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Macroecological Patterns of Estuarine Nematodes

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Abstract In the present study, we test whether large-scale patterns of estuarine nematodes are predicted by the "everything is everywhere" (EiE) hypothesis or by the moderate endemicity hypothesis (MEH). Specifically, we tested whether nematode genus richness and composition differ among geographical regions, latitudes, and between habitats (estuaries with and without mangroves). The meta-analysis included published data from 43 estuaries around the world. Only the most abundant genera (>1 % of relative abundance) were considered in the analysis. Each estuary was treated as an analytical unit. Results indicated that genus richness did not differ among geographical regions and between habitats, whereas latitude explained 36 % of the variability in genus richness. Genus richness assumed a bimodal pattern with higher values around the equator and in temperate regions. Canonical analysis revealed distinct nematode genus compositions in three main geographical regions and in both habitat types. These results suggest that nematodes are dispersion-limited and influenced by environmental conditions. The main conclusion is that large-scale patterns of estuarine nematodes are better predicted by the MEH, in line with studies of macroorganisms. Moreover, nematode genus turnover decreased with increasing latitude, a pattern already reported for harpacticoid copepods, land birds, vascular plants, mammals, and butterflies.

Keywords Latitudinal species richness pattern · Nematoda · Marine · Estuarine · Meta-analysis

Introduction

Macroecological patterns of microorganisms are a matter of current debate. The "everything is everywhere" (EiE) hypothesis (Baas-Becking 1934) posits that natural selection imposed by environmental and local conditions is more important for the generation of new species and the regulation of microorganism community structure than processes operating at larger scales, such as climate shifts and dispersion limitations (Fenchel and Finlay 2006). Although this hypothesis was primarily applied to ciliates (Finlay and Clarke 1999), it has been extrapolated to all organisms smaller than 2 mm (Fenchel and Finlay 2004). Facts that support this hypothesis are, e.g., the lack of latitudinal trends in local microorganism diversity (Hillebrand and Azovsky 2001; Hillebrand 2004a, b; Curini-Galletti et al. 2012), as well as the absence of biogeographical patterns and the cosmopolitan distribution of several species (Bik et al. 2010; Derycke et al. 2005; Fontaneto et al. 2008). Microorganism characteristics conducive to an EiE distribution pattern are high dispersal rates, high numbers of offspring, high local richness, and small regional turnover (Azovsky 2000; Hillebrand and Azovsky 2001).

By contrast, the moderate endemicity hypothesis (MEH), originally proposed for ciliates (Foissner 2008), predicts that microorganisms follow the same macroecological patterns as macroorganisms. Not all microorganism species are cosmopolitan, and endemicity occurs. Ciliates, for example, comprise much less cosmopolitan than restricted species (Foissner 2006; Azovsky and Mazei 2013). Moreover, the presence of

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latitudinal patterns in species diversity (Procter 1984; Lambshead et al. 2002) and species turnover (Azovsky et al. 2012), the differences in species composition among geographical regions (Fonseca and Soltwedel 2009; Sebastian et al. 2007), and the discovery of cryptic species in previously believed cosmopolitan species (Derycke et al. 2008; Fonseca et al. 2008) support the MEH.

The major cause for the contrasting views is the paucity of large-scale data sets of microorganisms in general (Azovsky and Mazei 2013). In particular, most of the large-scale studies on microscopic metazoans are based on regional data sets (but see Azovsky et al. 2012). So far, debates have mostly focused on large-scale patterns of microbes (Fenchel and Finlay 2004; Foissner et al. 2008; Azovsky and Mazei 2013) and, to a lesser extent, on micrometazoan taxa (Fontaneto 2006; Curini-Galletti et al. 2012). However, in contrast to protists, not all small marine benthic metazoans have dispersion stages, which is an important feature to be considered when studying macroecological processes (Curini-Galletti et al. 2012).

