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Meiofaunal communities in a tropical seagrass bed and adjacent unvegetated sediments with note on sufficient sample size for determining local diversity indices

Jian-Xiang Liao^{1*}, Hsin-Ming Yeh² and Hin-Kiu Mok¹

Abstract

Background: Seagrass beds are highly diverse and productive marine habitats for many associated organisms in nearshore coastal waters. The differences in abundance, diversity, and community structure of benthic invertebrates between seagrass beds and adjacent unvegetated sediments have been stated, whereas most studies are primarily focused on macrofauna or based on a comparatively long distance, i.e., more than 10 m. The present study is designed to test if the community structures of meiofauna, especially the free-living nematodes, differ between seagrass beds and adjacent unvegetated sediments on a meter scale.

Results: There are 21 meiofaunal taxa and 63 nematode genera that have been identified from a tropical seagrass bed of *Thalassia hemprichii* in Ludao, Taiwan. Although the compositions of higher meiofaunal taxa are undistinguished, according to correspondence analysis, the assemblages of nematode genera differ substantially between the seagrass bed and unvegetated sediments. Regarding the nematodes, approximately 50% of genera are restricted to the seagrass bed whereas 6% are restricted to unvegetated sediments, which indicate both habitats possessing distinct infaunas. The number of replicates for reasonable estimation of the local diversity index is calculated by the randomization technique. For local seagrass beds, only a single core is sufficient for reliably estimating meiofaunal diversity, but at least three cores or a sample size of 300 individuals is needed for the nematode community.

Conclusions: Nematode assemblages provide more particular differences between seagrass and unvegetated habitats than meiofaunal communities on small spatial scales. Both seagrass beds and adjacent unvegetated sediments harbor specific meiofaunal communities, and hence, the conservation strategy for seagrass should also consider the peripheral bare area of seagrass beds.

Keywords: Meiobenthos; *Thalassia hemprichii*; Community composition; Marine nematode; Randomization; Diversity index

Background

Seagrass beds, which distribute widely in tropical and temperate coastal regions, are one of the most productive marine ecosystems (Duarte and Chiscano 1999). Thalli, roots, and rhizomes of seagrasses offer associated animals microhabitats and shelters (Osenga and Coull 1983; Orth et al. 1984; Castel et al. 1989; Atilla et al. 2005). In

addition, various detritus and organic particles in seagrass beds enhance the density and heterogeneity of infauna (Hall and Bell 1993; Danovaro et al. 2002). Meiofauna, benthic organisms between 1 mm and 42 μm , is considered a trophic level between microfauna and macrofauna (animals larger than 1 mm). However, most studies dealing with seagrass beds merely focus on macrofauna, even though meiofauna can consume from 10% to more than 50% of the total primary production in a seagrass system (Danovaro et al. 2002). Moreover, most members of meiofauna are less influenced by hypoxia and predation than

* Correspondence: jianxiangliao@gmail.com

¹Department of Oceanography, National Sun Yat-sen University, Lienhai Road 70, Kaohsiung 80424, Taiwan

Full list of author information is available at the end of the article

those of macrofauna and have distinct responses to environmental changes (Josefson and Widbom 1988; Castel et al. 1989; Giere 2009). Among meiofaunal communities, free-living nematodes usually constitute the most abundant taxa, albeit seagrass studies of meiofauna have primarily focused on epifauna, i.e., harpacticoid copepods. Nematode assemblages shift consistently with ambient sediments, and they are considered an ecological indicator (Bongers and Ferris 1999).

The unvegetated area around seagrass patches facilitates infauna dispersal and can be a matrix habitat, but few seagrass studies have looked into this bare region (Boström et al. 2006). The abundance and community structure of nematodes show substantial differences between vegetated and peripheral unvegetated sites (Fisher and Sheaves 2003; Hourston et al. 2005; Monthum and Aryuthaka 2006; Fonseca et al. 2011; Leduc and Probert 2011), although no difference between both habitats has also been reported (Ndaro and Ólafsson 1999). The variability in nematode populations on a small spatial scale (centimeter scale) accounts for 30% and 43% in intertidal and shallow subtidal sediments, respectively (Hodda 1990; Li et al. 1997). However, the distances between samples or quadrats in most seagrass studies are separated by more than 10 m or unmentioned (except Hourston et al. 2005; 2 m), whereas the other unanticipated local environmental factors (e.g., water depth) exceed the effect of seagrass (Mills and Berkenbusch 2009). Comparisons between seagrass beds and peripheral unvegetated sediments at small-scale distances elucidate the seagrass effect on meiofaunal communities.

Diversity indices are widely used in ecological research, especially for comparative purposes. The Shannon-Wiener index (H') is the most popular one for measuring diversity in a community. Because of the sample size dependence, a pertinent sampling effort is required for comparison between various communities. The randomization technique has been used to estimate the sufficient sample size for obtaining an approximate value of the diversity index (Soetaert and Heip 1990). However, Hurlbert's modified rarefaction curve (Hurlbert 1971) or the expected species richness, $ES(n)$, a sample size-independent index of species richness (Sanders 1968), is much more often used to estimate the diversity of meiofauna (e.g., Shimanaga et al. 2004; Leduc et al. 2010). In addition, most relevant investigations are performed in temperate regions or the deep sea, but the same procedure may not be appropriate for tropical habitats. To our knowledge, there is an absent or scarce report on the marine meiofaunal communities in Taiwan, and a relevant method for determining local diversity indices might improve the future comparison with the other regions.

