but not in Mayotte. Vertically, differences were significant in the three islands ($p < 0.001$, Table 1). Redundancy analysis (RDA) was not performed on total meiofauna community data, due to an insufficient degree of taxonomic determination for each category of meiofaunal organism (multiple ecological/trophic niches represented within each taxon).

3.4. Nematode distribution

In Mayotte, nematode density ranged from 118 ± 55 (ZI) to 1156 ± 222 (MS) ind/10cm^3, vs 15 ± 17 (S7) to 782 ± 514 (S5) ind/10cm^3 in Martinique and 169 ± 164 (GO) to 2224 ± 771 (DE) ind/10cm^3 in Guadeloupe (Table A.4). No significant structuring of nematode density was identified between islands and stations, except for Mayotte ($P = 0.038$). Conversely, density variations were significant between horizons in the three islands (PERMANOVA, $P = 0.001$; Table 2).

The number of individuals identified at each station was sufficient to estimate the number of nematode genera (GS) in Martinique's stations, at MS (Mayotte), DE and FA (Guadeloupe; Fig. B.2). For all other stations, GS was still increasing at the chosen sample size, highlighting underestimation. 74 nematode genera were found in Guadeloupe, 65 in Mayotte and 28 in Martinique (see Table A.5 for details). The lowest GS was found at S7 (Martinique), with only 3 genera, and the highest at IN (Guadeloupe), with 48 genera. Significant horizontal structuring of GS was found in Mayotte and Guadeloupe ($P = 0.002$ and 0.005, respectively), but not in Martinique (Table 2). Vertically, PERMANOVA

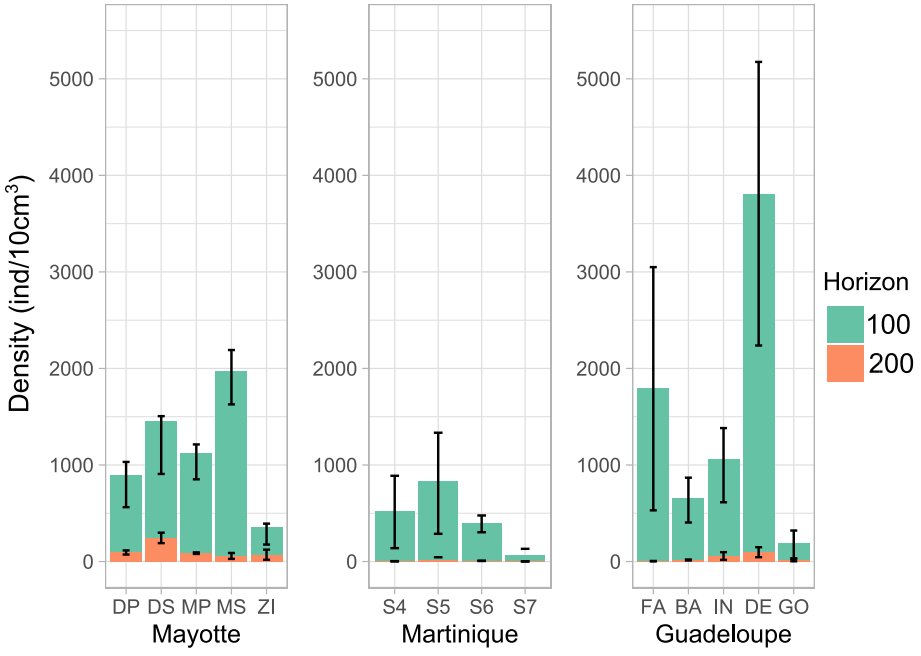

Fig. 4. Barplots of total meiofauna density (ind/10cm^3) in Mayotte, Martinique and Guadeloupe. Average values (± SD) are represented for each sediment layer (H100: 0–2 cm; H200: 2–10 cm) of each station on each island.

Table 1
Permutational analysis of variance (PERMANOVA) on meiofaunal taxa (density, number of taxa and community composition). 999 permutations were performed on the raw data, adding the terms sequentially. Bold *P* values indicate significant differences ($p < 0.05$). Only the significant pairwise comparisons are reported. Source = source of variation; DF = degrees of freedom; SS = sum of squares; R2 = mean sum of squares; F = pseudo-*F*; P = *p*-value; TS = number of meiofaunal taxa.