Estuaries have two interesting features that set them apart from other coastal habitats and make them particularly suitable for the study of macroecological patterns of meiofauna. First, they are well-delineated environments, where the freshwater meets the ocean, thereby creating distinct environmental conditions from the surroundings. Second, estuaries around the globe share several environmental characteristics, such as salinity oscillation, river runoff, high content of organic matter, accumulation of fine particles, and low levels of oxygen in the sediment (Elliot and McLusky 2002). These environmental characteristics shape estuarine benthic communities, rendering them different from adjacent marine and freshwater communities (Ferrero et al. 2008). However, estuaries are far from being a homogeneous system. They comprise a variety of complex ecosystems including mangrove forests in the tropics and extensive salt marshes in temperate zones (Elliot and McLusky 2002). Estuarine sediment composition largely depends on the sediment source and water currents (Peterson et al. 1984). Similarly, primary productivity is governed by local factors, such as water depth, nutrient input, and water turbulence (McIntyre and Cullen 1996). Regional differences in, e.g., rainfall regime or the size of the river catchment may also shape estuarine environmental conditions (Hutchings 1999; Cooper 2001, 2002). The question is whether such macroecological differences predominate over local factors in shaping microorganism communities. If so, the MEH is more likely to explain large-scale spatial patterns of microorganisms.

The objective of the present study is to test whether genus richness and composition of estuarine nematodes show macroecological patterns related to latitude, geographical region, and habitat type (i.e., estuaries with and without mangroves). In estuaries, nematodes show high densities (up to 10^6 individuals per square meter) and are represented by dozens of species (Heip et al. 1985). Based on the EiE hypothesis, we would expect to find several cosmopolitan taxa and no clear macroecological pattern across estuaries, i.e., no significant latitudinal trend in richness, no differences in terms of genus composition among geographical regions, and no differences between estuaries with or without mangroves (Fig. 1). Such expectations are plausible given the high selective pressure in estuarine systems through, e.g., salinity oscillations and physical disturbances. By contrast, based on the MEH we would expect macroecological patterns due to restricted regional and latitudinal distribution and limited turnover rates of taxa (Fig. 1). As nematode data at the species level are scarce and the majority of species remains undescribed, we investigated the patterns at the genus level. Studies on nematode community composition at the genus level have revealed macroecological patterns (Fonseca et al. 2010; Vanreusel et al. 2010) and are therefore suitable for comparisons of communities at the global scale.

Methods

We reviewed the literature on estuarine nematodes considering published studies that provide a nematode genus list. Given the limited information usually available in published data sets, the present meta-analysis was done on taxa with relative abundances of >1 %. We based our analyses on genera instead of species because in most ecological studies, nematodes are identified to genus level or assigned a putative rather than a real species name.

In the present meta-analysis, we included a total of 25 studies covering 43 estuaries (ESM Table 1). Europe and Australia were the two best-represented regions with 13 and 11 estuaries, respectively, while the remaining four regions (i.e., Asia, Africa, and North and South America) contained suitable data from less than five estuaries each. The different studies were very heterogeneous in terms of sampling intensity, tidal level, sediment depth, sampling size, and sampling season (ESM Table 1). While some studies presented detailed data from more than one station or sampling period, others only provided an average of the whole data set. To avoid potential bias, we defined each estuary with its average number of genera as an analytical unit. From experimental studies, we considered only the control samples. The average number of genera was used, since this measure has proven to be adequate to describe large-scale patterns of marine nematodes (for a comprehensive discussion, we refer to Boucher and Lambshead 1995; Lambshead et al. 2000).