The present study aims to inspect the community structure of meiofauna, particularly nematodes, which

are used to examine the difference between seagrass beds and adjacent unvegetated sediments on a meter scale. Meiofaunal samples were collected quantitatively from sediments below the sickle seagrass *Thalassia hemprichii* and peripheral unvegetated substrates in Ludaο, Taiwan. The sampling effort (i.e., the number of replicates) required for estimating the local diversity index in a seagrass habitat is determined using a randomization test to provide a basis for future experimental design of comparative researches.

Methods

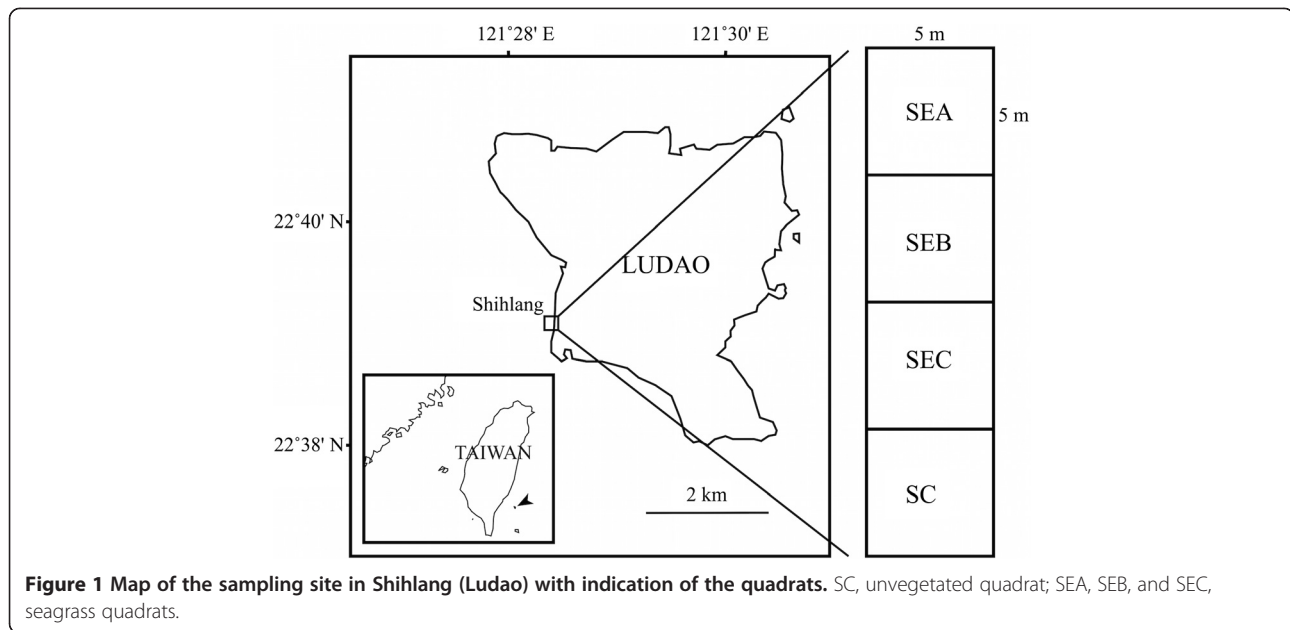
Study site and sampling methods

Shihlang is a recreational diving site in Ludaο, also known as Green Island, situated off the southeastern coast of Taiwan (Figure 1). The shore is composed of a sandy platform extending 50 m seaward and a *T. hemprichii* meadow (22°39'08" N, 121°28'25" E) in the littoral zone. Patches of seagrass distribute at a region 150 m in length and 12 m in width along the coast. The distance between the fringes of seagrass beds to the mean high water line is about 18 m. Because of the freshwater input, the salinity reaches approximately 20 to 25 practical salinity units (PSU) during low tide. Megafaunal bioturbators are frequently present, mainly composed of crustaceans and echinoderms.

Regarding the narrow distribution of the seagrass patches and avoiding intense environmental changes, four 5 × 5 m side-by-side sampling quadrats were selected: three seagrass patches and an adjacent unvegetated control quadrat. The vegetated quadrats densely grew *T. hemprichii* and patches with sparse region, where taking cores was avoided. Within each quadrat, five replicate cores for meiofauna were sampled by a lower end cutoff syringe (diameter = 2 cm), which was pushed into the sediment to a depth of 5 cm. On each sampling occasion, the replicates were at least 1 m apart from each other. All samples collected from the area were 20 m long and 5 m wide at approximately 30-cm water depth during low tide on 17 March 2012. Samples of meiofauna were anesthetized using 7% MgCl₂ solution to promote tissue relaxation and then preserved with formaldehyde to a final concentration of 4%. The sediment grain size profile was very similar to the sandy platform, and five additional replicate cores were taken for sediment granulometry as a reference.

