

Western Indian Ocean JOURNAL OF Marine Science

Volume 15 | Issue 2 | Jul – Dec 2016 | ISSN: 0856-860X

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Western Indian Ocean JOURNAL OF Marine Science

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ISSN 0856-860X



The spatial and temporal variations of nematofauna of recovering *Rhizophora mucronata* mangroves at Gazi Bay, Kenya

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Abstract

The spatio-temporal variations in physical sediment characteristics and nematode community assemblages were investigated and compared between a natural, a 10-year reforested, and a degraded *Rhizophora mucronata* mangrove ecosystem in Gazi Bay, Kenya. PCA showed a clear separation of the degraded site from both the natural and the 10 years reforested sites based TOM and silt/clay. The wet and the dry seasons of the natural and the 10 years reforested sites were also separated based on salinity and silt/clay. An nMDS and ANOSIM analysis on nematode community gave a clear spatial pattern, with both the natural and the 10 years reforested sites separated from the degraded site. The genera *Terschellingia* and *Pierickia* were dominant in the natural and the 10 years reforested sites respectively, and were responsible for the differences between both the natural and 10 years reforested sites, and the degraded site. The degraded site was characterised by high densities of the genus *Metachromadora*. This study shows that clear felling of mangroves leads to changes in nematode genera composition. It is also evident that the nematode community has fully re-established within 10 years of reforestation.

Keywords: mangroves, nematodes, reforestation, recolonisation, spatial, temporal.

Introduction

Mangroves are precious resources for multiple socio-economic and ecological uses. In the recent past, there has been significant development in mangrove research in Kenya, covering structure and function (Mutua *et al.*, 2011; 2013; Bosire *et al.*, 2003; 2004; 2005; Bouillon *et al.*, 2002; 2004a; 2004b; Mwashote and Jumba, 2002), which have provided a comprehensive understanding of this ecosystem. However, increased economic developments, witnessed in many countries, have led to massive destruction of these vital ecosystems (Netto and Galluci, 2003). Mostly, mangrove destruction is through unsustainable exploitation, eutrophication, unplanned coastal developments, and conversion for aquaculture. These activities are frequent along tropical and subtropical coastlines (Kairo and Abuodha, 2001; Netto and Galluci, 2003). Degradation of the floral component of mangrove ecosystems leads to direct impacts on the faunal structure

and function (Fondo and Martens, 1998; Bosire *et al.*, 2004). Among the marine benthos, Nematoda is a suitable taxon for use as an ecological indicator for benthic environments (Schratzberger *et al.*, 2000). According to Alongi *et al.* (1992), they are the most abundant meiobenthic group, have a ubiquitous distribution and high diversity. They are also restricted to the sediments throughout life and have a wide range of adaptations, which enables them exploit all littoral habitats (Higgins and Thiel, 1992; Kennedy and Jacobi, 1999). These traits ensure that the state and composition of nematode assemblages may be used to reflect the general health of the benthos (Kennedy and Jacobi, 1999).

According to Platt and Warwick (1980), nematodes are of major energetic importance, form a significant part of the diet of many other organisms, play vital roles in facilitating decomposition as well as influencing the stability of sedimentary environments, and