The 43 selected estuaries were located in six geographical regions (ESM Table 1). Whereas 17 tropical and subtropical estuaries were situated in the proximity of mangrove forests, 24 estuaries at subtropical and temperate latitudes had no mangroves. In a few cases,

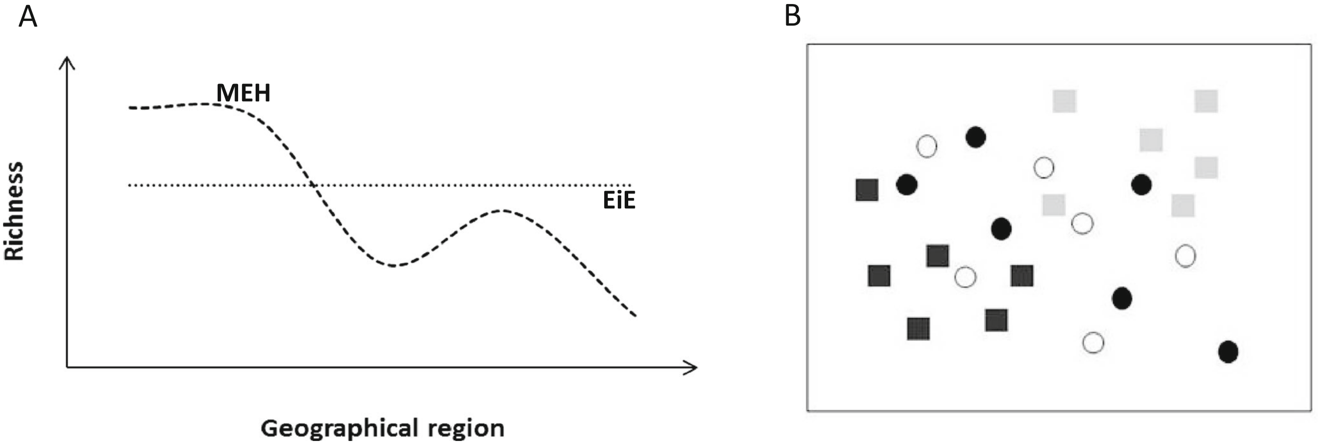

Fig. 1 Conceptual model contrasting the "everything is everywhere" (*EiE*) hypothesis with the "moderate endemicity" hypothesis (*MEH*). **a** Estuarine nematode species richness along geographical regions. *Dotted line* indicates no significant difference in regional species richness due to the cosmopolitan species distribution according to the EiE hypothesis. *Dashed line* indicates differences in regional species richness due to the limited species dispersal according to the MEH. **b** Estuarine nematode species composition from two distant estuaries. *Squares* indicate estuarine nematode assemblages structured according to the MEH (geographically limited distribution); *circles* indicate estuarine nematode communities structured according to the EiE hypothesis (cosmopolitan distribution)

the samples were taken at the mouth of the estuary and were therefore considered as "without mangroves" (Pittwater Port Hacking and Lake Conjola in Australia – Fonseca et al. 2011; Karwar, Mormugao, and Ratnagiri in India – Nanajkar and Ingole 2010; please see ESM Table 1).

To assess differences in the average number of genera between habitats (i.e., estuaries with and without mangroves) and among the six geographical regions, we applied one-way ANOVA tests. Latitudinal trends were investigated using third-order polynomial regressions. The best regression fit was calculated using the least squares estimation procedure applying the Gauss-Newton method. As visualized by a scatter plot, latitudinal genus richness trends were similar in both hemispheres; therefore, and because of the low number of studies per latitude in each hemisphere, we ran the regression analysis on the latitudinal distance of each estuary from the equator, i.e., we pooled the data from the northern and southern hemispheres. ANOVAs and regression analyses were performed with the software Statistica 10.

To assess patterns of nematode genus composition related to (1) habitat, (2) geographical region, and (3) latitude, we applied a canonical analysis of principal coordinates (CAP; Anderson and Robinson 2003; Anderson and Willis 2003) on a Bray-Curtis similarity matrix derived from a presence and absence data set. The significance of the canonical correlation coefficients was tested with a random permutation test (999 permutations). In order to visualize which nematode genera are characteristic of the different groups, we performed a vector overlay on the CAP-chart. Only genera with correlations $r > 0.2$ with at least one CAP-axis were used. Multivariate analyses were done with the software Primer v6 (Clarke and Gorley, 2006) with the add-on package PERMANOVA+ (Anderson et al. 2008).

