Biogeosciences Discuss., 9, 19019–19052, 2012
www.biogeosciences-discuss.net/9/19019/2012/
doi:10.5194/bgd-9-19019-2012

Biogeosciences
Discussions

Unravelling the environmental drivers of deep-sea nematode biodiversity and its relation with carbon remineralisation along a longitudinal primary productivity gradient

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Received: 29 November 2012 – Accepted: 3 December 2012 – Published: 20 December 2012

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Published by Copernicus Publications on behalf of the European Geosciences Union.

Abstract

Alongside a primary productivity gradient between the Galicia Bank region in the north-east Atlantic and the more oligotrophic eastern Mediterranean basin, we investigated the bathymetric (1200–3000 m) and longitudinal variation in several measures for nematode taxon (Shannon–Wiener genus diversity, expected genus richness and generic evenness) and functional diversity (trophic diversity, diversity of life history strategies, biomass diversity and phylogenetic diversity). Our goals were to establish the form of the relation between diversity and productivity (measured as seafloor particulate organic carbon or POC flux), and to verify the positive and negative effect of sediment particle size diversity (SED) and the seasonality in POC flux (SVI), respectively, as observed for other oceanographic regions and taxa. In addition, we hypothesized that higher taxon diversity is associated with higher functional diversity, which in turn stimulates carbon remineralisation rates by nematode assemblages (determined from biomass-dependent respiration estimates). Taxon diversity showed a positive linear relationship with seafloor POC flux. Both SED (against our expectations) and SVI (as expected) had a negative influence on several nematode diversity indices. We observed a positive linear relation between taxon diversity and carbon remineralisation, but none of the functional diversity indices computed in the present study provided a mechanism through which taxon diversity may promote this ecosystem function. The present results suggest potential repercussions of climate change on deep-sea ecosystem functioning, but further also emphasize the need for a better understanding of nematode functions and their response to evolutionary processes.

1 Introduction

By extrapolating species-accumulation curves from small deep-sea samples to the entire area of deep-sea sediment floor, Grassle and Maciolek (1992) estimated the total number of macrofaunal species in the deep sea to lie between 1 and 10 million.

More recently, the total number of eukaryotic species in the ocean (shallow and deep environments) was approximated at 2.2 million (Mora et al., 2011). Mokievsky and Azovsky (2002) gave an approximation of 10 000–20 000 marine nematode species with the majority inhabiting deep-sea sediments. To date 638 nematode species have been described from deep-sea habitats. This number, however, is a huge underestimate of deep-sea nematode species richness owing to the high resource requirement to obtain samples and describe species (Miljutin et al., 2010). The high diversity in the deep sea is believed to be generated and maintained by the actions of multiple factors that operate on different time (ecological and evolutionary) and spatial (local and regional) scales (Levin et al., 2001). Several theories have been proposed to explain the high diversity in the deep sea, such as the stability-time hypothesis (Sanders, 1968), the spatio-temporal mosaic theory (Grassle, 1989), the intermediate disturbance theory (Connell, 1978), and the dynamic equilibrium model (Huston, 1979).

The biodiversity within deep-sea sediments exhibits clear geographic variation. Potential inter-dependent drivers of regional variation in local diversity include productivity, boundary constraints, sediment heterogeneity, oxygen availability, hydrodynamic regimes and catastrophic physical disturbance (Levin et al., 2001). Gradients in these environmental factors co-determine local diversity by influencing the rates of local processes like resource partitioning, competition, predation, physical disturbance etc. Bathymetric variation in diversity is one of the most studied regional diversity trends (Danovaro et al., 2008b; Rex and Etter, 2010; Tecchio et al., 2011). Benthic diversity generally shows a hump-shaped bathymetric pattern, with a peak around 1500–2500 m depth (Rex and Etter, 2010; Stuart et al., 2003). However, the unimodal diversity-depth curve is not universal and the form of the association varies between regions (Stuart et al., 2003). The depth-related gradient in diversity is believed to be governed by productivity (i.e. the particulate organic carbon (POC) flux) and/or sediment characteristics (Gray, 2002; Stuart et al., 2003). Deep-sea diversity has been documented to vary positively (Glover et al., 2002; Lambshead et al., 2000, 2002), negatively (Gooday et al., 2012) or unimodally (Leduc et al., 2012a; McClain et al., 2012; Tittensor et al., 2011)

with productivity for different taxa and geographic regions. The diversity of sediment particles, which can be regarded as a measure of habitat heterogeneity, has a positive influence on macrofaunal (Etter and Grassle, 1992) and meiofaunal (Leduc et al., 2011) species diversity in the western North Atlantic and in the Pacific Ocean, respectively.

As a consequence of the worldwide ongoing decline in marine and terrestrial biodiversity (Pereira et al., 2010) there has been an explosion in the number of studies addressing the effect of biodiversity on the functioning of ecosystems (reviewed by Balvanera et al., 2006; Hooper et al., 2002; Stachowicz et al., 2007). There are four main possible impact scenarios of biodiversity on an ecosystem function: (1) no effect (null model); (2) all taxa (species/genera) contribute to ecosystem functioning (rivet hypothesis), (3) there is a minimum need of species, and all other species are redundant (redundancy model); (4) the effect is not predictable (idiosyncratic model) (Lawton, 1994; Naeem et al., 1995) According to different authors, the nature and strength of the relation between diversity and an ecosystem function depends on the environmental factors that drive diversity and ecosystem processes (Bengtsson et al., 2002; Cardinale et al., 2000) and the ecosystem function considered (Bolam et al., 2002; Hiddink et al., 2009; Naeem et al., 1995).