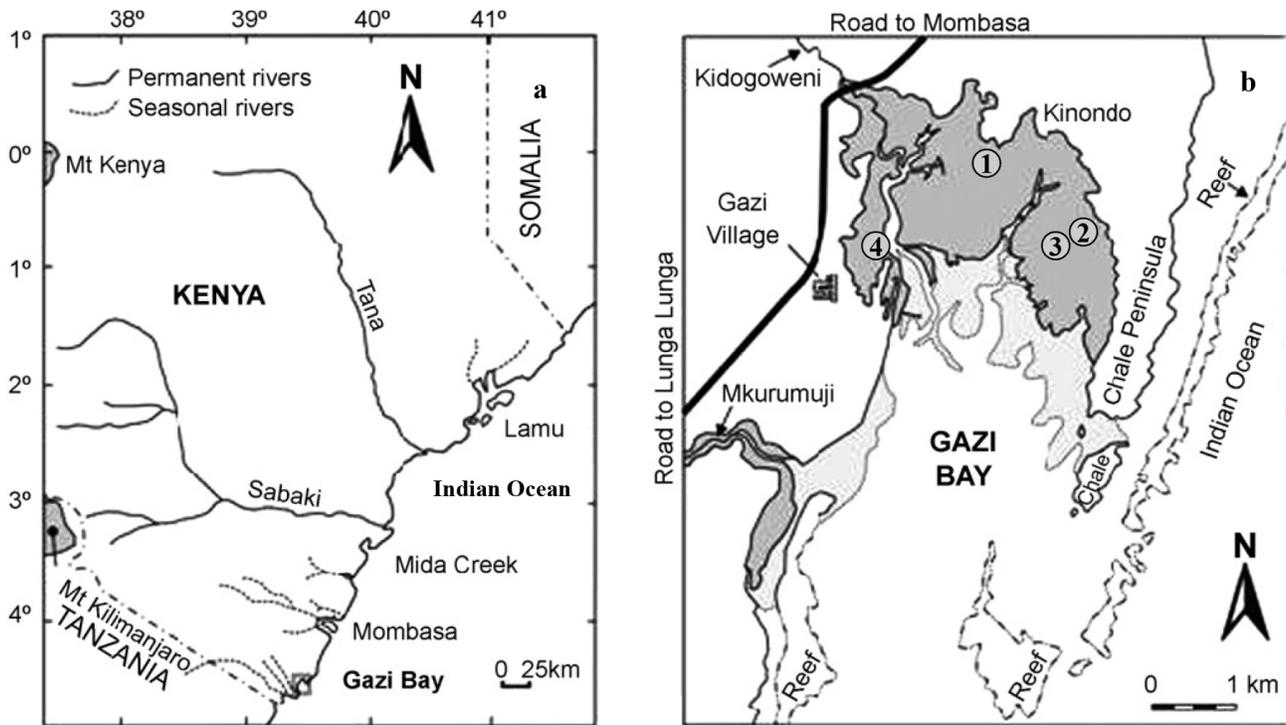


Figure 1. (a) Map of the Kenyan coast and (b) Gazi Bay, the study area. (1) Degraded site, (2) Natural site, (3) 10 years reforested site. (Adapted from Bosire *et al.*, 2004).

are potential indicators of environmental conditions. In addition, Giere (1993) notes that nematodes' diverse morphologies and adaptation to a wide variety of habitats makes them major players in the benthic ecosystem. Differences in benthic physico-chemical characteristics including temperature, depth, mean grain size, salinity, mangrove forest productivity and food availability are possible determinants of the development of different nematode communities among mangrove fringed estuaries (Alongi, 1987; Alongi and Sasekumar, 1992). Therefore, according to Platt and Warwick (1980), any general assessment of the ecology of intertidal habitats is incomplete if the nematofauna is not considered.

Several taxonomic descriptions of mangrove nematodes have been made from many parts of the world, especially in Australia by Nicholas *et al.* (1991), Brazil by Netto and Galluci (2003), and in India by Sasekumar (1994) and Chinnadurai and Fernando (2007). However, the Western Indian Ocean region, which includes the East African mangrove ecosystems, has received minimal coverage in nematofauna research. Only Muthumbi (1994) and Mwojoria (2007) have researched nematodes along the Kenyan coast. In addition, although mangrove restoration along the Kenyan coast was started in 1994 (Kairo and Abuodha, 2001), only Mwojoria (2007) studied nematode distribution

in reforested *S. alba* forests. His study recorded higher nematode densities from reforested *S. alba* compared to the natural site, though no significant differences between the two sites were found. However, no studies have been conducted on the nematodes of restored *R. mucronata* mangroves, which form the largest restoration projects in Gazi Bay. This is despite the understanding that nematodes comprise a large fraction of marine benthic communities. They also form a crucial component of the functioning of mangrove ecosystems and play a pivotal role in mangrove ecosystem restoration success (Field, 1999). Consequently, to better understand the effects of mangrove habitat loss and restoration, studies on the nematofaunal diversity of these ecosystems are crucial. This study is the first to be conducted in Kenyan mangroves that compares nematode community assemblages from natural, 10 years reforested, and degraded *R. mucronata* forest stands, with a view to highlight the effects of mangrove ecosystem degradation and restoration on nematode community structure. The study tries to answer the following questions: (1) Does mangrove clear felling lead to changes in the physico-chemical environment, both spatially and seasonally? (2) Does mangrove clear felling lead to alteration of nematode density and community composition? (3) Did the restoration of the *R. mucronata* mangrove ecosystem successfully create (after 10 years), a nematode

community assemblage comparable in density, community composition and diversity to that of the natural mangrove stand? And (4) to what extent do nematode communities show seasonal variations?

Materials and Methods

Study area

The study was conducted at Gazi Bay (4° 25' S and 39° 30' E) located on the southern part of the Kenyan coast (Fig. 1) about 50 km from Mombasa. The bay is protected from strong wave energy by the Chale Peninsula to the east and a fringing coral reef to the south (Tack and Polk, 1999). The site has natural mangrove forests, replanted sections, and totally degraded areas. Reforestation was started between 1991 and 1994 (Kairo, 1995, Kairo *et al.*, 2001).

Sampling and Sample processing

Sampling was done seasonally in September (Dry season) and December (Wet season) 2004. Three sampling plots measuring 25 m² each, and 50 m apart, were randomly selected at each site. In each of these plots, three sediment cores (6.4 cm diameter, 10 cm long) were collected at random for total organic matter (TOM) and grain size analysis. The TOM samples were oven-dried at 80°C for 24 h to remove all moisture. Thereafter, 10 g of the dried samples were ashed at 600°C for 6 h to obtain the ash-free dry weight (AFDW); TOM was calculated as the percentage of the ashed material. Interstitial sediment water samples were collected for measurement of salinity and temperature in a 5-10 cm hole dug in the sediment. Salinity was measured using an Atago optical refractometer. Additionally, from each of the sampling sites, 3 sediment cores for nematodes (3.2 cm internal diameter, 5 cm long) were taken at random and immediately fixed in 5 % formalin. In the laboratory, the samples were rinsed using tap water over a 1 mm sieve to exclude macrofauna and any debris, and collected

on a 38 µm sieve. The fraction retained on the 38 µm sieve was centrifuged three times at 6000 r.p.m. with MgSO₄ of specific density 1.28 for 10 minutes. Afterwards the supernatant was sieved over a 38 µm sieve to extract nematodes, rinsed with tap water to remove the MgSO₄, and stained with Rose Bengal. Nematodes were then counted under a dissecting microscope, and 200 individuals picked randomly. Afterwards, nematodes were fixed by transferring them from formalin to glycerol through a series of ethanol-glycerol solutions and mounted on glycerine slides (Warwick *et al.*, 1998). Identification of the nematodes was done to genera level using the pictorial keys of Platt and Warwick (1983; 1988) and Warwick *et al.* (1998).