Results

Genus Richness

A total of 241 genera from 43 estuaries were included in the present study. The five most common genera (i.e., *Theristus*, *Sabatieria*, *Daptonema*, *Terschellingia*, and *Viscosia*) occurred together in 29 estuaries, whereas each of the 81 genera was reported only once. There were no differences in genus richness between habitats (i.e., estuaries with and without mangroves; ANOVA, $F=0.91$, $p=0.347$) or among regions (ANOVA, $F=2.27$, $p=0.118$; Fig. 2). Instead, latitude explained 36 % of the variability in genus richness as shown by the least squares polynomial regression ($F=73.15$, $p<0.001$). Average genus richness per estuary assumed a polynomial pattern of higher richness around the equator and in temperate regions (between 30° and 60°) and lower richness between latitudes 20° and 30° in both hemispheres (Fig. 3a, b).

Genus Composition

There were strong and significant relationships between assemblage structure and the three factors latitude, region, and habitat, as indicated by the canonical correlation ($\delta^2=$

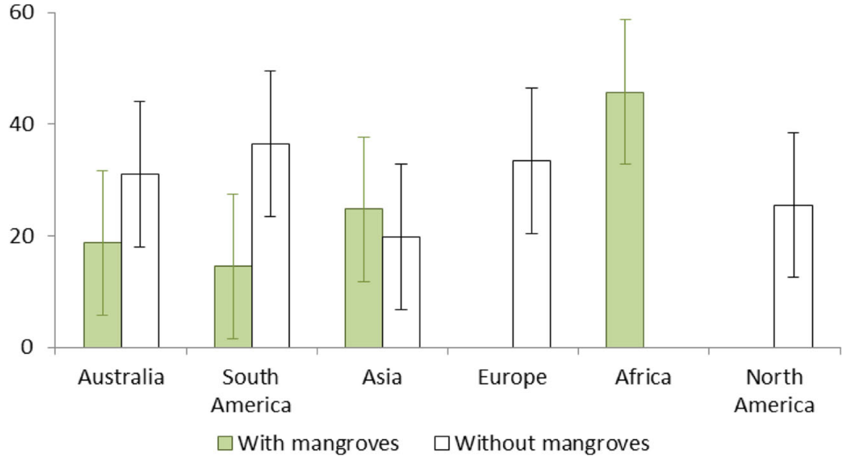

Fig. 2 Average number of nematode genera (*G*) (±95 % confidence intervals) in estuaries with and without mangroves across geographical regions

0.85, $p<0.001$). The first three axes together explained 38 % of the variability in genus composition.

There was a positive relationship with latitude indicating that genus composition changed gradually from the equator to higher latitudes (CAP1 $r=0.92$; Fig. 4a). Moreover, the scattering of the data decreased with increasing latitude, which indicates a decreased turnover in genus composition (Fig. 4a). The analysis also indicated a clear association with geographical region (CAP2 $r=-0.94$; Fig. 4b). The genus composition of the 43 estuaries was distinct among three major geographical regions: (1) Europe and North America; (2) Africa, East Asia, and India; and (3) South America and Australia (Fig. 4b). Finally, nematode assemblages were distinct between habitats (CAP3 $r=0.96$; Fig. 4c). The factors latitude and habitat were partially correlated ($r=0.70$). When removing latitude from the analysis, the model remained largely the same with a slightly lower delta ($\delta^2=0.73$, $p<0.001$) and with a stronger correlation between species composition and habitat than with geographical region. When removing latitude and habitat, the correlation between species composition and geographical region became non-significant ($\delta^2=0.04$; $p=0.20$).