Laboratory procedures

Meiofaunal samples were stained with 0.5 g/L Rose Bengal for 1 h and washed through sieves of 1,000- and 42-μm mesh size. All the meiofauna retained on the 42-μm sieve were extracted, counted, and identified to the major taxon level under a stereomicroscope. From each replicate, 100 nematodes (or all individuals if fewer) were picked out, transferred to pure glycerol, mounted onto permanent slides, and identified to the genus level



using the pictorial keys (Platt and Warwick 1988; Warwick et al. 1998). The trophic types of nematodes were classified by the morphology of buccal cavities (Wieser 1953). For granulometric analysis, sediment samples were first washed with freshwater to remove salt, dried at 60°C for 48 h, and then separated out on mesh sizes of 1,000, 500, 250, 125, and 62 μm .

Statistical analyses

Multivariate and univariate statistical methods were used to discriminate meiofaunal communities and nematode assemblages between seagrass beds and unvegetated sediments. Community structures were examined using classification and ordination methods to test the consistency of the core replicates. Cluster analysis based on the similarity of the Morisita-Horn index (Horn 1966), which was independent of sample size and diversity, was conducted to group the subsamples. The unweighted pair group method with arithmetic mean (UPGMA) was used to construct the dendrograms. Correspondence analysis (CA) was selected as the ordination method for appropriating to species abundance data. Scaling type 1 (Legendre and Legendre 1998) was chosen for preserving the chi-square distances between sites. For meiofauna and nematode assemblages, the abundance data were square root transformed to reduce the skewness before the multivariate analysis. The square root transformation was used to balance between retaining quantitative information and downweighting the dominant taxa.

The randomization technique was used to calculate a sufficient number of replicates for achieving a reasonable estimate of the diversity index in the sampling site (Soetaert and Heip 1990). According to the results of

cluster analysis and CA, if the replicates from identical quadrats were not clustered an obvious group, the abundance data of these replicates were pooled. The numbers of individuals among the core replicates were highly variable, so the mean abundance of meiofauna was chosen as a representative sample size for calculating efficiency. Regarding nematodes, 100 individuals, the most commonly selected number for taxonomic identification, were used to simulate a given sample. All abundance data of seagrass beds were pooled for the randomization simulation by Yeh's computer program (Yeh and Ohta 2002). Pooled data were randomly selected to achieve the predetermined number of sample sizes. The significant differences of ten replicates of the Shannon-Wiener index (H') among every dissimilar sample sizes were examined using the Kruskal-Wallis test. Dunn's test for multiple comparisons was used to determine which values differed significantly if the Kruskal-Wallis test revealed a significant difference.

Results

Environmental and biological variables

The quadrats covered an area 20 m long and 5 m wide, where salinity was approximately 20 PSU during the sampling occurrence at low tide. Sediment grain sizes ($n = 5$) showed peaks around coarse (500 to 1,000 μm) or very coarse (1,000 to 2,000 μm) sand, with the average median grain size $537 \pm 51 \mu\text{m}$ and very few silt (<62 μm) contents (<1%).

A total of 21 meiofaunal taxa were identified in the present study (Table 1). Meiofaunal density in the top 5 cm of sediments varied between 188 and 2,978 individuals 10 cm^{-2} , whereas mean densities showed 1,172 and 1,345 individuals 10 cm^{-2} for vegetated and unvegetated

Table 1 Abundance of higher meiofaunal taxa from seagrass beds and adjacent unvegetated sediments at Shihlang, Ludao

Higher meiofaunal taxa	Seagrass (n = 15)		Unvegetated (n = 5)	
	Mean	SD	Mean	SD
Acari	1.5	2.0	1.3	0.6
Amphipoda	3.2	4.8	0.6	0.3
Bivalvia	0.2	0.8	0.6	0.3
Ciliophora	11.0	11.2	3.8	1.0
Copepoda	160.7	201.6	607.6	82.3
Cnidaria	0.8	1.9	1.3	0.6
Foraminifera			0.6	0.3
Gastropoda			1.3	0.3
Gastrotricha	3.6	4.0	0.6	0.3
Hirudinea	0.2	0.8		
Isopoda	7.4	15.8		
Nauplius	16.6	45.1	138.9	30.6
Nematoda	853.3	731.1	475.8	126.0
Nemertea	1.1	2.0		
Oligochaeta	5.9	8.2		
Ostracoda	5.7	7.1	22.3	4.7
Polychaeta	71.5	97.6	69.4	12.6
Rotifera	0.2	0.8		
Sipuncula	0.4	1.1	0.6	0.3
Turbellaria	28.7	20.5	15.3	4.3
Undetermined egg			4.5	1.0

The mean and standard deviation (SD) of each meiofaunal taxon are shown in individuals per 10 cm².

sites, respectively. Nematoda was the most abundant taxon (72.8%) in the seagrass quadrats, followed by Copepoda (13.7%) and Polychaeta (6.1%). However, Copepoda accounted for 45.2% and dominated the unvegetated site, followed by Nematoda (35.4%), nauplius (10.3%), and Polychaeta (5.2%). The remaining groups represented less than 6% of total meiofauna.

Regarding nematodes, densities within each sample ranged from 51 to 2,682 individuals 10 cm⁻². A total of 63 nematode genera belonging to 20 families were identified from 1,680 individuals (Table 2). Ten genera (6.3% of total) were restricted to unvegetated sediments, and 30 genera (47.6%) solely occurred in seagrass beds. *Daptonema* was the most dominant genus and accounted for similar percentages in both habitats, whereas most genera (44 genera) made poor contributions (<1% of total abundance). Four genera, i.e., *Daptonema*, *Perspiria*, *Robbea*, and *Paralinhomoeus*, contributed 50.2% to the total nematode abundance at seagrass sites, whereas three genera, i.e., *Daptonema*, *Longicyatholaimus*, and *Spirinia*, made a larger contribution to the abundance (60.1%) at the adjacent unvegetated site.