Statistical analysis

Data on sediment physical characteristics and nematode community were analysed using PRIMER (v.5) and STATISTICA (v.6). Principal Component Analysis (PCA) ordination using Euclidean distances was used to reveal variation between sites and seasons based on physical sediment characteristics. Non-metric multidimensional scaling (nMDS) ordination of square root-transformed data using the Bray-Curtis similarity coefficient was used to reveal similarities between the study sites in terms of nematode community composition. Variability in nematode density between and within sites was tested using analysis of similarity (ANOSIM). Differences in environmental characteristics between sites and seasons, and nematode density, was analysed using ANOVA, while post hoc analysis was performed using Tukey's Honest Significant Difference test. Data was first tested for normality using Levene's test before being subjected to ANOVA.

Results

Environmental characteristics

The spatial and temporal variations in sediment physical characteristics are shown in Table 1.

Table 1. Spatial and Temporal averages (Mean ± SE; n = 3) of sediment physical characteristics in the study sites and seasons.

Parameter	Sites and Seasons					
	WNat	DNat	WRefo10	DRefo10	WDegr	DDegr
TOM (%)	48.1±6.6	48.4±5.4	32.1±3.9	33.9±0.3	3.3±0.7	2.8±0.4
Sand (%)	39.1±9.8	19.2±3.6	32.5±2.6	28.1±2.6	78.7±1.8	81.6±6.2
Silt/Clay (%)	60.9±9.8	80.8±3.6	67.5±2.6	71.9±2.6	21.3±1.8	18.4±6.2
Salinity (PSU)	30.3±2.1	38.3±0.6	32±1	39.7±0.6	43.3±1.5	46±1
Temperature (OC)	28.7±1.2	28.7±0.4	29±0.9	28±0.2	31.3±1.4	34±1

Two-Way ANOVA showed significant differences in TOM between sites (ANOVA; $F = 856.63$, $df = 2$, $p < 0.05$). However, there was neither any seasonal differences within sites observed, nor was the interaction between seasons and sites significant. The wet and dry seasons within the natural site recorded significantly higher mean sediment TOM ($48.1\% \pm 6.6$ and $48.4\% \pm 5.4$ respectively) than all the other sites. The lowest TOM levels ($3.3\% \pm 0.7$ and $2.8\% \pm 0.4$) were recorded from the degraded site during both wet and dry seasons respectively.

There were significant differences in sand content between sites, between seasons within sites, and the interaction between seasons and sites (ANOVA; $F = 185.36$, $df = 2$, $p < 0.05$; $F = 8.29$, $df = 1$, $p < 0.05$; $F = 7.37$, $df = 2$, $p < 0.05$ respectively). The degraded site recorded significantly sandier sediments ($81.6\% \pm 6.2$ and 78.7 ± 1.8) during the dry and wet seasons, respectively, than the natural and the 10 years reforested sites.

However, only the natural site recorded significant seasonal differences in sand content where the dry season recorded significantly lower sand content ($19.2\% \pm 3.6$) than the wet season (39.1 ± 9.8), and lower than all the other sites ($p < 0.05$).

The proportion of silt/clay was significantly different between sites, between seasons, and the interaction between seasons and sites was also significant (ANOVA; $F = 185.36$, $df = 2$, $p < 0.05$; $F = 8.29$, $df = 1$, $p < 0.05$; $F = 7.37$, $df = 2$, $p < 0.05$, respectively). Both the natural and the 10 years reforested sites recorded significantly higher silt/clay content ($p < 0.05$) during both seasons than the degraded site. Significant seasonal differences in silt/clay within sites were recorded within the natural site, where the dry season recorded significantly higher silt/clay fractions ($80.8\% \pm 3.6$) than the wet season ($60.9\% \pm 9.8$). The high sand content during the wet season in the natural site shows that surface runoff probably deposited sandy from the surrounding terrestrial systems. The wet and dry seasons within the degraded site recorded the lowest silt/clay content ($21.3\% \pm 1.8$ and $18.4\% \pm 6.2$ respectively).

The level of salinity was significantly different between sites, between seasons, and the interaction between sites and seasons was also significant (ANOVA; $F = 120.25$, $df = 2$, $p < 0.05$; $F = 108.4$, $df = 1$, $p < 0.05$; $F = 8.81$, $df = 2$, $p < 0.05$, respectively). The degraded site recorded significantly higher salinity ($p < 0.05$) during both dry and wet seasons (46 ± 1 and 43.3 ± 1.5 PSU, respectively), than the natural and the 10 years reforested sites, which recorded the lowest salinity during