Numerous biodiversity-ecosystem function studies related taxon diversity (i.e. the diversity of taxa, with taxa indicating species, genera or other taxonomic levels), and primarily taxon richness (i.e. the number of taxa), to the rate of ecosystem processes, assuming this diversity measure serves as an adequate surrogate for functional diversity (Naeem and Wright, 2003). However, taxa may differ in their contribution to total functional diversity (degree of redundancy and singularity) and/or total abundance (commonness-rarity), resulting in a huge variety in possible relationships between taxon and functional diversity (Cadotte et al., 2011; Naeem and Wright, 2003). Moreover, the nature of the relation between taxon and functional diversity depends on the measure of functional diversity employed (Naeem and Wright, 2003). Analogous to taxon diversity, different aspects of functional diversity can be measured, namely richness, divergence and evenness (Mason et al., 2005). Numerous univariate and multivariate indices have been developed that fall into one of these categories (Weiher, 2011). Because functional diversity provides a direct mechanistic link between diversity and ecosystem functioning, a growing amount of research has been devoted to the effect of functional – instead of taxon – diversity on ecosystem functioning (Díaz and Cabido, 2001; Petchey et al., 2004; Reiss et al., 2009). In many studies where both functional and taxon diversity were related to the rate of ecosystem processes, functional diversity or composition explained a greater portion of ecosystem functioning than traditional measures of taxon diversity (Díaz and Cabido, 2001; Petchey et al., 2004).

Contrary to taxon diversity, phylogenetic diversity entails the evolutionary relationships amongst taxa (Vellend et al., 2010). When it is difficult to identify or measure those properties that are relevant to the ecosystem function under study, phylogenetic diversity may be a useful proxy for functional diversity, since it often encompasses most of the variation in functional traits within a community (Cadotte et al., 2011; Srivastava et al., 2012). The rationale behind this approach is that phylogenetic relatedness usually indicates ecological resemblance, i.e. the more closely related two individuals are, the higher the likelihood that they are functionally similar (but see Gravel et al., 2012; Srivastava et al., 2012). Cadotte et al. (2008, 2009) discovered that phylogenetic diversity was a better predictor of ecosystem functioning than both species and functional group richness.

Moreover, not only individuals belonging to different species may differ in functional characteristics, also considerable intraspecific variability in functional traits is known to occur (Bolnick et al., 2011; Messier et al., 2010). This finding calls for a trait-based instead of a taxon-based approach in examining the effect of diversity on ecosystem functioning.

Deep-sea nematodes are highly diverse (Lambshead and Boucher, 2003), and owing to their omnipresence they can be used to study broad-scale geographic patterns in diversity (Lambshead et al., 2002) as well as the importance of diversity to ecosystem functioning (Danovaro et al., 2008a). Here, we investigated the variation in nematode

taxon and functional diversity along longitudinal (reaching from the Galicia Bank in the northeast Atlantic to the eastern Mediterranean basin) and bathymetric (1200–1900–3000 m) gradients within deep-sea sediments. The first aim of this study was to identify potential environmental drivers (i.e. magnitude and variability in seafloor particulate organic carbon (POC) flux and sediment particle size diversity) of nematode taxon and functional diversity. Specifically, we explored the form of the diversity-productivity curve (unimodal, positive or negative) by characterizing the relationship between nematode diversity and the magnitude of the POC flux to the seabed. For the seasonal variability in seafloor POC flux and sediment particle size diversity we expected a negative and positive influence, respectively, on nematode taxon and functional diversity measures. Our second aim was to determine how nematode diversity relates to ecosystem functioning. Concretely, we presumed that a higher taxon diversity results in a higher functional diversity, which in turn stimulates carbon remineralisation. The rate of carbon remineralisation by the nematode community was assessed by estimating respiration rates from biomass measurements.

2 Materials and methods

2.1 Study region and sampling strategy

Sediment samples were collected at 1200, 1900 and 3000 m water depth along a longitudinal transect spanning the Galicia Bank in the northeast Atlantic and the Mediterranean basin (Fig. 1, Table 1). The regions that were sampled were, from west to east, the Galicia Bank region, and the Algerian, Algero-Provençal, Ionian and Levantine basin in the Mediterranean Sea. Samples comprised either sub-samples from box cores taken with multicorer cores or actual multicorer samples. We used cores with differing surface areas, but standardized subsamples of maximum 100 nematodes per sediment layer were used for diversity analysis (see Sect. 2.3). Sediment cores were sliced horizontally per cm down to 5 cm, and from 5 to 10 cm sediment depth. Next, these sediment sections were fixed in 4 % formaldehyde.