Estuaries at higher latitudes (Fig. 4a) were mainly characterized by four genera: *Axonolaimus*, *Leptolaimus*, *Chromadorita*, and *Hypodontholaimus* as indicated by the superimposed genus vectors on the canonical axes (Fig. 5a). South American and Australian estuaries (Fig. 4a) were characterized by higher frequencies of *Parodontophora*, *Desmodora*, and *Trissonchulus*, whereas African, East Asian, and Indian estuaries (Fig. 4a) were characterized by higher frequencies of *Marylynnia*, *Halalaimus*, and *Paracomesoma* (Fig. 5a). Estuaries with mangroves (Fig. 4c) were characterized by the

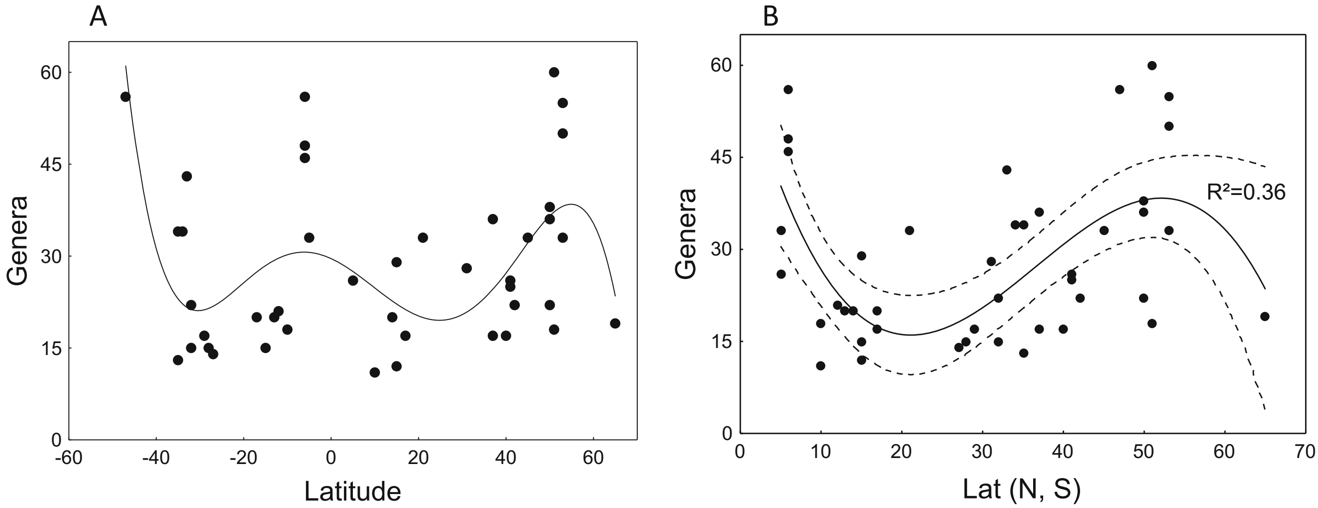

Fig. 3 Number of nematode genera in each estuary plotted against latitude (degrees) considering both hemispheres separately (**a**) and together (**b**). *Solid line* indicates third-order polynomial regression. *Dashed lines* indicate 95 % confidence intervals. Coefficient (R^2) of determination of the regression analysis