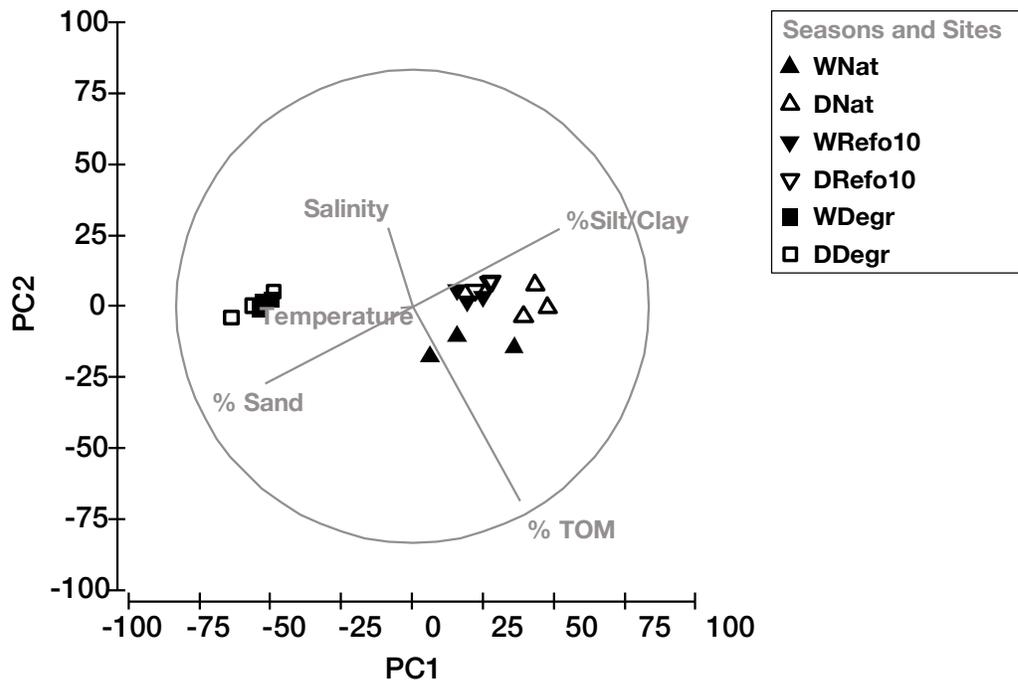


Figure 2. Sediment physical characteristics: output of Principal Component Analysis (PCA) on sites and seasons. WNat; Wet season Natural site, DNat; Dry season Natural site, WRefo10; Wet season 10 years reforested site; DRefo10; Dry season 10 years reforested site, WDegr; Wet season Degraded site and DDegr; Dry season Degraded site.

the wet season (30.3 ± 2.1 and 32 ± 1 PSU, respectively). Seasonal salinity differences were recorded from both the natural and the 10 years reforested sites, where the dry season recorded significantly higher salinity ($p < 0.05$) than the wet season. There were significant differences in temperature between sites, and the interaction between seasons and sites (ANOVA; $F = 36.95$; $df = 2$, $p < 0.05$; $F = 5.95$, $df = 2$, $p < 0.05$, respectively). However, no significant differences between seasons within sites were observed. The degraded site recorded significantly higher temperatures ($34 \text{ }^\circ\text{C} \pm 1$ and 31.3 ± 1.4) during the dry and wet seasons respectively ($p < 0.05$) than the natural and the 10 years reforested sites.

Figure 2 shows the ordination of sites and seasons within sites based on sediment physical characteristics data. The PCA output showed a clear separation of the degraded site from both the natural and the 10 years reforested sites. Principal components (PC) 1 and 2 explained 99 % of the variability (PC 1, 96 %; PC 2, 3 %). On the first principal component, the natural and the 10 years reforested sites, with the highest TOM and silt/clay, were separated from the degraded site having sandier sediments and low TOM. The separation of sites along the second principal component was less pronounced, though it separated the wet and dry

seasons within the natural and the 10 years reforested sites, based on salinity and silt/clay fraction.

Nematode community assemblages

A total of 76 nematode genera, belonging to 24 families were identified. Out of these, 62 genera belonging to 23 families were recorded from the 10 years reforested site, while 60 genera belonging to 23 families were recorded from the natural site. The degraded site recorded 33 genera belonging to 18 families. The dominant families in the natural site were Linhomoeidae (31 %) and Desmodoridae (14 %). The families Linhomoeidae (32 %) and Comesomatidae (26 %) were the most abundant families in the 10 years reforested site, while Desmodoridae (29 %), Cyatholaimidae (15 %) and Anoplostomatidae (14 %) contributed the highest relative densities in the degraded site.

Total nematode densities and major nematode genera

Total nematode densities within sites and seasons are shown in Figure 3. The natural and the 10 years reforested sites recorded higher densities during both wet and dry seasons (1635 ± 640 , 2110 ± 1100 , 1410 ± 356 and 1804 ± 958 Ind./10 cm² respectively) than the degraded site (436 ± 169 and 398 ± 182). There were significant differences between sites (ANOVA; $F = 17$, $df = 2$,