Meiofauna						
Variable	Source	DF	SS	R2	F	P
Between Islands						
Density (.10 cm^3)	Island	2	1.8878	0.08237	3.5904	1
	Residual	80	21.0322	0.91763		
TS	Island	2	1.6922	0.23473	12.269	1
	Residual	80	5.5170	0.76527		
Comm. Comp	Island	2	1.9884	0.16681	8.0084	1
	Residual	80	9.9316	0.83319		
Mayotte						
Density (.10 cm^3)	Station	4	0.8867	0.15157	1.1166	0.407
	Residual	25	4.9633	0.84843		
	Horizon	1	3.2989	0.56391	36.207	**0.001**
	Residual	28	4.359	0.43609		
TS	Station	4	0.08592	0.07975	0.5417	0.782
	Residual	25	0.99145	0.92025		
	Horizon	1	0.48072	0.4462	22.559	**0.001**
	Residual	28	0.59666	0.5538		
Comm. Comp.	Station	4	0.49944	0.17723	1.3463	0.213
	Residual	25	2.31857	0.82277		
	Horizon	1	0.80314	0.285	11.161	**0.001**
	Residual	28	2.01487	0.715		
Martinique						
Density (.10 cm^3)	Station	3	0.6285	0.09572	0.6704	0.748
	Residual	19	5.9376	0.90428		
	Horizon	1	3.3202	0.50565	21.48	**0.001**
	Residual	21	3.246	0.49435		
	Station	3	0.18488	0.11039	0.7859	0.556
	Residual	19	1.48986	0.88961		
	Horizon	1	0.9637	0.57543	28.462	**0.001**
	Residual	21	0.71104	0.42457		
Comm. Comp.	Station	3	0.77623	0.26322	2.2626	**0.028**
	Residual	19	2.1728	0.72678		
	Horizon	1	0.63376	0.21491	5.7484	**0.001**
	Residual	21	2.31527	0.78509		
Guadeloupe						
Density (.10 cm^3)	Station	4	1.5917	0.18474	1.4162	0.233
	Residual	25	7.0243	0.81526		
	Horizon	1	3.4588	0.40144	18.779	**0.001**
	Residual	28	5.1572	0.59856		
TS	Station	4	0.80287	0.29038	2.5576	0.056
	Residual	25	1.96198	0.70962		
	Horizon	1	0.79185	0.2864	11.238	**0.001**
	Residual	28	1.97299	0.7136		
Comm. Comp.	Station	4	1.0902	0.26178	2.2163	**0.025**
	Residual	25	3.0743	0.73822		
	Horizon	1	0.9106	0.21867	7.8361	**0.001**
	Residual	28	3.2539	0.78133		

identified significant structuring on each island ($p < 0.05$ for all).

In all islands, the nematode community was structured at the scale of the station, with significant differences in composition between stations, but not between islands. To support this result, pairwise PERMANOVA on presence-absence matrices found significant variations in Mayotte between DS and ZI, MP and ZI, and MS and ZI ($p < 0.05$ for all; Table 2). In Martinique, the strongest differences were recorded between S4 and S6 and between S5 and S6 ($p < 0.03$; Table 2). In Guadeloupe, the horizontal variation was mainly due to pairwise differences between FA and DE, BA and IN, BA and DE, and IN and GO ($p < 0.05$ for all; Table 2). Only *Daptonema*, *Desmodora* and *Terschellingia* were present and dominant in all islands (Table A.5).

Nematode community composition significantly varied between sediment depths in Mayotte, Guadeloupe (PERMANOVAs, $P = 0.001$) and Martinique ($P = 0.012$; Table 2).

Table 2
Permutational analysis of variance (PERMANOVA) on nematodes (density, number of taxa and community composition). 999 permutations were performed on the raw data, adding the terms sequentially. Bold *P* values indicate significant differences (<0.05). Only the significant pairwise comparisons are reported. Source = source of variation; DF = degrees of freedom; SS = sum of squares; R2 = mean sum of squares; F = pseudo-*F*; P = *p*-value; GS = number of nematode genera.