Consistency of core replicates

The univariate analyses cannot detect any significant differences in meiofaunal abundance, nematode abundance, and nematode diversity between seagrass and unvegetated habitats. According to the multivariate analysis, most subsamples were clustered at a high similarity level (>0.80) for higher meiofaunal taxa, whereas replicates of various habitats were undetermined and combined randomly (Figure 2a). For nematode genera, all replicates from the seagrass quadrats were clustered to a single group at a similarity level of 0.51, whereas one unvegetated replicate was highly dissimilar from the others (Figure 2b).

The results of CA were similar to what cluster analysis displayed. For higher meiofaunal taxa, the eigenvalues of the first three axes were 0.207, 0.145, and 0.078 and accounted for 27.7%, 19.5%, and 10.4% of the variation, respectively (Figure 3a). Except for one seagrass replicate (SEC3 in Figure 3a, which possessed rare taxa, i.e., the only rotifer in this study and a sipunculan) in the second quadrant, the other replicates were positioned near the origin and distributed along the first axis. A seagrass replicate (SEB5 in Figure 3a, which possessed the fewest nematodes showing a low nematode/copepod ratio as in the unvegetated samples) and the unvegetated samples were aggregated together. For nematode genera, the eigenvalues of the first three axes were 0.582, 0.287, and 0.254 and accounted for 21.5%, 10.6%, and 9.4% of the variation, respectively (Figure 3b). In addition to one unvegetated replicate (SC4 in Figure 3b, which revealed an extremely distinct generic composition from the other replicates: 71 individuals of *Longicyatholaimus*, 10 of *Mesacanthion*, and 2 rare taxa, *Oxystomina* and *Thalassironus*, only appearing in this sample) in the fourth quadrant, the other replicates were distributed along the second axis. All seagrass replicates were located near the origin and well separated from the replicates of unvegetated sediments. The non-metric multidimensional scaling (MDS) ordination for meiofauna and nematodes (data not shown) both represented a considerable degree of similarity to the results of CA but with a high stress value (0.16).

Cluster analysis and CA revealed that the nematodes showed dissimilar community structures between seagrass beds and unvegetated sediments. Therefore, the randomization test was constructed afterward only according to the seagrass samples.

Randomization test

All of the 15 cores from seagrass quadrats were combined in this analysis. For meiofauna, the mean abundance of the seagrass samples (i.e., 368 individuals) was used to simulate a sample size for the randomization test. The cumulative diversity curve (Figure 4a) flattened from the first sample size ($n = 368$) to the total abundance ($n = 5,521$; $H' = 1.0$), and the Kruskal-Wallis test showed no significant

Table 2 Percentages of nematode genera from seagrass beds and adjacent unvegetated sediments at Shihlang, Ludao

Nematode genus	Family	Trophic type	Seagrass	Unvegetated
<i>Acanthonchus</i>	Cyatholaimidae	2A	0.2	0.0
<i>Alaimella</i>	Leptolaimidae	1A	0.1	0.0
<i>Anticoma</i>	Anticomidae	1A	1.3	0.3
<i>Bathyeurystomina</i>	Enchelidiidae	2B	0.2	0.0
<i>Calyptonema</i>	Enchelidiidae	2B	0.2	0.0
<i>Camacolaimus</i>	Leptolaimidae	2A	0.5	0.0
<i>Chromadorina</i>	Chromadoridae	2A	1.1	0.0
<i>Chromadorita</i>	Chromadoridae	2A	6.1	3.4
<i>Daptonema</i>	Xyalidae	1B	21.2	23.3
<i>Demonema</i>	Selachnematidae	2B	0.3	0.0
<i>Desmodora</i>	Desmodoridae	2A	0.1	0.6
<i>Desmodorella</i>	Desmodoridae	2A	0.0	0.3
<i>Desmolaimus</i>	Linhomoeidae	1B	1.2	0.3
<i>Dichromadora</i>	Chromadoridae	2A	0.0	0.6
<i>Diodontolaimus</i>	Leptolaimidae	2A	1.1	0.0
<i>Elzalia</i>	Xyalidae	1B	0.8	0.3
<i>Epsilonema</i>	Epsilonematidae	1A	1.7	2.0
<i>Eubostrichus</i>	Desmodoridae	1A	0.0	1.1
<i>Eurystomina</i>	Enchelidiidae	2B	0.2	0.3
<i>Filoncholaimus</i>	Oncholaimidae	2B	0.1	0.0
<i>Gammanema</i>	Selachnematidae	2B	0.2	0.3
<i>Graphonema</i>	Chromadoridae	2A	0.0	6.0
<i>Halalaimus</i>	Oxystominidae	1A	0.5	0.0
<i>Halaphanolaimus</i>	Leptolaimidae	1A	0.2	0.0
<i>Halichoanolaimus</i>	Selachnematidae	2B	0.4	0.9
<i>Leptolaimus</i>	Leptolaimidae	1A	0.5	0.0
<i>Longicyatholaimus</i>	Cyatholaimidae	2A	0.0	22.1
<i>Megadesmolaimus</i>	Linhomoeidae	1B	0.5	0.0
<i>Mesacanthion</i>	Thoracostomopsidae	2B	0.1	3.2
<i>Metachromadora</i>	Desmodoridae	2A	4.9	0.9
<i>Metalinhomoeus</i>	Linhomoeidae	1B	3.0	0.0
<i>Meyersia</i>	Oncholaimidae	2B	0.5	0.3
<i>Microlaimus</i>	Microlaimidae	2A	0.2	0.0
<i>Molgolaimus</i>	Desmodoridae	1A	0.9	0.0
<i>Neochromadora</i>	Chromadoridae	2A	2.5	0.0
<i>Odontanticoma</i>	Anticomidae	2A	0.1	0.0
<i>Oncholaimus</i>	Oncholaimidae	2B	2.0	1.4
<i>Oxystomina</i>	Oxystominidae	1A	0.0	0.6
<i>Paracyatholaimus</i>	Cyatholaimidae	2A	0.9	0.0
<i>Paralinhomoeus</i>	Linhomoeidae	1B	7.4	3.4
<i>Perspiria</i>	Desmodoridae	2A	13.4	0.6
<i>Phanoderma</i>	Phanodermatidae	2A	0.2	0.0
<i>Phanodermella</i>	Phanodermatidae	1A	0.2	0.0
<i>Pomponema</i>	Cyatholaimidae	2A	0.6	2.0