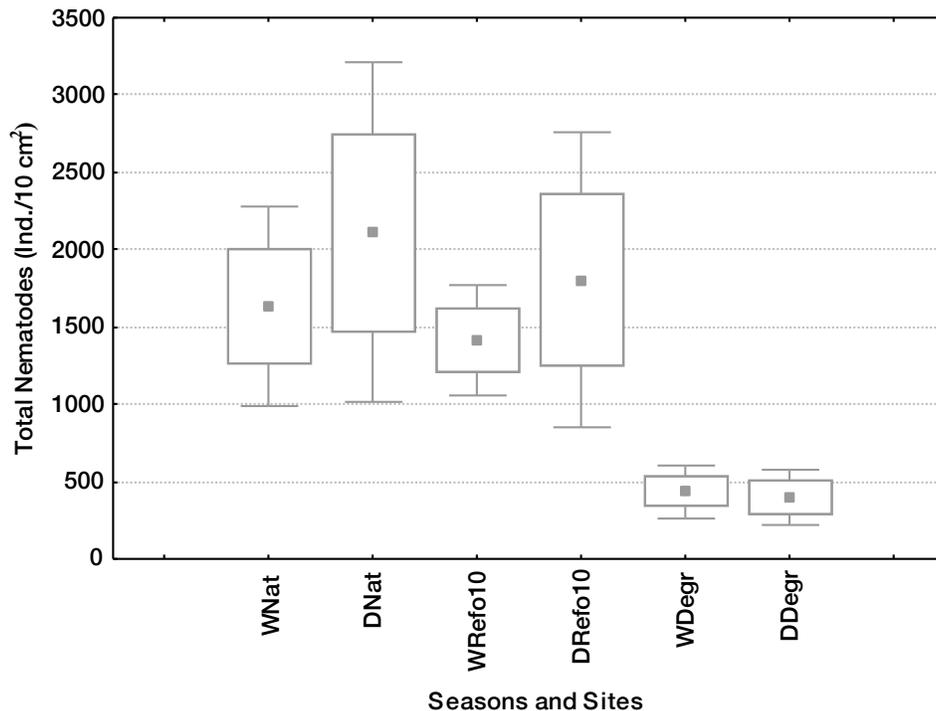


Figure 3. Spatial and temporal variations in nematode densities. WNat; Wet season Natural site, DNat; Dry season Natural site, WRefo10; Wet season 10 years reforested site; DRefo10; Dry season 10 years reforested site, WDegr; Wet season Degraded site and DDegr; Dry season Degraded site.

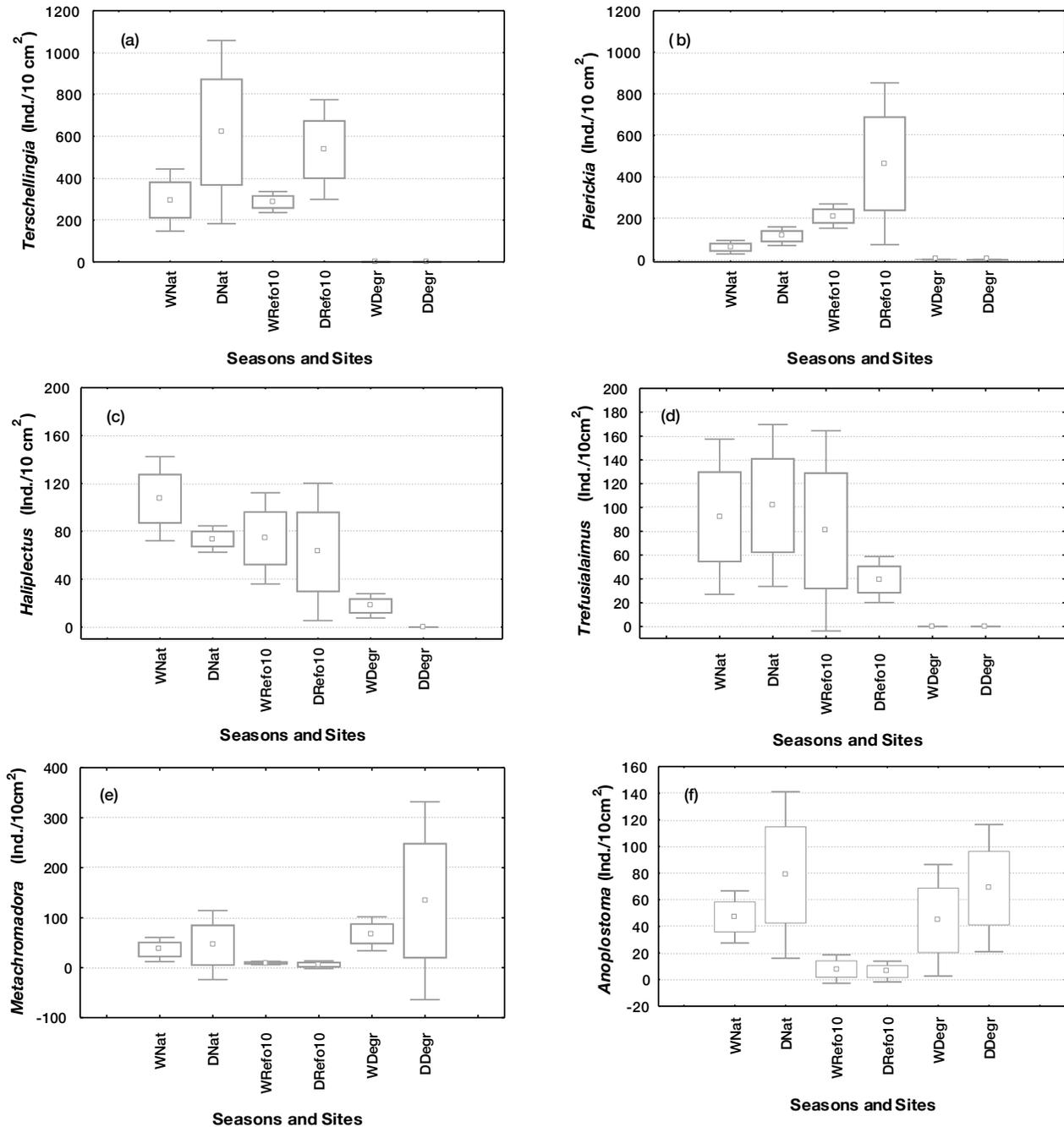


Figure 4a-f. Spatial and temporal variation in numerical abundance of the major nematode genera; (a) *Terschellingia*, (b) *Pierickia*, (c) *Haliplectus*, (d) *Trefusialaimus*, (e) *Metachromadora* and (f) *Anoplostoma*. WNat; Wet season Natural site, DNat; Dry season Natural site, WRefo10; Wet season 10 years reforested site; DRefo10; Dry season 10 years reforested site, WDegr; Wet season Degraded site and DDegr; Dry season Degraded site.