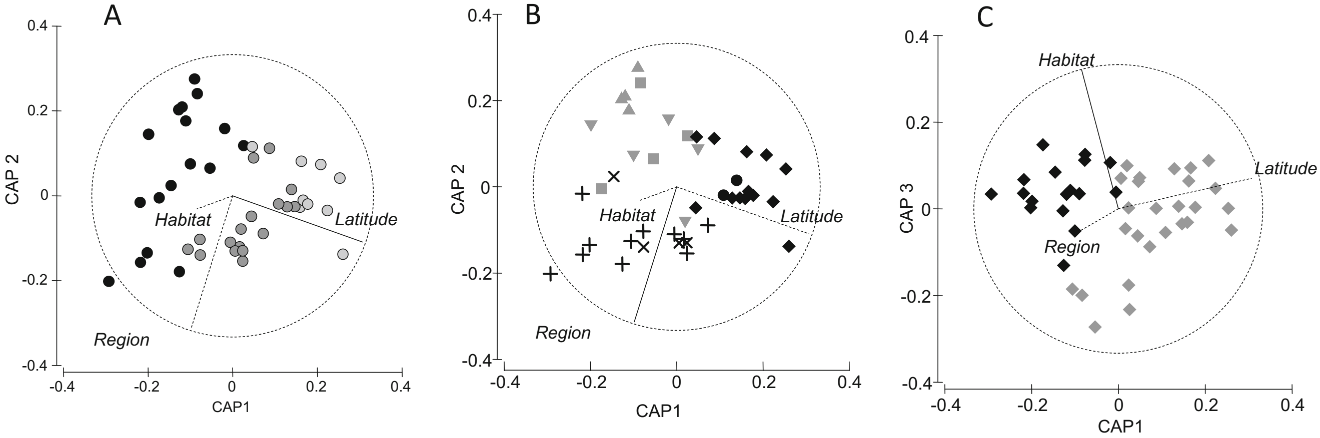

Fig. 4 Scatter plots of the first three axes of the canonical analysis of principal coordinates (*CAP*) which best explained the structure of the estuarine nematode assemblages. **a** First two axes (*CAP1*, *CAP2*) representing the latitudinal gradient. *Black dots* indicate estuaries at tropical latitudes (0° to 27°); *dark gray dots* indicate estuaries at latitudes between 27° and 50°; *light gray dots* indicate estuaries at higher latitudes (>50°). **b** *CAP1* and *CAP2* representing the different geographical regions: *black symbols* indicate European (*diamonds*) and North American (*circles*) estuaries; *crosses* indicate South American (*multiplication signs*) and Australian (*plus signs*) estuaries; *gray symbols* indicate Indian (*squares*), South Asian (*inverted triangles*), and African (*triangles*) estuaries. **c** *CAP1* and *CAP3* representing the habitat (presence and absence of mangroves): *black diamonds* indicate estuaries with mangroves; *gray diamonds* indicate estuaries without mangroves

genera *Parodontophora*, *Desmodora*, *Trissonchulus*, and *Terschellingia* (Fig. 5b).

Discussion

There are at least three lines of evidence rejecting the EiE hypothesis and supporting the MEH for estuarine nematodes. First, there was not a single genus common to all estuaries. The most widespread genera occurred in 29 of 43 estuaries, while one third of all genera (81) appeared only once. Although this has to be interpreted with caution, since our data set only comprised the dominant genera (relative abundance >1 %), it was nevertheless evident that comparable environmental conditions across the globe did not result in the same set of dominant taxa. Second, there was a relation between latitude and both genus richness and composition, and third, there was a significant effect of region and habitat on the structure of nematode assemblages. The 43 estuaries were separated in three main regions: (1) The North Atlantic representing Europe and North America, (2) The Indian Ocean representing Africa, India, and East Asia, and (3) the southern regions representing Australia and South America. These findings indicate that estuarine nematodes may be, to some extent, dispersion limited, which leads to distinct large-scale patterns (Foissner 2008), in contrast to microorganisms, which seem to be rather cosmopolitan (Finlay and Clarke 1999; Fenchel and Finlay 2004, 2006; Fontaneto 2006).

The only evidence supporting the EiE hypothesis is the influence of the presence of mangroves on nematode genus composition. Genus composition in estuaries with mangroves