2.2 Environmental variables

Granulometric data were available for the top 5 cm of the sediment, and were averaged over the five sediment depth layers. Sediment particle size diversity (SED) was computed as the Shannon–Wiener diversity index based on the percent dry weight of 10 particle size classes (i.e. < 4, 4–38, 38–63, 63–125, 125–250, 250–500, 500–800, 800–1000, 1000–1600, > 1600 µm) (Etter and Grassle, 1992; Leduc et al., 2011). The seasonal variability in surface primary productivity (SVI) was calculated as the coefficient of variation (i.e. standard deviation divided by the mean) of monthly NPP values (Lutz et al., 2007), which were extracted from the Vertically Generalised Production Model (VGPM; resolution: 1°) (Behrenfeld and Falkowski, 1997) and downloaded from http://www.science.oregonstate.edu/ocean.productivity/. We considered SVI as a proxy for the intermittency with which organic matter is deposited at the deep-sea bed. The VGPM estimate of NPP values was based on satellite measurements of sea surface temperature (SST), surface water chl-*a* concentrations, and photosynthetically active radiation. Data on the particulate organic carbon (POC) flux to the seafloor (abbreviated as POC in the remainder of the text) were approximated on the basis of SVI values following Lutz et al. (2007).

2.3 Nematode diversity

The formaldehyde-fixed sediment samples were washed over a 32-µm mesh sieve and the meiofauna extracted from the sediment by Ludox centrifugation (Heip et al., 1985). From each sediment slice, ±100 nematodes were identified to genus level. Diversity indices were calculated for the top 0–10 cm of each sediment core and hence signify point diversity values. Genus diversity was evaluated as expected genus richness EG(18), Pielou's evenness index (J'), as well as the Shannon–Wiener diversity index

(H', ln), which incorporates both the number of genera and their relative abundances. Functional diversity was assessed using the following metrics:

- On the basis of the morphology of the buccal cavity, nematode genera can be appointed to one of the following four feeding types: selective deposit-feeder (1A), non-selective deposit-feeder (1B), epistrate feeder (2A) and predator/scavenger (2B) (Wieser, 1953). Nematode *trophic diversity* (TD) was computed as the reciprocal of the trophic diversity index given by Heip et al. (1988):

  $$\text{TD} = \frac{1}{\sum_{i=1}^{4} q_i}$$

  with q_i = the relative abundance of feeding type i. Consequently, the value of TD varied between 1 (all individuals belong to the same feeding guild) and 4 (all 4 feeding types comprise the same number of individuals). Since the four feeding guilds were represented in all sediment cores studied, TD could be considered as a measure of trophic evenness (sensu Mason et al., 2005).

- Based on their life history strategies, nematode genera can be assigned a c–p score ranging between 1 (colonisers: short generation time, high reproduction rate and colonisation ability and tolerant towards pollution and disturbance) and 5 (persisters: long life cycle, low reproduction potential, sensitive to disturbance and pollution) (Bongers, 1990). Monhysterid genera were assigned to the c–p 2 class ("general opportunists") as advised by Bongers et al. (1995), and as such there were no nematodes belonging to c–p class 1 ("enrichment opportunists"). We calculated the Shannon–Wiener diversity index based on the partitioning of nematode individuals over these 4 c–p classes, and termed this *c–p diversity*.

- As phylogenetic diversity measures, we calculated average *taxonomic distinctness* based on quantitative (Δ^*) and presence–absence data (Δ^+) (both indicative of average relatedness), as well as the *variation in taxonomic distinctness*

(Λ^+, a measure for the imbalance of the taxonomic tree) (Clarke and Gorley, 2006; Clarke and Warwick, 2001; Warwick and Clarke, 1998). Since Λ^+ indicates functional unevenness, and higher values point to less functionally diverse communities, we used $1/\Lambda^+$ to quantify functional evenness. The two taxonomic distinctness metrics measure functional divergence. We used the following taxonomic levels to calculate these phylogenetic diversity indices: class, subclass, order, suborder, superfamily, family and genus, according to the classification by De Ley et al. (2006), and assumed equal step length.

- Finally, we measured length (L, µm) and width (W, µm) of all nematodes that were mounted on slides for identification purposes to estimate individual wet weight (WW) using Andrassy's (1956) formula, adjusted for the specific gravity of marine nematodes (i.e. $1.13\,\mathrm{g\,cm^{-3}}$; µg WW = $L \times W^2/1\,500\,000$). Individual biomass (B) in terms of $\mu\mathrm{g\,C\,ind^{-1}}$ was then calculated as 12.4 % of WW (Jensen, 1984). Next, we calculated *biomass diversity* (BD) using a Shannon–Wiener diversity expression adapted for continuous variables according to Quintana et al. (2008). The computation was performed in the Diversity08 software available at http://limnolam.org/.

Taxon (genus) and phylogenetic diversity indices were calculated in Primer v6 (Clarke and Gorley, 2006).

In addition to these diversity indices, we computed the *maturity index* (MI) of a nematode assemblage as the weighted average of the individual genus c–p values:

$$\mathrm{MI} = \sum_{i=1}^{n} v(i) f(i)$$

with $v(i)$ = the c–p value of genus i and $f(i)$ = the relative abundance of that genus (Bongers, 1990; Bongers et al., 1991, 1995). Hence, the higher the relative abundance of nematode genera with a high c–p score, the higher the value of MI. This functional response measure gives an idea about how stable the environment is nematodes live in.