$p < 0.05$) with the natural and the 10 years reforested sites recording significantly higher densities than the degraded site. However, no seasonal differences were observed within sites.

The genera *Terschellingia*, *Pierickia*, *Haliplectus*, *Trefusialaimus*, *Metachromadora* and *Anoplostoma* were the most dominant in all the sites and accounted for 22 %, 11 %, 4 %, 4 %, 4 % and 3 % respectively) of the overall nematode density. Figure 4a-f shows the densities

of the major nematode genera recorded. *Terschellingia* (Fig. 4a) recorded the highest densities in both the natural and the 10 years reforested sites during both the wet and the dry seasons (296 ± 148 , 620 ± 437 , 286 ± 50 and 537 ± 238 Ind./10cm² respectively). *Terschellingia* was totally absent from the degraded site. Densities of *Terschellingia* were significantly different between sites (ANOVA; $F = 245.3$, $df = 2$, $p < 0.05$) even though no seasonal differences within sites were observed.

The densities *Pierickia* (Fig. 4b) were highest in the 10 years reforested site during both dry and wet seasons (462 ± 390 and 211 ± 59 Ind. / 10cm^2 respectively). The natural site recorded intermediate densities (114 ± 45 and 61 ± 32 Ind. / 10cm^2) during the dry and wet seasons. However, significantly lower densities of *Pierickia* (ANOVA; $F = 82.57$, $df = 2$, $p < 0.05$) were recorded in the degraded site (1 ± 2 and 2 Ind. / 10cm^2). No seasonal differences within sites were observed.

The genus *Haliplectus* (Fig. 4c) recorded high densities in the natural and the 10 years reforested sites (107 ± 35 , 73 ± 11 , 74 ± 38 and 63 ± 57 Ind. / 10cm^2) during the wet and dry seasons, respectively. The degraded site recorded significantly lower densities of *Haliplectus* only during the wet season (18 ± 10 Ind. / 10cm^2 ; ANOVA; $F = 67.86$, $df = 2$, $p < 0.05$) than both the natural and the 10 years reforested sites. Only the degraded site showed significant seasonal differences in densities of *Haliplectus*, with no *Haliplectus* at all recorded during the dry season (ANOVA; $F = 24.67$, $df = 2$, $p < 0.05$).

The genus *Trefusialaimus* (Fig. 4d) was not recorded in the degraded site while the natural and the 10 years reforested sites recorded densities of 92 ± 65 , 101 ± 68 and 80 ± 84 , 40 ± 19 Ind. / 10cm^2 in the wet and dry seasons, respectively. Lack of *Trefusialaimus* in the degraded site explains the observed significant differences between sites (ANOVA; $F = 92.13$, $df = 2$, $p < 0.05$).

The densities of *Metachromadora* (Fig. 4e) was highest in the degraded site with densities of 134 ± 198 and 68 ± 34 Ind. / 10cm^2 recorded during the dry and wet seasons, respectively. The densities of this genus were very low in the natural (45 ± 69 and 36 ± 24 Ind. / 10cm^2) and the 10 years reforested sites (6 ± 8 and 9 ± 3 Ind. / 10cm^2). Due to the great variation in densities of *Metachromadora*, especially in the degraded site during the dry season, no significant differences between sites and between seasons within sites were observed.

The densities of *Anoplostoma* (Fig. 4f) were highest in the natural site (78 ± 62 and 47 ± 20 Ind. / 10cm^2) and the degraded site (69 ± 48 and 45 ± 42 Ind. / 10cm^2) during the dry and wet seasons, respectively. The 10 years reforested site recorded significantly lower densities (6 ± 8 and 8 ± 11 Ind. / 10cm^2) of *Anoplostoma* (ANOVA; $F = 3.97$, $df = 2$, $p < 0.05$) compared to the natural and the degraded sites.

An nMDS analysis (Fig. 5) of nematode genera densities and community composition produced two

clear clusters. The natural and the 10 years reforested sites formed one cluster which was separated from the degraded site. However, no separation of seasons within sites was observed. ANOSIM further confirmed the spatial patterns within the nMDS, with the natural site being very similar to the 10 years reforested site irrespective of the season ($R < 0.5$). The degraded site was significantly different from both the natural and the 10 years reforested sites in all seasons ($R > 0.5$). In addition, ANOSIM showed no significant seasonal differences within sites ($R = -0.111$, 0.111 and 0.444) for the natural, the 10 years reforested and the degraded sites. SIMPER analysis showed that the genera *Terschellingia*, *Pierickia* and *Haliplectus* were the main genera responsible for the high similarity observed within the natural and the 10 years reforested sites. The genera *Paracanthochus* and *Metachromadora* contributed to the similarity observed within the degraded site. The observed differences between the degraded site and both the natural and the 10 years reforested sites were mainly explained by the genera *Terschellingia*, *Pierickia*, and *Trefusialaimus*, among others. The degraded site recorded the lowest densities of these genera.