Nematodes						
Variable	Source	DF	SS	R2	F	P
Between Islands						
Density (.10 cm^3)	Island	2	1.203	0.05845	2.3591	1
	Residual	76	19.3780	0.94155		
GS	Island	2	1.1767	0.05879	2.3422	1
	Residual	75	18.8394	0.94121		
Comm. Comp	Island	2	2.7320	0.078	3.1747	1
	Residual	75	32.2710	0.92195		
Mayotte						
Density (.10 cm^3)	Station	4	1.6200	0.28246	2.4604	**0.038**
	Residual	25	4.1152	0.71754		
	Horizon	1	2.0744	0.3617	15.867	**0.001**
	Residual	28	3.6607	0.6383		
GS	Station	4	1.2864	0.45182	5.1514	**0.002**
	Residual	25	1.5608	0.54818		
	Horizon	1	0.28417	0.09981	3.1044	**0.015**
	Residual	28	2.56306	0.90019		
Comm. Comp.	Station	4	2.4853	0.26099	2.2072	**0.001**
	Residual	25	7.0374	0.73901		
	Horizon	1	1.0038	0.10541	3.2993	**0.001**
	Residual	28	8.5189	0.89459		
	DS vs ZI	1	1.0718	0.2757	3.8059	**0.02**
	MP vs ZI	1	0.7635	0.1884	2.3218	**0.03**
	MS vs ZI	1	0.8696	0.2086	2.6272	**0.01**
Martinique						
Density (.10 cm^3)	Station	3	0.789	0.14906	0.8758	0.569
	Residual	15	4.5043	0.85094		
	Horizon	1	2.4144	0.45613	14.258	**0.001**
	Residual	17	2.8788	0.54387		
GS	Station	3	0.34554	0.14893	0.8712	0.528
	Residual	15	1.98304	0.85161		
	Horizon	1	1.2005	0.51555	18.092	**0.002**
	Residual	17	1.1281	0.48455		
Comm. Comp.	Station	3	2.2282	0.37209	2.9629	**0.001**
	Residual	15	3.7602	0.62791		
	Horizon	1	0.5729	0.09567	1.7985	**0.012**
	Residual	17	5.4155	0.90433		
	S4 vs S6	1	1.0335	0.31114	4.0651	**0.018**
	S5 vs S6	1	1.0656	0.32829	4.8874	**0.03**
Guadeloupe						
Density (.10 cm^3)	Station	4	1.4871	0.17811	1.3544	0.266
	Residual	25	6.8622	0.82189		
	Horizon	1	3.4382	0.41182	19.605	**0.001**
	Residual	28	4.9109	0.58818		
GS	Station	4	1.3749	0.39427	3.9054	**0.005**
	Residual	24	2.1123	0.60573		
	Horizon	1	0.8389	0.24057	8.5528	**0.001**
	Residual	27	2.6483	0.75943		
Comm. Comp.	Station	4	3.14554	0.30913	2.6847	**0.001**
	Residual	24	7.0296	0.69087		
	Horizon	1	0.7745	0.07612	2.2246	**0.001**
	Residual	27	9.4005	0.92388		
	FA vs DE	1	0.6987	0.2294	2.6798	**0.01**
	BA vs IN	1	1.0208	0.2862	4.0106	**0.05**
	BA vs DE	1	0.8599	0.2515	3.3616	**0.03**
	IN vs GO	1	0.8483	0.2035	2.5555	**0.03**

3.5. Response of dominant nematode genera to local environmental variations

3.5.1. Mayotte

The RDA was performed on a reduced dataset of 18 dominant genera (>5 % of total nematode density): *Cobbia*, *Dagda*, *Daptonema*, *Desmodora*, *Desmolaimus*, *Desmoscolex*, *Halalaimus*, *Halichoanolaimus*, *Laimella*, *Metalinhomoeus*, *Molgolaimus*, *Monhystrella*, *Neochromadora*, *Onchium*, *Perspiria*, *Sphaerolaimus*, *Spilophorella* and *Terschellingia*. The first two axes of the RDA (R^2_{adj} = 0.35; P = 0.001 based on 999 permutations) explained 21 % and 14 % (P = 0.001 for both) of the variation in dominant nematodes (Fig. 5a). The most powerful predictors were pH, TOC:TN ratio (P = 0.001 for both), sand % (P = 0.002), Cr (P = 0.006), salinity (P = 0.008), Pb (P = 0.012), bacterial abundance (P = 0.014), Ni (P = 0.06) and Hg (P = 0.15). The genera with the highest variability among stations were *Spilophorella*, *Terschellingia* and *Daptonema* (SCBD = 0.20, 0.13 and 0.12, respectively). Vertically, aside of *Terschellingia* and *Spilophorella* (SCBD = 0.19 and 0.10, respectively), the other genera contributing most were *Halalaimus* (0.17), *Cobbia* (0.12) and *Neochromadora* (0.10). *Terschellingia* and *Halalaimus* showed a positive relationship with bacterial abundance, high TOC:TN ratio, Ni and sand %, and a negative correlation with salinity and Hg. On the contrary, *Spilophorella* was negatively related to sand %, Cr, Pb, pH and high TOC: TN ratio, but positively related to salinity. *Daptonema* and *Cobbia* were positively related with Cr, Pb and pH (Fig. 5a). The depth factor explained a further 15 % of the total variation in dominant nematodes.