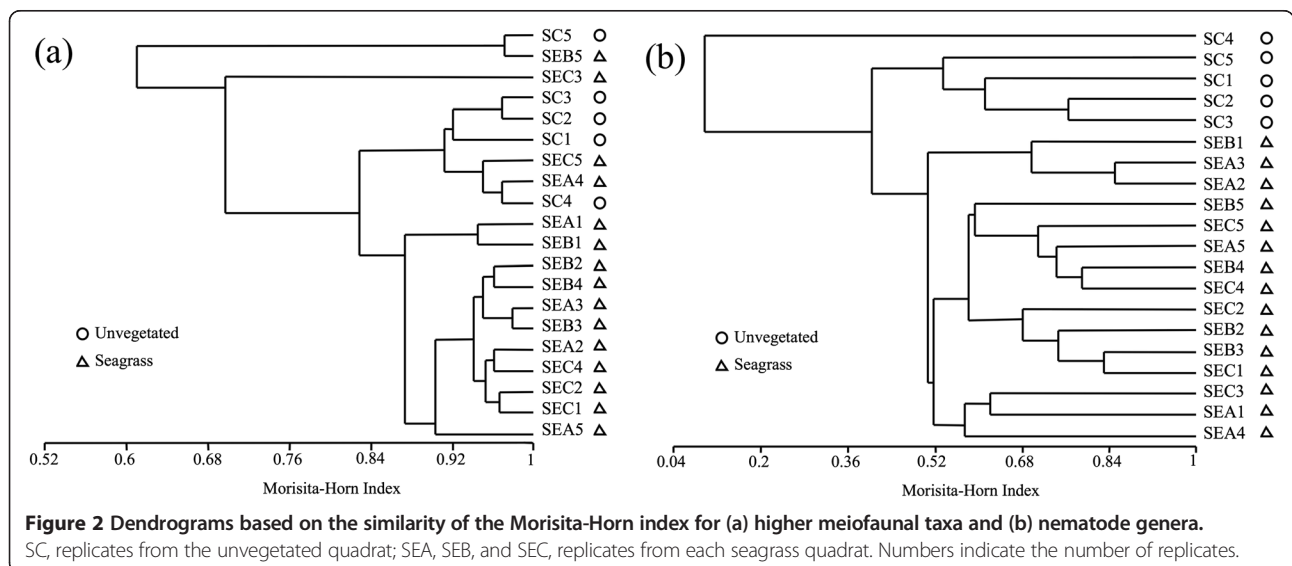
Table 2 Percentages of nematode genera from seagrass beds and adjacent unvegetated sediments at Shihlang, Ludao (Continued)