Discussion

Spatial variation

Mangroves are an important resource both ecologically and socio-economically because of the services and goods they provide. Along the Kenyan coast, mangroves have been clear cut in the past to provide goods such as fuel wood and building materials, leading to loss of ecosystem services (Kairo and Abuodha, 2001). Reforestation efforts have been initiated in order to remedy the effects of forest loss. One of the main aspects in the evaluation of the success of an ecological restoration project, is to determine how far all ecosystem components have re-established, and to what extent their functions have been restored (Ellison, 2000). In this respect, only the study by Mwojoria (2007) has documented the most abundant and species rich metazoan taxon, the nematode communities, in reforested *S. alba* mangrove sediments in Kenya. Additionally, data on nematode colonisation of reforested mangrove ecosystems on a global scale is also rare and most studies have dealt with macrofauna and meiofauna up to higher taxa level (Khalil, 2001; Bosire *et al.*, 2004; Mutua *et al.*, 2011; Mutua *et al.*, 2013; Mutua *et al.*, 2014). Therefore, these results provide the first account of nematodes associated with mangrove sediments in natural, reforested and degraded *R. mucronata* mangroves.

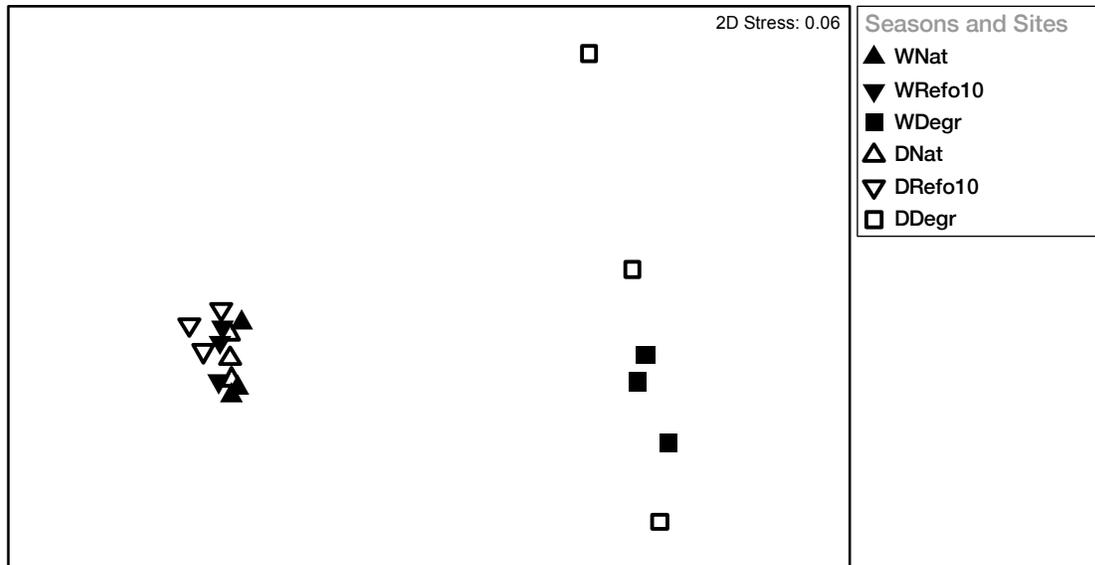


Figure 5. Nematode genera community assemblage: Output of non-metric Multi Dimensional Scaling (nMDS) on square root transformed nematode genera densities data showing affinities between sites and between seasons within sites, WNat; Wet season Natural site, DNat; Dry season Natural site, WRefo10; Wet season 10 years Reforested site, DRefo10; Dry season 10 years Reforested site, WDegr; Wet season Degraded site and DDegr; Dry season Degraded site.

The results of this study show that nematodes are very diverse within the studied mangrove sediments, with a total of 76 genera belonging to 24 families recorded. Mwojoria (2007) recorded 72 genera belonging to 24 families, with densities ranging from 1638 to 1292 Ind./10cm² from *S. alba* mangroves in Gazi Bay, which is similar to the results of the current study (2110 to 1685 Ind./10cm²). The total density of nematodes and number of genera recorded are also similar to those reported from other mangrove systems in India (Chinnadurai and Fernando, 2007), Brazil (Netto and Galluci, 2003) and Zanzibar (Ndaro and Olafsson, 1999). The density of nematodes was not different between the natural and the 10 years reforested sites, despite the differences in TOM. These similarities can be linked to the fact that the supply of fresh organic material as food for benthos is more or less equal in both the reforested and the natural sites. In addition, Bosire *et al.* (2003) and Mutua *et al.* (2011; 2013; 2014) found that reforestation usually alters sediment physico-chemical conditions and ultimately restores the functional importance of nutrient fluxes, among other functions.