2.4 Nematode respiration

Individual nematode respiration rates (R; $\mu\mathrm{g\,C\,ind^{-1}\,d^{-1}}$) were calculated on the basis of individual biomass (B) using the formula of de Bovée and Labat (1993):

$$R = 0.0449 \times B^{0.8554} \times \exp(\ln Q10/10(T-20))$$

with $Q10 = 2$, and T = temperature (°C; measured at the seabed at each site). Nematode community respiration rates ($\mu\mathrm{g\,C\,(10\,cm)^{-2}\,d^{-1}}$) were computed as the product of R with nematode community biomass ($\mu\mathrm{g\,C\,(10\,cm)^{-2}}$).

2.5 Data analysis

Geographic (longitudinal and bathymetric) and environmental trends (relationship with POC, SVI and SED) in nematode diversity, as well as the relationship between diversity and community respiration were evaluated with multiple linear regression. To account for region-specific bathymetric patterns in diversity, we included an interaction term between depth and longitude in our models. In the regression of respiration against diversity, we included nematode community biomass as an independent variable to account for confounding biomass effects on respiration rates. Relationships amongst taxon and functional diversity indices, and between diversity and biomass, were explored with Spearman rank correlations, corrected for multiple testing using the method of Benjamini and Yekutieli (2001). Here we used correlation analysis because we did not assume a relationship of functional dependence between these variables (Zar, 2010).

For the linear regression analysis, partial residual plots were used to examine the linearity of the relationship between the dependent and independent variables (Moya-Laraño and Corcobado, 2008). The other assumptions of linear regression (homogeneity of variances, normally distributed residuals, absence of outliers) were checked visually on the basis of the residual plots (Zuur et al., 2010). Additionally, normality of the residuals and homogeneity of variances were tested using a Shapiro–Wilk test and a non-constant variance score test, respectively. When the variance inflation factors of the independent variables exceeded 5, indicative of multicollinearity, variables were centered (i.e. from each observation the average of the variable was subtracted). When assumptions were not met, either the dependent or one of the independent variables was log-transformed or the quadratic term of an independent variable was added. Models with and without quadratic terms were compared with an anova "lack of fit" test. Our samples were clustered per region (Fig. 1) and thus we checked for spatial autocorrelation which can lead to an increased chance of type I errors (i.e. falsely rejecting the null hypothesis) (Dormann et al., 2007). We conducted global Moran's I tests on the residuals of all linear regression models (Plant, 2012), which showed no significant spatial autocorrelation. Nevertheless, to account for the dependencies between samples collected in the same region, we fitted a linear mixed effects (LME) model with region as a random factor and the aforementioned independent variables as fixed effects to our data. When the likelihood ratio (LL ratio) test indicated that the random region effect was not statistically significant (Pinheiro and Bates, 2000), this term was removed and we proceeded with the linear regression model (LM).

All statistical analyses were conducted in R (R core Team, 2012) with the packages car (linear regression assumption checks; Fox and Weisberg, 2011), spdep (test for spatial autocorrelation; Bivand, 2012), psych (correlation analysis with a correction for multiple testing; Revelle, 2012), and nlme (fit LME models; Pinheiro et al., 2012). Graphs were generated with the ggplot2 package (Wickham, 2009). To visualize significant longitude-depth interactions, we assigned stations to classes of approximate water depth, i.e. 1200, 1900 and 3000 m depth and plotted these as a function of longitude. For the multiple regression models, the isolated effects of independent variables on nematode diversity or respiration were shown using partial regression plots. We

added the means of the raw variables to the residuals displayed on the axes to place these on the same scale as the raw variables (Moya-Laraño and Corcobado, 2008).

3 Results

3.1 Longitudinal and bathymetric patterns in nematode diversity

The phylogenetic diversity indices Δ^*, Δ^+ and $1/\Lambda^+$ and the index of biomass diversity (BD) showed no trend with water depth or longitude. The diversity of life history strategies or c–p diversity (range: 0.92–1.25) declined with depth in the linear regression model (LM; estimate $\pm$SE $= -2.88 \pm 1.23 \times 10^{-5}$, $P < 0.05$), but in the linear mixed effects model (LME) with the statistically significant random region effect (LL ratio = 6.57, $P = 0.01$), this relation became insignificant (LME, estimate $\pm$SE $= -1.75 \pm 1.16 \times 10^{-5}$, $P = 0.14$). For diversity index H', the likelihood ratio (LL ratio) test indicated that the inclusion of the random region effect resulted in a significant improvement of the regression model with depth and squared longitude as independent fixed variables (LL ratio = 19.59, $P < 0.001$). The effect of squared longitude on H' was only marginal in the LME model (estimate $\pm$SE $= -0.0007 \pm 0.0004$, $P = 0.07$). Nevertheless, this index (range: 2.40–3.76) showed a decline along the longitudinal (Fig. 2a) and bathymetric (LME, estimate $\pm$SE $= -0.00024 \pm 0.00003$, $P < 0.001$; Fig. 2b) axis. Expected genus richness EG(18) (10.52–14.10) displayed a hump-shaped pattern with longitude, with a peak between 0 and 10° longitude (LM, longitude: estimate $\pm$SE $= 0.03 \pm 0.01$, $P = 0.01$, squared longitude: estimate $\pm$SE $= -0.0026 \pm 0.0007$, $P < 0.01$; Fig. 2c), and a linear inverse relationship with water depth (LM, estimate $\pm$SE $= 0.0008 \pm 0.0001$, $P < 0.001$; Fig. 2d). Values of Pielou's evenness J' (0.78–0.96; Fig. 2e), trophic diversity TD (2.87–3.71; LM, estimate $\pm$SE $= 0.008 \pm 0.003$, $P < 0.01$ Fig. 2f), and the maturity index MI (2.57–3.06; LM, estimate $\pm$SE $= 0.004 \pm 0.002$, $P < 0.05$; Fig. 2g) increased from west to east. There were no significant interactions between longitude and depth, except for J' (LM, $P < 0.001$). The magnitude of the longitudinal increment in J' depended on water depth, with the smallest rise apparent at the shallowest stations (Fig. 2e).