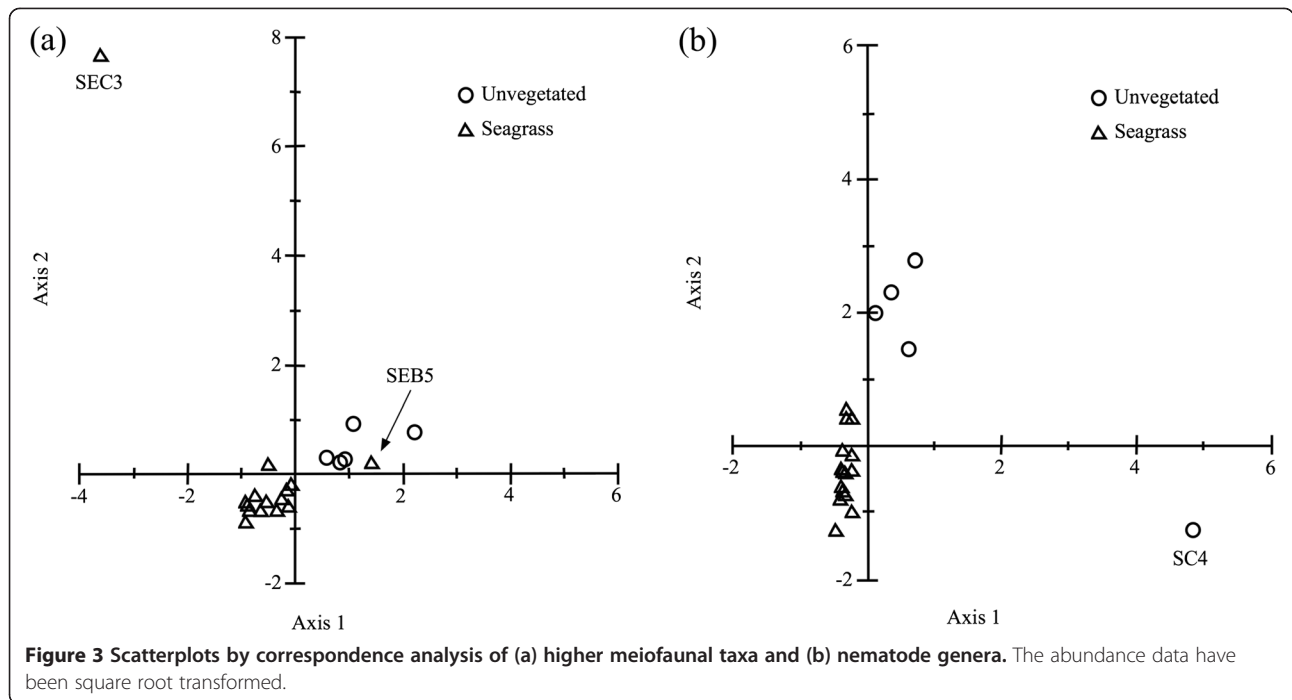
<i>Prochromadorella</i>	Chromadoridae	2A	0.4	0.6
<i>Promonhystera</i>	Xyalidae	1B	0.1	0.0
<i>Pseudocella</i>	Leptosomatidae	2A	0.3	0.0
<i>Pseudochromadora</i>	Desmodoridae	2A	5.9	1.7
<i>Pseudonchus</i>	Desmodoridae	2B	0.0	1.7
<i>Rhinema</i>	Monoposthiidae	2A	0.9	0.0
<i>Robbea</i>	Desmodoridae	1A	8.1	0.6
<i>Spilophorella</i>	Chromadoridae	2A	2.6	4.3
<i>Spirinia</i>	Desmodoridae	2A	0.5	14.7
<i>Steineria</i>	Xyalidae	1B	0.9	0.0
<i>Symplocostoma</i>	Enchelidiidae	2B	0.1	0.0
<i>Symplocostomella</i>	Enchelidiidae	2B	0.1	0.0
<i>Synonchus</i>	Leptosomatidae	2A	0.1	0.0
<i>Thalassironus</i>	Ironidae	2B	0.0	0.9
<i>Thalassomonhystera</i>	Monhysteridae	1A	0.1	0.0
<i>Theristus</i>	Xyalidae	1B	3.2	0.0
<i>Trichotheristus</i>	Xyalidae	1B	0.0	0.3
<i>Vasostoma</i>	Comesomatidae	2A	0.0	0.3
<i>Viscosia</i>	Oncholaimidae	2B	1.7	0.9

The percentages of the ten most dominant nematode genera for both habitats are shown in italics. Trophic type: 1A, selective deposit feeder; 1B, non-selective deposit feeder; 2A, epistrate feeder; 2B, predator or omnivore.

difference among the cumulative sample sizes. For nematodes, 100 individuals, the most commonly selected number for taxonomic identification, were used to simulate a given sample. After the two replicates ($n = 200$) were pooled, the cumulative diversity curve (Figure 4b) flattened to the total number of individuals ($n = 1,332$; $H' = 2.9$). The Kruskal-Wallis test showed a significant difference among various sample sizes ($p < 0.001$). Only

100 and 200 individuals revealed significant differences from the other cumulative sample sizes. The cumulative sample size of 200 nematodes merely shows a significant difference with 1,300 individuals but is indistinguishable from the ultimate sample size ($n = 1,332$) by Dunn's test (Figure 4b). For reliably estimating the local diversity index of nematode genera, a cumulative sample size of at least 300 individuals is recommended.