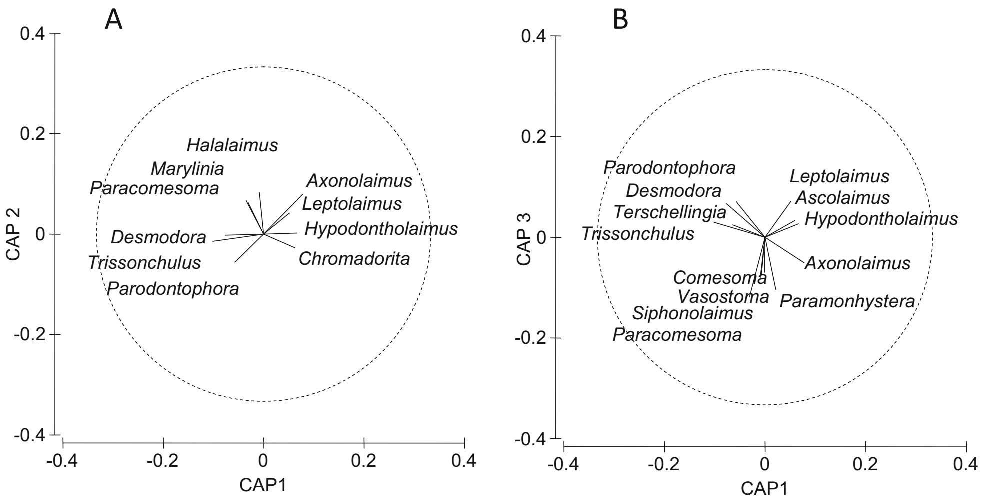

Fig. 5 Superposition of nematode genus frequencies on the first three axes of the canonical analysis of principal coordinates as shown in Figure 4. **a** Characteristic nematode genera over the latitudinal gradient (Fig. 4a) and of the different geographical regions (Fig. 4b). **b** Characteristic nematode genera of habitats with and without mangroves (Fig. 4c)

was significantly different from that in estuaries without mangroves. This result is in line with the idea that habitat type is important in shaping nematode assemblages (Vanreusel et al. 2010). Very little is known about the biology of estuarine nematodes, making it difficult to understand why genus composition differs between estuaries with and without mangroves. The genera that dominated mangrove estuaries belong to different feeding guilds (sensu Moens and Vincx 1997) and taxonomical orders (sensu Hodda 2007), indicating little taxonomical or functional overlap. Differences in root systems and leaf decomposition processes may be key factors shaping the different communities (Alongi 1987).

Each estuary comprised, on average, only approximately one tenth of the total number of genera (241), which indicates a high turnover among estuaries. The turnover of taxa is the result of the relation between habitat heterogeneity and connectivity (Logue et al. 2011), and a high turnover indicates that local diversity is principally shaped by local conditions. This implies that estuarine nematode assemblages were, to some extent, spatially disconnected and exposed to different environmental conditions due to the discrete and variable geological formation of estuaries (Elliot and McLusky 2002). In contrast to our findings, most microorganism species tend to have a cosmopolitan distribution and can be found in any local assemblage (Fenchel and Finlay 2004; Fontaneto et al. 2006; Azovsky and Mazei 2013; Curini-Galletti et al. 2012). Multivariate analyses further indicated that turnover decreased with increasing latitude. Since we merged the data from both hemispheres for the analysis, the observed decrease in turnover with latitude does not reflect a decrease in dispersion with increasing latitude. Instead, the pattern reflects the more heterogeneous environmental conditions. A decrease in species turnover with increasing latitude has been reported for small mammals (Qian et al. 2009), land birds (Koleff et al. 2003, but see Gaston et al. 2007), vascular plants (Qian and Ricklefs 2007), butterflies (Andrew et al. 2012), and harpacticoid copepods (Azovsky et al. 2012). All these studies suggest that habitat complexity may be a major cause for the observed latitudinal trend.