3.2 Environmental drivers of nematode diversity

Indices Δ^*, Δ^+ and $1/\Lambda^+$, c–p diversity and BD did not relate to seasonal variability in primary productivity (SVI), sediment particle size diversity (SED) or seafloor POC flux (POC). For both H' (LL ratio = 27.61, $P < 0.001$) and J' (LL ratio = 21.98, $P < 0.001$) the region effect was significant. However, in the LME model constructed for J', the effect of SVI became insignificant upon inclusion of the random region effect (estimate ±SE = 0.04±0.17, $P = 0.79$). H' showed a linear positive relationship with the logarithm of seafloor POC flux (LME, estimate ±SE = 2.76 ± 0.20, $P < 0.001$; Fig. 3a), while EG(18) related positively and linearly to untransformed POC (LM, estimate ±SE = 0.33 ± 0.05, $P < 0.001$; Fig. 3c). SED had a negative influence on H' (LME, estimate ±SE = −0.41 ± 0.16, $P < 0.05$; Fig. 3b) and TD (LM, estimate ±SE = −0.52 ± 0.20, $P = 0.01$; Fig. 3e). Both EG(18) (LM, estimate ±SE = −6.00 ± 1.12, $P < 0.001$; Fig. 3d) and MI (LM, estimate ±SE = −0.57 ± 0.20, $P < 0.01$; Fig. 3f) decreased with increasing values of SVI.

3.3 Relationship between nematode taxon and functional diversity

After correcting for multiple testing, expected genus richness EG(18) correlated positively with c–p diversity (Spearman rank, $r = 0.58$, $P < 0.05$; Fig. 4). The other taxon diversity indices did not relate to any of the functional diversity measures.

3.4 Effect of diversity on respiration rates in nematode communities

Logarithmically transformed nematode community biomass showed a positive linear relationship with respiration, and thus for higher biomass values the increase in community respiration rate was less pronounced than for lower values (LM, estimate ±SE = 0.10±0.01, $P < 0.001$; Fig. 5a). Biomass related inversely to J' (Spearman rank,

$r = -0.70$, $P < 0.001$), and positively with H' ($r = 0.54$, $P < 0.05$). After accounting for biomass (by including this variable in the multiple regression models), H' (LM, estimate ±SE = 0.16 ± 0.04, $P < 0.001$), EG(18) (LM, estimate ±SE = 0.06 ± 0.02, $P < 0.001$) and J' (LM, estimate ±SE = 1.82 ± 0.35, $P < 0.001$) had a positive and linear relationship with nematode community respiration rates (Fig. 5b–d). For the regression of respiration against biomass and J', we removed one observation (one of the samples from station GB3000, Table 1) to comply with the assumptions of linear regression. The random effect of region was never statistically significant. None of the functional diversity indices, or the functional response MI, was related significantly to community respiration.

4 Discussion

4.1 Longitudinal and bathymetric patterns in nematode diversity

One of the first steps in unravelling the drivers of biodiversity constitutes the description of broad-scale geographic patterns. Our nematode genus abundance data revealed a slightly nonlinear decrease in Shannon–Wiener diversity (H') with increasing longitude, while expected genus richness (i.e. EG(18)) displayed a unimodal longitudinal trend. The different west-east trends for these two taxon diversity indices may be ascribed to the fact that, in contrast to EG(18), H' is dependent on sample size (Soetaert and Heip, 1990), which declined with longitude. Nevertheless, consistent with our findings for genus Shannon–Wiener diversity, earlier work reported a drop in nematode species diversity between the northeast Atlantic and the southern Adriatic Sea (Danovaro et al., 2009a), as well as alongside the longitudinal axis in the Mediterranean basin (Danovaro et al., 2008b, 2009b, 2010). Furthermore, we detected an eastward incline in nematode generic evenness (J'). This observation does not corroborate with the study of Danovaro et al. (2008b), who found no longitudinal pattern in the evenness of nematode species. Studies on other faunal groups in the deep Mediterranean revealed either comparable diversity in the western, central and eastern Mediterranean (megafauna) (Tecchio et al., 2011), or a decline along the longitudinal axis (foraminiferans) (Danovaro et al., 2010).