This study further shows that the 10 years reforested site is similar in nematode community assemblage to the natural site, but the two are significantly different from the degraded site. This is a clear indication of the effects of mangrove clear felling on the structure, function and biodiversity of mangrove ecosystems. Mangrove clear felling removes vegetation cover

exposing the sediment to tidal erosion which leads to removal of the fine sediments and detritus, since these are easily re-suspended by tidal currents. The dense root network in the natural and the 10 years reforested sites ensures that tidal currents are slowed down and re-suspension is reduced (Wolanski *et al.*, 1992), leading to fine sediment and organic matter deposition. Fine sediments, rich in detritus, form the food for benthic fauna, directly or indirectly by providing the medium which supports microphytobenthos growth, and in this way, forms essential food materials for benthic fauna (Snelgrove *et al.*, 1997; Pavlyuk, 2004; Chinnadurai and Fernando, 2007).

Mangrove derived detritus has been shown to be of low nutritional value (Bosire *et al.*, 2005; Alongi and Christoffersen, 1992) and acts as a repellent to nematode colonisation due to high tannin content (Alongi, 1987). However, nematodes may excrete substances which stimulate soil micro-organisms, and produce exo-enzymes which initiate decomposition of complex molecules from mangrove detritus (Ruess *et al.*, 2001; Ekschmitt *et al.*, 1999). These substances would promote the establishment and growth of bacterial populations that take over organic matter decomposition, ensuring that both nematodes and bacteria feed on the nutritious 'soup' of dissolved organic matter (DOM) and particulate organic matter (POM) released (Snelgrove *et al.*, 1997; Riemann and Helmke, 2002). It has also been shown that the bacterial biomass

associated with detritus may not be sufficient to meet detritivores' carbon and energy requirements (Blum *et al.*, 1988). However, the presence of fungi, in substantial proportions in the detritus, increases the microbial detrital biomass sufficiently to provide detritivores with their nutritional requirements (Blum *et al.*, 1988; Snelgrove *et al.*, 1997). This is in addition to the mangrove-derived detritus whose nutritional value is increased through microbial decomposition (Skov and Hartnoll, 2002).

Total canopy removal by clear-felling exposes mangrove sediments to intense solar radiation, which leads to increased interstitial water temperature and salinity. Bosire *et al.* (2003; 2004) recorded significantly higher interstitial water temperature and salinity in degraded *R. mucronata* sites compared to natural and reforested sites. Increased temperature and salinity impacts negatively on the benthic fauna due to increased environmental stress (Sasekumar, 1994). Salinity also affects the osmoregulation in meiofaunal species and hence could be a community regulator by determining the physiological activity of marine organisms (Ingole and Parulekar, 1998). Additionally, increased sediment temperature leads to desiccation, which kills or limits growth of microflora, removes water from plant cell cytoplasm and changes the chemical status of organic materials which are important media for microbial growth (Mfilinge *et al.*, 2002).

Studies by Sjolting *et al.*, (2005) indicate that low Redox Potential in degraded mangrove sediments due to lack of oxygen, and ultimately accumulation of organic matter, also leads to increased anoxicity and high sulphide concentrations. This creates inhospitable habitats for most benthic fauna and ultimately leads to impoverished faunal abundances. This probably explains the low densities of nematodes recorded from the degraded site in the current study.

The genus *Terschellingia* is known to be a low oxygen consumer and is dominant in muddy sediments rich in organic matter (Schratzberger and Warwick, 1998a; 1998b). Therefore, its dominance in both the natural and the 10 years reforested sites reflect its ability to exploit these organically rich, but oxygen poor habitats. The genus *Metachromadora* was dominant in density in the degraded site which also recorded the highest sand content. Studies by Schratzberger *et al.* (2004) as well as those of Long and Othman (2005) have also documented high densities of *Metachromadora* in sandy sediments. Similarly, Mwojoria (2007) recorded

high densities of *Metachromadora* from degraded *S. alba* in Gazi Bay. These high densities were related to the ability of this genus to burrow, and hence increased competitive ability especially in search of food. *Metachromadora* is also known to be eurytolerant to fluctuating environmental conditions, probably due to its thick cuticle, hence its high abundance in the exposed degraded site (Long and Othman, 2005).

Seasonal variation

Seasonal variations of plant and animal populations are the rule in nature and several abiotic and biotic variables may account for the temporal variation in benthos. Temperature and food availability have been cited as the main factors explaining seasonal changes in the abundance of benthos (Olafsson and Elmgren, 1997). The absence of seasonal differences within sites in nematode densities and community composition in the present study, may be explained by the lack of seasonal trends in TOM (an indicator of food availability) and temperature, which are key factors influencing nematode densities in mangrove sediments. Although sand and silt/clay showed significant seasonal variation in the natural site, they did not influence nematode densities. Lack of seasonal trends in nematode densities have also been documented from mangroves in South Africa (Dye, 1983). However, the genus *Haliplectus* showed significant differences between seasons in the degraded site, with higher densities recorded during the wet season. This difference may be linked to organic matter input from terrestrial runoff from the surrounding farmlands which flooded this site during the rainy season (personal observation). This genus is a selective deposit feeder hence may have been responding to the availability of diverse detrital material introduced by flood waters.

Conclusions

The study shows that mangrove clear-felling restricts nematode colonisation due to the resulting unfavourable conditions that result from canopy removal. The study also shows that mangrove reforestation modifies sediment conditions leading to recovery of the systems ecological functions, such as nematode colonisation. Seasonal variations in nematode communities were not very evident except in the degraded site where abiotic conditions were unfavourable. These findings further support mangrove reforestation efforts as this provides continuity of the systems ecological functions, which will ensure that there is sustainability of ecological services, economic benefits and ultimately biodiversity conservation.

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