3.5.2. Martinique

The RDA performed on the 8 dominant genera (*Anticyathus*, *Daptonema*, *Desmodora*, *Haliplectus*, *Microlaimus*, *Molgolaimus*, *Spirinia* and *Terschellingia*) explained 36 % of their variability (R^2_{adj} = 0.36, P = 0.001), with the depth factor explaining a further 8 % (Fig. 5b). TOC (P = 0.001), As (P = 0.008), Hg and Cu (P = 0.31 for both) defined the first two significant canonical axes (P = 0.001 and 0.023), which explained 34 % and 15 % of the variability of dominant nematodes, respectively. *Haliplectus* (SCBD = 0.34), *Desmodora* (0.20), *Terschellingia* (0.16) and *Spirinia* (0.12) contributed most to the horizontal variability between S6, S7 and S4, S5 on axis 1. *Desmodora* and *Haliplectus* were associated with high TOC content and As concentration, unlike *Terschellingia* and *Spirinia*. *Desmodora* (SCBD = 0.82) was responsible for most of the variability at depth, which mainly concerned differences between the sediment layers of S6 (Fig. 5b).

3.5.3. Guadeloupe

The RDA was performed on the 25 dominant genera: *Anoplostoma*, *Chromadora*, *Chromadorina*, *Cobbia*, *Daptonema*, *Desmodora*, *Desmoscolex*, *Gomphionema*, *Halalaimus*, *Haliplectus*, *Halomonhystera*, *Leptepsilonema*, *Linhomoeus*, *Marylynnia*, *Metacyatholaimus*, *Microlaimus*, *Monhystrella*, *Paradesmodora*, *Parodontophora*, *Perspiria*, *Spilophorella*, *Syringolaimus*, *Terschellingia*, *Thalassomonhystera* and *Theristus* (Table A.5). The forward-selected variables Pb, Al, Co, Clay (P = 0.001 for all), V, Hg (P = 0.002), Zn (P = 0.013), TN (P = 0.016), PAHs (P = 0.06), salinity (P = 0.029), Cu (P = 0.045) explained 52 % (R^2_{adj} = 0.52) of the variability in dominant genera, with a further 6 % explained by the depth factor. *Terschellingia*, *Theristus*, *Metacyatholaimus*, *Haliplectus*, *Paradesmodora*, *Perspira* and *Desmodora* (SCBD = 0.15, 0.10, 0.09, 0.09, 0.08, 0.08 and 0.07, respectively) contributed most to horizontal variability between stations. At depth, Guadeloupe stations are fairly homogeneous in community composition, with *Perspira*, *Marylynnia* and *Terschellingia* contributing the most (SCBD = 0.16, 0.13 and 0.12, respectively). Contaminants (Pb, Cu, Hg, Zn, PAH, V and Co) and total nitrogen (TN) were responsible for differences between communities of BA and FA vs. DE and IN on axis 1. At DE and IN, ecological conditions (high TN, PAHs, Pb, Cu and Hg concentrations) opposite to those at BA and FA were associated with the flourishing of *Paradesmodora*, *Perspira* and *Desmodora*. Axis 2 mainly separated GO from other stations (DE and FA in particular). Salinity, TN, clay % and Al were responsible for differences between communities, with *Terschellingia*, *Desmodora*, *Paradesmodora*, *Perspira* and *Metacyatholaimus* favoring high salinity and TN, and *Theristus* and *Thalassomonhystera* low salinity, low TN and high clay % (Fig. 5c).

4. Discussion

4.1. Widespread contamination of mangrove sediments

Existing studies on metal and organic contamination in our study areas focus on the main polluted areas of the islands, i.e. Fort-de-France Bay (Mille et al., 2006), Pointe-à-Pitre (Bernard, 1995) and Malamani (Herteman et al., 2011). Our results show that anthropogenic activities on each island affects mangrove plots far from towns and agricultural fields, with specific sources of pollutants trapped in sediments (Tables A.1 to A.3). Station FA, isolated on a small island in the middle of the Guadeloupe National Park, is surprisingly the most contaminated with phthalates. BA, which is also isolated, is contaminated with As and Cu. Station ZI (Mayotte) is impacted by several metals (Cr, Cu, As, Pb, Zn and Ni), which exceed the concentrations harmful for benthic fauna indicated in NOAA guidelines for marine sediments (Table A.1; Buchman, 2008). Toxicity thresholds were also exceeded for PAHs, Cu, Pb and Hg at stations DE and IN, while As exceeded the effect range low (Table A.3; Buchman, 2008) at all stations and depths in Guadeloupe. The ERL was exceeded for pesticides in the deepest horizon of samples from Mayotte and Martinique, where sediments recorded contamination over time. Fiard et al. (2024) recently showed that two pesticides specific to phytosanitary products (dieldrin and total DDT) exceeded regulatory thresholds in mangrove sediments from Martinique.

Similar environmental conditions in the French West Indies only occurred between stations close to each other (HCPC results), suggesting specific environmental constraints at each group of stations along the coastline. On the other hand, in Mayotte, stations located far apart, i.e. on the east and west coasts, were similar (MP and DS, ZI and DS), suggesting the absence of obvious barriers separating mangrove patches along the coastline. However, a sampling strategy over a larger area would be required to validate these trends.