The functional diversity index TD and the functional response index MI both increased from west to east. The longitudinal cline in TD was primarily governed by the higher contribution of feeding type 2B (predators/scavengers) to nematode standing stock in the east (Pape et al., 2012). Representatives of this feeding type are generally not opportunistic, and can be classified as either intermediate between opportunists and persisters (c-p score = 3), or as persisters (c-p score = 4–5) (Bongers and Ferris, 1999; Bongers et al., 1991). Consequently, the higher proportion of predators/scavengers within nematode communities in the eastern part of our study area yielded higher MI values which point to the diminished seasonal variability in organic matter input.

We noticed a decline in taxon diversity indices H' and EG(18) with increasing water depth, contrasting with numerous previous reports of a unimodal diversity-depth trend (Menot et al., 2010; Rex and Etter, 2010; Stuart et al., 2003). However, the depth range covered here is fairly narrow (1026–3072 m, Table 1) and diversity may be depressed at shallower depths. In other words, it is possible that our samples fell within the descending section of the unimodal bathymetric diversity curve. Danovaro et al. (2010), who considered a larger depth range than us, discovered a hump-shaped bathymetric trend in nematode species diversity, albeit only in the eastern Mediterranean basin. In contrast, Tselepides et al. (2000) described a decrease in macrofaunal diversity between 40 and 1570 m water depth along the Cretan continental margin. Rex and Etter (2010) speculated that when nutrient loadings become very scarce, as is the case in the Mediterranean, there is a shift from a fully unimodal diversity-depth curve towards just the ascending portion. Alternatively, the absence of a peak in diversity at intermediate water depths may be related to the unusually warm (13 °C) and isothermal water column in the Mediterranean basin (Tyler, 2003). Unimodal diversity-depth trends are generally found in open oceans like the Atlantic and the Pacific

where temperature decreases rapidly (to barely a few degrees) with depth. Opposed to Danovaro et al. (2009a) and Danovaro et al. (2010), bathymetric diversity patterns did not vary between the different regions that were sampled.

Clearly, there were several dissimilarities between the present results and those of Danovaro et al. (2008b) and Danovaro et al. (2010) regarding bathymetric and longitudinal trends in nematode diversity. This divergence may be attributed to the different taxonomic levels (genera and species, respectively) and sediment depth intervals that were investigated (0–10 and 0–1 cm, respectively). For deep-sea nematodes inhabiting the Kenyan continental margin, it has been shown that patterns in genus diversity may differ substantially from species diversity trends (Muthumbi et al., 2011). In contrast, Leduc et al. (2012b) found very comparable environmental trends in species and genus diversity at the continental slope of New Zealand.

4.2 Environmental drivers of nematode diversity

Productivity and its mediation of biological interactions has been proposed as a potential mechanism for the commonly observed unimodal bathymetric and linear latitudinal diversity gradients in deep-sea sediments (Levin et al., 2001; Stuart et al., 2003). The magnitude of seafloor POC flux had a positive impact on nematode taxon diversity, measured as H' and EG(18), consistent with earlier work (Glover et al., 2002; Lambshead et al., 2002). It was shown that seafloor POC flux declines from the northeast Atlantic to the eastern Mediterranean and with depth (Pape et al., 2012), and hence this environmental factor may partly explain the observed bathymetric and longitudinal gradients in taxon diversity (see 4.1). The detection of a positive association between diversity and productivity does not necessarily negate the existence of a hump-shaped productivity–diversity curve. The productivity gradient considered in this study may occupy only the left, ascending limb of the unimodal diversity-productivity curve (Levin et al., 2001). In support, in the Atlantic and the Gulf of Mexico, Menot et al. (2010) found a diversity peak at an organic carbon flux of 10–15 $\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ for several macrofaunal phyla, which is the maximum value of seafloor POC flux observed in our study area.

In the deep sea, the mean and variance of productivity are generally positively related (Rex and Etter, 2010). Along our longitudinal transect, the most westward located Galicia Bank region received the highest and most variable POC input (Pape et al., 2012). Regions with higher seasonal variability in surface productivity displayed lower expected genus richness, in agreement with the research of Corliss et al. (2009) on deep-sea benthic foraminiferans in the north Atlantic. The negative relation implies that a stable food supply is an essential prerequisite for the establishment and maintenance of high biodiversity in deep-sea nematode assemblages. A pulsed nutrient loading may suppress diversity by limiting resource exploitation to certain periods of the year (Rex and Etter, 2010). Additionally, higher seasonality resulted in a reduced maturity index, governed by the increased contribution of colonisers or opportunists to nematode standing stock (Bongers and Ferris, 1999; Bongers et al., 1991). It is believed that these nematodes can cope better with variable environmental conditions such as those induced by pulsed organic matter input. Thus, seasonal variability in sedimentation may be an additional factor driving geographic patterns in taxon diversity and the maturity index of nematode communities.