The separation of estuaries based on genus composition in three main geographical regions further supports the idea that estuaries are discrete environments where the faunal composition is dictated by distance, environmental heterogeneity, or both. Our results revealed that more taxa were shared among close estuaries, which is in agreement with the general straightforward effect of distance (Condit et al. 2002). On the other hand, environmental characteristics may be regionally structured (Legendre 1993; Bahn and McGill 2007); therefore, the higher environmental similarity among European estuaries may explain the greater amount of common species compared to estuaries from different (and more distant) geographical regions. While the first hypothesis is based on dispersion limitation, the second is based on the spatial autocorrelation of habitat heterogeneity. These two hypotheses are not mutually exclusive (Cottenie 2005; Chase and Myers 2012) but at the moment our results are insufficient to disentangle them. Interestingly, however, lacustrine nematodes and freshwater ciliates show global patterns similar to those reported here. A meta-analysis covering lakes from 13 countries of four continents (Asia, Africa, America, and Europe) revealed four distinct nematode assemblages, each characteristic of one continent (Fontaneto 2006). European lakes share more lacustrine nematode taxa among each other than with African lakes and vice versa. The global distribution of ciliates has been found to be coherent with the split of the Pangea (Foissner et al. 2008). Taken together, our data provide further evidence for the MEH—both estuarine and lacustrine nematodes are not randomly distributed at large spatial scales.

Nematode genus richness was mainly structured by latitude rather than by region and habitat. The lack of differences among geographical regions and between habitats is probably due to the fact that different regions and habitats are situated at several latitudes and therefore include sites with low and high genus richness. Genus richness of estuarine nematodes assumed a bimodal pattern, with peaks at the equator and around temperate latitudes. Although we did not expect such a pattern based on a previous study (Hillebrand 2004b), it matches that of soil nematodes (Procter 1984; Boag and Yeates 1998) and deep-sea nematodes (Lambshead et al. 2000; Lambshead et al. 2002) remarkably well. A possible cause for this pattern may be the total carbon stock in the sediments. Deep-sea and estuarine sediments as well as terrestrial soils contain more carbon in equatorial and temperate regions compared to subtropical and polar regions. Carbon stock in soils in temperate regions is as high as at the equator, although the latter shows much higher aboveground biomass and productivity (Midgley et al. 2010). In the deep sea, the sedimentary carbon stock is mainly the result of the particulate organic carbon flux (i.e., surface primary productivity and subsequent settlement; Smith et al. 1997). Consequently, equatorial and temperate latitudes feature the highest deep-sea carbon stock values. Data on carbon stock in estuarine systems are relatively scarce. Biomass and productivity of mangrove forests and salt marshes decline with increasing latitude (Ellisson 2002; Kirwan et al. 2009), whereas salt marsh extent is greatest at temperate latitudes (Odum 1988). This oversimplified model evidently needs further support. However, at face value, the amount of available energy in the system seems to dictate the latitudinal pattern of free-living nematodes (Hawkins et al. 2003).

Although terrestrial, lacustrine, estuarine, and deep-sea nematodes show comparable macroecological patterns, the congruence is merely indicative. Similar to other meta-analyses, the current data set suffers from several limitations, namely (1) the great variety in sampling and analytical methodologies applied in the different studies, (2) the limitation to abundant genera, (3) the limited geographical coverage, and (4) the lack of environmental variables. Given all these limitations, the present results need to be interpreted with caution. A larger data set would be needed to test whether the macroecological pattern of species richness observed with our limited data set is supported. Similarly, our study provides evidence that nematode composition at the large scale is better explained by the MEH than by the EiE hypothesis, but the exclusion of rare genera from the analyses inevitably favors the MEH over the EiE hypothesis. Unlike macroorganism inventories, studies on small organisms always face a tradeoff between the number of samples on the one hand and spatial resolution and hence diversity estimation on the other hand (Hewitt 1998). This limitation, combined with the taxonomic problems and the low number of specialists, highlights the need for standard methodologies and data sharing in order to render the discovery of macroecological trends possible. Irrespective of the question which hypothesis is more applicable, the present study highlights an interesting aspect of the EiE hypothesis: in the present study, nematode composition was apparently largely shaped by environmental heterogeneity, which in fact is in line with the EiE hypothesis. Nevertheless, if habitats were spatially structured over different scales, then similar environmental conditions would never occur and "everywhere" would not exist. Unless microorganisms have very little environmental requirements, it is most likely that, just like macroorganisms, nematodes and other microorganisms largely reflect the structured environment they have adapted to.

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