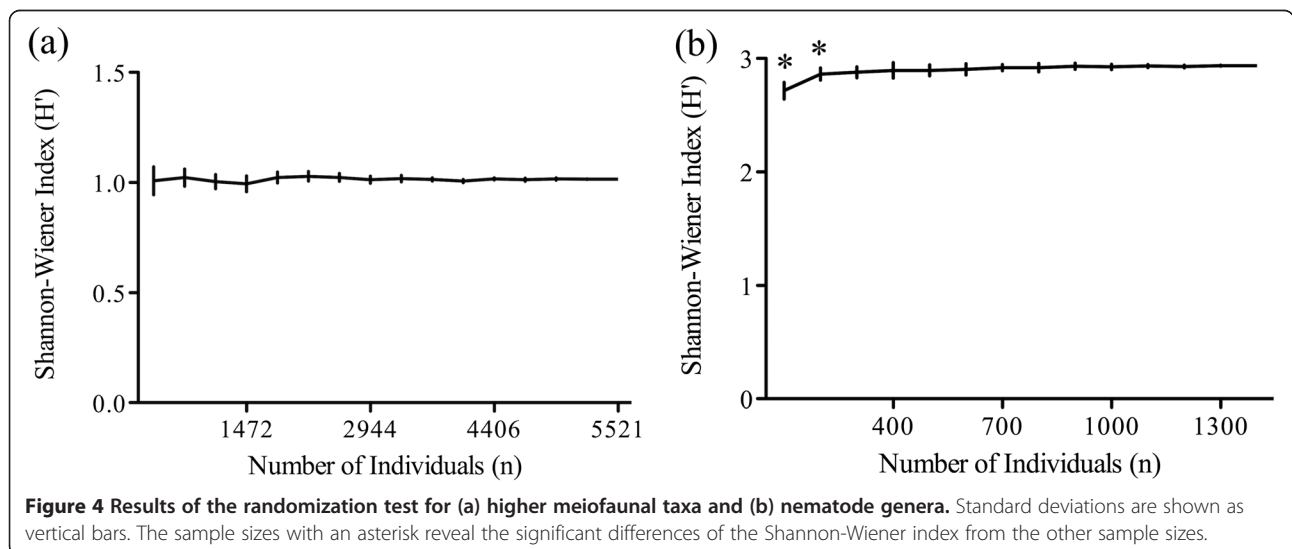




Discussion

According to the multivariate analyses, the nematode abundance and diversity recorded in the seagrass bed being higher than those in the adjacent unvegetated sediments are consistent with previous studies (Castel et al. 1989; Danovaro et al. 2002; Hourston et al. 2005; Monthum and Aryuthaka 2006; Leduc and Probert 2011). However, an unexpected pattern was observed in this study where copepods display a reverse trend to nematodes, i.e., the abundance of copepods inside the seagrass bed is lower than that in the unvegetated area. Most surveys have mentioned that copepod densities are higher in seagrass

beds (e.g., Hicks 1986; Ansari and Parulekar 1994; Ndaro and Ólafsson 1999; De Troch et al. 2001), but a contrary result has also been reported (Leduc and Probert 2011). Shallow seagrass beds may not substantially influence the abundance of copepods as the deeper ones do (De Troch et al. 2001). The abundance of copepods is positively related to the coarser sediments (Coull 1985), whereas sediments underneath seagrass are commonly finer than those of unvegetated areas. In addition, the dense canopies of seagrasses prevent the growth of microphytobenthos, which are the main diet of copepods (Leduc et al. 2009; Leduc and Probert 2011). The epibenthic and interstitial



copepod taxa have distinct environmental demands and stress endurance (Hicks 1986; Giere 2009), so classifying subgroups of copepods may clarify their preference for the microhabitats in seagrass beds.

The seagrass samples bear a rough resemblance in meiofauna as revealed by multivariate analyses but with exceptions. The differences in meiofaunal communities between seagrass beds and adjacent unvegetated sediments may be hardly detectable at a meter scale, and most higher meiofaunal taxa, e.g., copepods and nauplii, have substantially higher dispersal rates than nematodes, which affect their temporary local distribution (Commito and Tita 2002). The active seagrass-associated taxa could forage for foods in peripheral unvegetated sediments but keep close to seagrass beds (Orth et al. 1984). The wave disturbance and salinity changes in the coastal region tend to mitigate small-scale patchiness and local diversity of nematodes (Lambshhead and Boucher 2003). However, the compositions of nematode genera have various arrangements in this study, even at a scale within several meters.

Regarding the trophic types of nematodes, epistrate feeders (2A; trophic type by Wieser 1953) are generally dominant in sandy sediments and non-selective deposit feeders (1B) are highly abundant in muddy regions, whereas a recent study has pointed out that the trophic structure is coupling with the potential food sources rather than the other environmental factors (Danovaro and Gambi 2002). *Daptonema*, which possesses the highest percentage (>20%) in both habitats, dominates wide seagrass habitats, especially in sandy sediments (Ndaro and Ólafsson 1999; Hourston et al. 2005; Fonseca et al. 2011). Although *Daptonema* has been treated as a non-selective deposit feeder, many trophic studies have found that they also feed on diatoms at the surface of sand grains and can be regarded as epistrate feeders (Heip et al. 1985; Moens and Vincx 1997). Comparing with the uniform distribution of *Daptonema*, most epistrate feeders (most members of Chromadoridae and Desmodoridae), which have the highest relative dispersal rate of nematodes (Commito and Tita 2002), show a substantial patchy colonization in this study. Many studies have also stated the dominance of epistrate feeders in seagrass sediments (e.g., Hopper and Meyers 1967; Ndaro and Ólafsson 1999; Danovaro and Gambi 2002; Fonseca et al. 2011). The seagrass samples consisted of 8.1% of *Robbea*, a selective deposit feeder (1A), which is coated with particular ectosymbiotic bacteria and occurred extremely rare (0.6%) in unvegetated sediments. A similar deep-dwelling genus, *Catanema*, also dominates Australian seagrass beds (Fisher 2003; Fisher and Sheaves 2003).