In contrast to Leduc et al. (2011) (nematode species and genera) and Etter and Grassle (1992) (macrofaunal species), we detected lower instead of higher diversity (measured as H') in areas with increased sediment heterogeneity. However, contrary to the present study which considered ten different grain size classes (see Sect. 2.2), Leduc et al. (2011) used only five sediment grain size classes in his calculation of SED without subdividing the mud fraction ($< 63\,\mu$m) of the sediment. Leduc et al. (2011) found no effect of SED on nematode trophic diversity, whereas we uncovered an inverse relationship between SED and TD. We stress that the trends described here do not imply causal relationships, and that the decrease in nematode diversity with increasing SED may be driven by a confounding, unmeasured environmental factor. Moreover, our SED calculation and that of Etter and Grassle (1992) and Leduc et al. (2011) was based on dry-sieved sediment fractions and it is possible that this

measure of particle diversity is not representative for the in situ size distribution of aggregated sediment particles (Levin et al., 2001; Snelgrove and Butman, 1994).

4.3 Link between nematode taxon and functional diversity

Our results showed that nematode communities with higher taxon diversity were characterized by a greater variety of life history strategies (higher c–p diversity). This finding strongly suggests that higher taxon diversity ensures that important ecosystem processes experience enhanced resistance against environmental fluctuations or resilience following disturbance, evidencing a positive long-term effect of diversity on ecosystem functioning (Loreau, 2000). We found no links between the other taxon and functional diversity measures, and hence the presence of a relationship between taxon and functional diversity depended on the type of functional traits considered. However, the functional diversity indices computed here might not encompass the entire array of functions performed by the nematode community. For instance, the feeding type classification scheme based on buccal morphology (Wieser, 1953) may be too coarse to represent a truthful proxy for resource partitioning. In support, De Mesel et al. (2003) observed that shallow-water nematode species belonging to the same feeding guild had a differential influence on cordgrass decomposition rates. The validity of our results concerning the association between taxon and functional diversity in other oceanographic regions remains to be tested as it is partly determined by the degree of redundancy and singularity within a community, as well as by biogeography and biotic interactions (Hooper et al., 2002; Naeem and Wright, 2003).

4.4 Effect of diversity on respiration rates in nematode communities

The present study demonstrated a positive linear relationship between taxon diversity (H', EG(18) and J') and daily respiration rates for deep-sea nematode communities. The form of the relation indicates that all genera contributed more or less equally to the decomposition and remineralisation of organic matter, which is in line with the rivet hypothesis (Lawton, 1994; Naeem et al., 1995). Contrary to expectations, we found no proof for functional diversity as a mechanistic link between taxon diversity and ecosystem functioning since none of the functional diversity indices employed (including phylogenetic diversity) had a measurable impact on community respiration. A possible explanation for the lack of a significant association between the functional diversity indices and ecosystem functioning is that the functional diversity measures used here are not important for the ecosystem function under study, although they may well be for other functions performed by nematodes. For instance, a nematode community which comprises a wide variety of differently sized individuals (high BD) may create more diversified microburrow networks within the sediment. This type of cryptobioturbation and bioirrigation may in turn stimulate small-scale, yet important biogeochemical processes (Aller and Aller, 1992; Pike et al., 2001). Moreover, as mentioned in Sect. 4.3, the metrics may not adequately represent true functional diversity. Finally, it is possible that environmental conditions (apparently not those investigated here) influencing both functional diversity and respiration rates vary among sites, resulting in an absence of an across-site pattern even when significant biodiversity effects exist within each locale (Cardinale et al., 2000; Hiddink et al., 2009; Loreau, 2000).

Phylogenetic diversity may serve as a proxy for functional diversity when related taxa are functionally similar (Cadotte et al., 2008, 2009). The present study did not demonstrate a significant effect of phylogenetic diversity on community respiration. The lack of a relation between phylogenetic diversity and ecosystem functioning may be because (1) functionally important traits do not have a strong phylogenetic signal (or in other words, closely related taxa do not have similar functional trait values), (2) the signal is reduced because of community assembly, or (3) traits that determine dominance are not important for the function under study (Srivastava et al., 2012). The fact that we failed to uncover a link between taxon and phylogenetic diversity, whereas community respiration was affected positively by taxon diversity, implies that the phylogenetic diversity indices used here do not serve as good surrogates for the diversity of traits important for community respiration.

The different form of the biodiversity-function curve in the present study (linear) and that of Danovaro et al. (2008a) (exponential) is in all probability related to the different measures that were used to define ecosystem functioning (nematode respiration rates vs. prokaryote biomass and production, bacterial organic matter decomposition and total faunal biomass, respectively). As demonstrated for shallow marine and terrestrial systems, different ecosystem processes can respond very dissimilarly to changes in biodiversity (Bolam et al., 2002; Naeem et al., 1995).

Since climate change is already affecting the pattern of POC flux to the deep-sea bottom and will continue to do so (Danovaro et al., 2001; Ruhl et al., 2008; Smith et al., 2008), the links between the magnitude and variability in POC flux and taxon diversity, on the one hand, and between taxon diversity and ecosystem functioning, on the other hand, suggests that this global phenomenon will modify, or already is modifying, the functioning of deep-sea ecosystems.