4.2. Sediment organic matter sources

In our study, the carbon isotopic composition of sediment emphasizes prominent mangrove signature in all sites (mean values in $\delta^{13}C$ ranging from −26.6 to −28.6 ‰; Tables A.1 to A.3), when compared with $\delta^{13}C$ values of mangrove litter and leaves (−27.1 to −30.5 ‰ depending on species; Venkatesalu et al., 2008; Gontharet et al., 2014 Ray et al., 2018), microphytobenthos (−15.9 to −20.9 ‰; Gontharet et al., 2014; Ray et al., 2018) and marine phytoplankton (−22 ‰; Cifuentes et al., 1996). The $\delta^{13}C$ values in sediments of all three islands are lower than those recorded in mangrove sediments from French Guiana (FG) (−22.9 to −24.5 ‰; Gontharet et al., 2014). Associated with high TOC:TN ratios (20–30 vs. 7–8 in FG), they highlight a lower relative amount of organic matter (OM) derived from marine sources in the sediments of our study sites (see Gontharet et al., 2014 for review). This result is partly explained by the low tidal range in the French West Indies (<0.5 m) and shorter immersion time of the mud banks. Within each island, the small variations in $\delta^{13}C$ values between sites (from −0.3 ‰ in Mayotte to −1.2 ‰ in Martinique) underline the overall predominance of terrestrial-plant-derived TOC as food source for benthic organisms.

In contrast, the $\delta^{15}N$ signature (Tables A.1 to A.3; from −0.6 to 4.8 ‰ overall) shows variations of a factor of three to five between sites on each island, highlighting spatial variations in nitrogen sources. In particular, in Martinique, the negative values of $\delta^{15}N$ recorded at S4 and S6 (Table A.2), associated with lowest acidic pH and negative Redox potentials (sub-oxic to anoxic conditions), likely indicate nitrogen