Freshwater input in the sampling site (20 PSU during sampling occurrence) allows salinity-tolerant nematodes, including *Chromadorita*, *Daptonema*, *Metachromadora*,

Metalinhomoeus, *Paralinhomoeus*, *Pomponema*, *Spilophorella*, *Spirinia*, and *Theristus* (Heip et al. 1985), to occur as the dominant genera. The salinity stress drives the abundance of few euryhaline species while rich nutrient supply by seagrass creates a luxuriant microbial food resource, which attracts the rare deposit-feeding nematodes from peripheral sediments (Fisher and Sheaves 2003). Definite differences are present in nematode assemblages between both habitats, and shifts in nematode generic composition have occurred on a meter scale. For Chromadoridae, *Chromadorina* and *Neochromadora* are restricted to seagrass beds, whereas *Dichromadora* and *Graphonema* are restricted to unvegetated sediments. For Desmodoridae, *Robbea*, *Metachromadora*, *Perspiria*, and *Pseudochromadora* are dominant in seagrass beds, whereas *Eubostrichus*, *Pseudonchus*, and *Spirinia* are restricted to or dominant in unvegetated sediments. Various genera of the same family may have distinct preferences for vegetated and unvegetated habitats, or the distribution pattern could be the competitive result in which similar species compete for the plentiful food sources in seagrass sediments. In addition to the chromadorids, desmodorids, and xyalids common to both habitats, linhomoeids (e.g., *Paralinhomoeus* and *Metalinhomoeus*) are obviously occurring in seagrass beds, whereas cyatholaimids (e.g., *Longicyatholaimus*) dominate in unvegetated sediments. Linhomoeids are also restricted to the seagrass beds in Australia, and it has been suggested that they are tolerant to high organic matter content and hypoxia in the sediments underneath seagrasses (Fonseca et al. 2011). *Paralongicyatholaimus*, which resembles *Longicyatholaimus*, is the dominant genus in seagrass beds and adjacent unvegetated area in Thailand (Monthum and Aryuthaka 2006).

Regarding local seagrass beds, only a single core or a cumulative sample size of 368 individuals is sufficient for estimating the diversity of meiofauna, but at least three cores or a cumulative sample size of 300 individuals is needed for nematode diversity. The taxonomic categories (family, genus, or species) obviously influence the requirements of appropriate sample sizes. The Shannon-Wiener index (H'), used as a criterion for the randomization test, is less sample size dependent than Hill's N_1 index (Hill 1973; Soetaert and Heip 1990), but H' has still been applied extensively to compare community diversity and provides an appropriate estimate for a community structure. The diversity of nematodes ($H' = 2.9$), albeit only for genera, is lower than the species diversity in Thailand (3.4 to 3.7; Monthum and Aryuthaka 2006) but resembles the Australian values (2.66 to 3.5; Fisher and Sheaves 2003). The nematode assemblages dominate by a small number of taxa but still show moderate diversity in tropical seagrass beds (Fisher and Sheaves 2003).

At least 300 individuals are recommended for steady estimation of the local diversity of nematode genera.

However, 6 out of 15 of the seagrass samples and 3 out of 5 of the unvegetated samples possess less than 100 individual nematodes in this study. The use of cores with fairly wide diameters (e.g., 3.6 cm) is suggested for achieving reliable quantitative data. A similar result showed that two 10-cm² subsampling cores are required to monitor nematode genus diversity in subtidal stations of the North Sea (Li et al. 1997). Water flows or bioturbated activities improve oxygen penetration in sandy habitats and then induce vertical migration of nematodes to a deeper (beneath 5 cm) sediment layer (Steyaert et al. 2003; Giere 2009). The seagrass bed in Shihlang possesses a large amount of coarse sands, where nematodes tend to distribute more deeply (McLachlan et al. 1977; Heip et al. 1985), and thus, the vertical profile of the nematode community can be clarified by sampling deeper than 5- or 10-cm depths (Steyaert et al. 2003; Leduc and Probert 2011).

Conclusions

The community structure of marine nematode genera distinguishes the seagrass habitats from adjacent unvegetated sediments at a scale within several meters, whereas higher meiofaunal taxa are undetermined according to multivariate analysis. The copepod abundance is unexpectedly higher in peripheral unvegetated habitats than in seagrass beds in the present study. Classifying copepods into epibenthic or interstitial subgroups may elucidate their preference for microhabitats. Regarding nematodes, *Daptonema*, a non-selective deposit feeder, dominates both habitats. *Longicyatholaimus* is abundant and restricted to unvegetated sediments, whereas some genera, e.g., *Perspiria* and *Robbea*, are restricted to dominating in sediments under seagrass. According to randomization analysis, only a single core can reliably estimate meiofaunal diversity, whereas three cores are sufficient to estimate the local diversity of nematodes. Albeit the unvegetated areas may not contain as diverse infauna as vegetated sediments, they could be a matrix habitat and provide corridors between fragmented seagrass patches (Boström et al. 2006). In addition, both habitats compose specific infauna, and the unvegetated site should also be considered in the conservation strategy for seagrass.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

JXL designed and carried out the experiment. JXL and HMY analyzed the data. JXL, HMY, and HKM finalized the manuscript. All authors read and approved the final manuscript.

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Author details

¹Department of Oceanography, National Sun Yat-sen University, Lienhai Road 70, Kaohsiung 80424, Taiwan. ²Coastal and Offshore Resources Research Center, Fisheries Research Institute, Yugang North 3rd Road 6, Kaohsiung 80672, Taiwan.

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