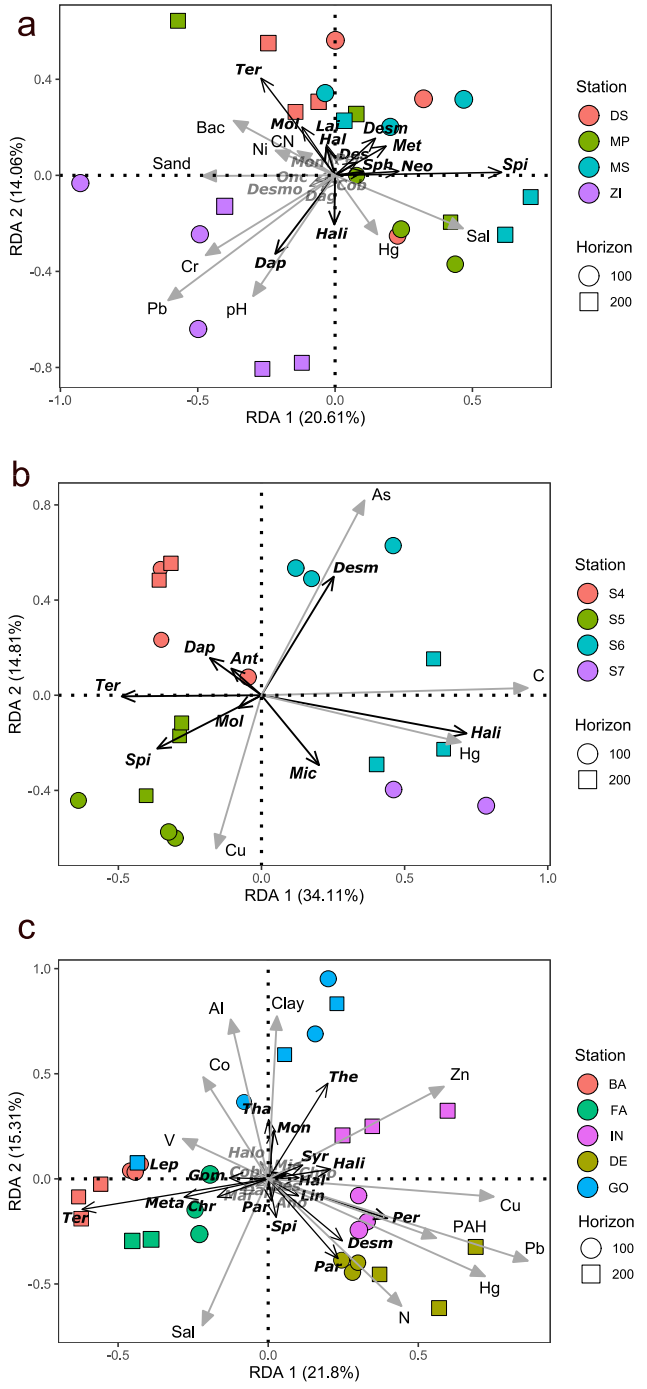

Fig. 5. Redundancy analysis (RDA) based on Hellinger-transformed abundances of dominant nematodes and environmental variables after forward selection for Mayotte (a), Martinique (b) and Guadeloupe (c). Black arrows indicate dominant nematode genera and gray arrows the terms of the model. Genera whose coordinates do not exceed 0.1 in absolute value are shown transparent. Al = Aluminium; As = Arsenic; Bac = bacterial abundance; C = total organic carbon; CN = TOC:TN ratio; Co = Cobalt; Cu = Copper; Cr = Chromium; Hg = Mercury; N = total nitrogen; Ni = Nickel; PAH = polycyclic aromatic hydrocarbons; Pb = Lead; Sal = salinity; Zn = Zinc; *Ant* = *Anticyathus*; *Ano* = *Anoplostoma*; *Dag* = *Dagda*; *Dap* = *Daptonema*; *Desm* = *Desmodora*; *Des* = *Desmoscolex*; *Desmo* = *Desmolaimus*; *Chr* = *Chromadora*; *Chro* = *Chromadorina*; *Cob* = *Cobbia*; *Gom* = *Gomphionema*; *Hal* = *Halalaimus*; *Hali* = *Haliplectus*; *Lai* = *Laimella*; *Lin* = *Linhomoeus; Mar* = *Marylynnia*; *Meta* = *Metacyatholaimus*; *Mic* = *Microlaimus; Mol* = *Molgolaimus*; *Mon* = *Monhystrella; Neo* = *Neochromadora*; *Onc* = *Onchium*; *Per* = *Perspiria*; *Spi* = *Spilophorella*; *Sph* = *Sphaerolaimus*; *Syr* = *Syringolaimus; Tha* = *Thalassomonhystera*; *Ter* = *Terschellingia*; *Par* = *Paradesmodora*.

fixation by microorganisms (highest bacterial abundance in S4) and denitrification. In Guadeloupe, ^{15}N enrichment at DE and IN (Table A.3) may reflect organic matter degradation in which bacteria have preferentially used the lighter isotope (^{14}N; Cifuentes et al., 1996) and the inflow of marine water via the Rivière Salée.

4.3. Meiofauna distribution

To our knowledge, this is the first study to report information on the structure of meiofauna communities in Martinique and Mayotte. As the total number of meiofaunal taxa (TS) is a function of sample size and sampling effort, we found that for most stations, sample size was sufficient to characterize meiofauna community diversity, with the exception of stations GO, BA and IN. Insufficient sample size or sampling effort in the latter would result from higher heterogeneity in environmental conditions and associated meiofaunal community in Guadeloupe, compared with the two other islands (Fig. 3 and Table A.4). This hypothesis is sustained by the results of the PERMANOVA on nematodes (numbers of significant differences in pairwise comparisons of nematode community composition; Table 2). Systematically lower TS values at stations in Martinique, compared with Guadeloupe and Mayotte (Table A.4), were associated with sub-oxic to anoxic conditions, denitrification (see Section 4.2), and contaminant concentration peaks varying from site to site (e.g. Mn and Fe at S4, phenols at S6, phthalates and pesticides at S6 and S7).

The results of PERMANOVA combined with HCPC suggest that the sedimentary environment acts as a filter, generating specific meiofaunal communities at station scale in Martinique and Guadeloupe (Table 1, Fig. 3). The heterogeneity (in Martinique and Guadeloupe) or homogeneity (in Mayotte) of community composition between island stations reflects that of the sedimentary environment, even though variability between replicas can blur differences between stations. In Mayotte, horizontal homogeneity contrasts with vertical heterogeneity in sedimentary conditions and meiofaunal composition and density. Kinorhynchs were only sampled at Mayotte stations (all except ZI; Table A.4). Their absence at ZI, combined with a 6 to 9-fold decrease in ostracod density at ZI (Table A.4), suggests a high sensitivity of these taxa to metallic and organic contaminants, which is in line with the literature (Ruiz et al., 2013; Gyedu-Ababio and Baird, 2006).

Sharp decreases in copepod and polychaete densities were observed with lower salinity in Guadeloupe and Martinique (18 at GO and 24 at S5). For much greater salinity variations than in our study, copepods reduce their respiration rate, become dormant or, in some cases, die (Finney, 1979). In Guadeloupe, the proximity of the Goyave River explains desalting at GO. This river probably drains all the metalloids from the agricultural watershed to the mangrove areas. The most negative redox potential and highest archaea abundance at GO (Tables A.3 and A.4) imply that these freshwater-influenced mangrove sediments are oxygen-poor and unsuitable for most meiofaunal organisms. For example, some polychaetes need oxidized, TOC-enriched sediments for feeding and ventilation in mangroves (Michaud et al., 2022). By comparison, the slightly improved redox conditions at DE are due to the continuous inflow of marine water via the Rivière Salée, as evidenced by the salinity values and ^{15}N enrichment of the sediments (Table A.3). In Guadeloupe, high concentrations of multiple metal contaminants may also contribute to the lowest diversity and abundance of meiofaunal taxa at GO (Table A.4). The latter would be the result of the combined effect of multiple disturbances, rather than single contaminants (Fleeger et al., 2007; Thor et al., 2021), which we cannot distinguish in the present study.

4.4. Nematode community distribution

In this study, the distribution of the different nematode genera showed particular horizontal and vertical patterns (PERMANOVAs), suggesting the presence of sediment patches suitable for a restricted pool of the total diversity of genera on each island. The spatial extent of a patch, which implies homogeneous environmental conditions, was not limited to a single station, but to pairs of stations not far apart. In Martinique, S6 and S7 are closer to each other than to S4 and S5 (Fig. 5b). Moreover, community composition is not significantly different between S4 and S5 on the one hand, and between S6 and S7 on the other (Table 2). In Guadeloupe, FA resembles BA and DE resembles IN, while the two pairs of stations are clearly separated on axis 1 of the RDA (Fig. 5c) and their community compositions are significantly different (Table 2). The latter suggests that similar environmental conditions lead to similar genus composition at stations a few kilometers apart. Between groups of similar stations and others, dispersion should not be a limiting factor, given the distance between them (Derycke et al., 2008). Thus, a stronger environmental filtering is responsible for the differences observed in community composition between groups of stations. Our results in Martinique and Guadeloupe are consistent with the nested diversity patterns due to environmental filtering identified in mangrove sediments by Brustolin et al. (2021). Conversely, the horizontal homogeneity observed between study sites at Mayotte is more consistent with greater dispersal between stations or more spatially homogeneous anthropogenic pressures.

SCBD analyses showed that vertical variability in genus composition in all islands was due to a combination of genera responsible for horizontal variability and other genera present in both layers but dominant exclusively at depth. These genera constituted a subset of the diversity in surface sediments, suggesting a nested diversity pattern between sediment layers. Among dominant genera, those that contribute most to horizontal variability also contribute most to vertical variability. Among rare genera (<5 % of total density), the surface sediments were richer and more diversified than the deeper horizons. Consequently, the genera present in the deeper layers may not be the most specialized, as is often indicated in the literature (Vieira and Fonseca, 2013 and references therein), but the most versatile, capable of thriving in different conditions. Vieira and Fonseca (2013) hypothesized that communities living deep in the sediment are highly dependent on the dispersal of surface communities, which in turn are dependent on dispersal and environmental gradients, which is consistent with our findings.

For each island, however, there remains a proportion of variance not explained by the environmental parameters we have considered, suggesting that other factors such as biotic interactions play an important role in structuring the nematode community (see Spedicato et al., 2023 for review).

4.5. Specific responses of dominant nematodes to environmental variables

In this study, the effect of environmental variables on nematode communities is island-specific. *Terschellingia* and *Daptonema*, dominant in all three islands, show contrasted responses to the surrounding environment (Fig. 5). These two genera, ubiquitous and often dominant in mangroves (Spedicato et al., 2023 and references therein), are found in a wide variety of sedimentary conditions and levels of contamination in other ecosystems (Ridall and Ingels, 2021). Experimental and in situ studies have shown that *Terschellingia* survives periods of anoxia (Soetaert et al., 1995; Armenteros et al., 2010; Alves et al., 2013; Semprucci and Balsamo, 2015; Yen et al., 2020) and organic matter enrichment (Krishnapriya et al., 2021), which is consistent with our results in Mayotte only (Fig. 5). *Daptonema* is tolerant to low concentrations of heavy metals (Heininger et al., 2007) and is particularly dependent on sand % (Vincx et al., 1990), which is also in line with our results in Mayotte. Our study and the literature support the hypothesis that the heterogeneous responses of these genera are due to their versatility. It remains to be determined whether the variability of response between species underlies the versatility of a given genus, as we have identified the taxa at the genus level.

Several other nematode genera showed uniform responses between study areas. *Desmodora* (one of the three genera dominant on all islands) thrived in organic matter-enriched sediments and tolerated organic contaminants. This response is not new in mangroves (Michelet et al., 2021), but it is at odds with what is observed in several other ecosystems (see Ridall and Ingels, 2021 for references). *Desmodora* is also a versatile and resistant genus. Given the huge differences in environmental conditions between ecosystems, it is likely that one (or more) species of *Desmodora* has specifically adapted to thrive in mangrove sediments. We are not aware of the existence of specific physiological adaptations of *Desmodora*, thus tailored experiments could be conducted to shed light on the mechanisms behind its tolerance. *Desmodora* was reported to be tolerant to heavy metals (Somerfield et al., 1994), which agrees with our results in Martinique and Guadeloupe (Fig. 5). However, in Mayotte, *Desmodora* is absent from ZI, where metal concentrations are on average the highest of the three islands, suggesting that toxicity thresholds have been exceeded. Our results support the conclusion that particularly versatile genera respond differently to given sedimentary conditions depending on sites.

On the other hand, some genera showed similar responses across study areas, for instance *Spilophorella* and *Perspira* in Mayotte and Guadeloupe, thriving in sediments with high salinity (as already observed by Xu et al., 2016) and contaminated by mercury. *Haliplectus* and *Microlaimus* thrived in organic-enriched, metal-contaminated sediments in Guadeloupe and Martinique. *Haliplectus* is reported to be resistant to contamination from shrimp farms in Brazil and *Microlaimus* to various sources of pollution from port and mariculture activities (Venekey and Gomes de Melo, 2016; Ridall and Ingels, 2021).

On another hand, we found a very different pool of dominant nematodes in 2019 at approximately the same locations as that sampled in the Rivière Salée (Guadeloupe) by Boucher and Gourbault in 1990. They found *Terschellingia* and *Cobbia* to be dominant, whereas these two genera were dominant only at stations far from the inlet in our study. *Metalinhomoeus* and *Gomphionema*, which were also dominant in 1990, were exclusive to the most pristine stations and absent in the heavily contaminated sediments of the Rivière Salée in 2019. Lastly, *Croconema* was not recorded in our study, although it was dominant in Boucher and Gourbault (1990). The latter did not quantify contaminants in their study, but it is likely that local industrial activities have radically altered sedimentary conditions and the nematode community in the meantime.

5. Conclusions

In the present study of French overseas mangroves, we hypothesized that mangrove sediments around urban centers and agricultural land are more contaminated than sediments far from anthropogenic activities, but our results show that contamination affects mangroves regardless of distance from the source of contamination. We also hypothesized that specific environmental conditions would filter out nematode communities that are also specific to each station, thus generating high horizontal and vertical heterogeneity. Contrary to our initial hypothesis, we found a certain homogeneity in Mayotte and between pairs of stations in Guadeloupe and Martinique, due to similar environmental conditions. A strong environmental gradient is necessary to "filter" a given set of taxa or genera and generate spatial heterogeneity, as was the case between groups of stations in the Caribbean. As expected, some nematode genera showed consistent responses between study areas, although only *Desmodora* reacted similarly across all islands. However, our hypothesis of a uniform response was only partially validated, as many other genera showed island-specific responses. Finally, we hypothesize that the responses to environmental forcing of the nematode genera present in the different study areas could be due to a high versatility of the species or to the presence of different species. Further studies are required to validate

this hypothesis. In the same way, the generalization of some results (upscaling) or the confirmation of some trends put forward in this study would require increasing sampling effort and sample size. Further studies should also address temporal variability in sediment characteristics and meiofaunal community composition linked to the alternation of dry and rainy seasons in the study areas.

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CRediT authorship contribution statement

Adriana Spedicato: Conceptualization, Methodology, Software, Formal Analysis, Investigation, Writing - Original Draft, Visualization. **Daniela Zeppilli:** Conceptualization, Validation, Resources, Writing - Review & Editing, Supervision. **Gérard Thouzeau:** Conceptualization, Methodology, Validation, Investigation, Writing - Review & Editing, Supervision. **Philippe Cuny:** Conceptualization, Methodology, Investigation, Resources, Writing - Review & Editing, Project administration, Funding Acquisition. **Cécile Militon:** Conceptualization, Methodology, Investigation, Resources, Writing - Review & Editing. **Léa Sylvi:** Methodology, Investigation. **Cédric Hubas:** Conceptualization, Methodology, Software, Validation, Formal Analysis, Investigation, Resources, Data Curation, Writing - Review & Editing. **Guillaume Dirberg:** Conceptualization, Investigation, Writing - Review & Editing, Project administration, Funding Acquisition. **Ronan Jézéquel:** Methodology, Validation, Investigation, Resources, Writing - Review & Editing. **Guerric Barrière:** Investigation, Writing - Review & Editing. **Loïc N. Michel:** Investigation, Resources, Writing - Review & Editing. **Tânia Nara Bezerra:** Investigation, Resources, Writing – review & editing. **Emma Michaud:** Conceptualization, Methodology, Validation, Investigation, Resources, Writing - Review & Editing, Supervision, Project administration, Funding Acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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