5 Conclusions

Several of the nematode diversity indices that we calculated displayed significant bathymetric and longitudinal patterns, which may be partly ascribed to variations in the rate and seasonality of organic matter deposition, and in sediment heterogeneity. Accounting for confounding biomass effects, we observed a positive linear relationship between nematode taxon diversity and carbon remineralisation. The fact that none of the indices of functional diversity, including phylogenetic diversity, provided a mechanistic link between taxon diversity and remineralisation rates suggests that these indices did not encompass the entire array of nematode functional traits that are of importance to carbon remineralisation. Our results suggest potential repercussions of climate change on nematode carbon remineralisation rates in the deep sea. In light of the progressive change in global climatic patterns, it is clear that we urgently need to improve our knowledge regarding the functions that nematodes perform within deep-sea sedimentary ecosystems and how these are affected by evolutionary processes.

Acknowledgements. This research received funding through the ESF-EuroDEEP BIOFUN project (FWO project number 3G067007) and the European Commission's Seventh Framework Programme HERMIONE project (grant number 226354), as well as through the FWO project GA00612W. We are indebted to the crew and scientific personnel during expeditions aboard the R/V *Belgica* (Belgica cruise 2008/13b), R/V *Pelagia* (cruises 64PE295-296 and 64PE314), R/V *Urania* (BIOFUN cruise 2008) and *Sarmiento de Gamboa* (BIOFUN 2009 Trans-Mediterranean cruise). Bart Beuselinck and Niels Viaene are thanked for granulometric analyses. We appreciated the help of Niels Viaene in measuring nematode biovolume and extracting the meiofauna, and that of Annick Van Kenhove and Guy De Smet in preparing slides for nematode identification. Last but not least, the authors greatly appreciated the statistical advice provided by Carl Van Gestel.

References

Aller, R. C. and Aller, J. Y.: Meiofauna and solute transport in marine muds, Limnol. Oceanogr., 37, 1018–1033, 1992.

Balvanera, P., Pfisterer, A. B., Buchmann, N., He, J.-S., Nakashizuka, T., Raffaelli, D., and Schmid, B.: Quantifying the evidence for biodiversity effects on ecosystem functioning and services, Ecol. Lett., 9, 1146–1156, 2006.

Behrenfeld, M. J. and Falkowski, P. G.: Photosynthetic rates derived from satellite-based chlorophyll concentration, Limnol. Oceanogr., 42, 1–20, 1997.

Bengtsson, J., Engelhardt, K., Giller, P., Hobbie, S., and Lawrence, D.: Slippin' and slidin' between the scales: the scaling components of biodiversity-ecosystem functioning relations, in: Biodiversity and Ecosystem Functioning: Synthesis and Perspectives, vol. 18, 209–220, 2002.

Benjamini, Y. and Yekutieli, D.: The control of the false discovery rate in multiple testing under dependency, Ann. Statist., 29, 1165–1188, 2001.

Bivand, R.: spdep: spatial dependence: weighting schemes, statistics and models, R package version 0.5-53, 2012.

Bolam, S. G., Fernandes, T. F., and Huxham, M.: Diversity, biomass, and ecosystem processes in the marine benthos, Ecol. Monogr., 72, 599–615, 2002.

Bolnick, D. I., Amarasekare, P., Araújo, M. S., Bürger, R., Levine, J. M., Novak, M., Rudolf, V. H. W., Schreiber, S. J., Urban, M. C., and Vasseur, D. A.: Why intraspecific trait variation matters in community ecology, Trends Ecol. Evol., 26, 183–192, 2011.

Bongers, T.: The maturity index: an ecological measure of environmental disturbance based on nematode species composition, Oecologia, 83, 14–19, 1990.

Bongers, T. and Ferris, H.: Nematode community structure as a bioindicator in environmental monitoring, Trends Ecol. Evol., 14, 224–228, 1999.

Bongers, T., Alkemade, R., and Yeates, G.: Interpretation of disturbance-induced maturity decrease in marine nematode assemblages by means of the maturity index, Mar. Ecol.-Prog. Ser., 76, 135–142, 1991.

Bongers, T., De Goede, R. G. N., Korthals, G. W., and Yeates, G. W.: Proposed changes of c–p classification for nematodes., Russ. J. Nematol., 3, 61–62, 1995.

Cadotte, M. W., Cardinale, B. J., and Oakley, T. H.: Evolutionary history and the effect of biodiversity on plant productivity, P. Natl. Acad. Sci. USA, 105, 17012–17017, 2008.

Cadotte, M. W., Cavender-Bares, J., Tilman, D., and Oakley, T. H.: Using phylogenetic, functional and trait diversity to understand patterns of plant community productivity, Plos One, 4, e5695, doi:10.1371/journal.pone.0005695, 2009.

Cadotte, M. W., Carscadden, K., and Mirotchnick, N.: Beyond species: functional diversity and the maintenance of ecological processes and services, J. Appl. Ecol., 48, 1079–1087, 2011.

Cardinale, B. J., Nelson, K., and Palmer, M. A.: Linking species diversity to the functioning of ecosystems: on the importance of environmental context, Oikos, 91, 175–183, 2000.

Clarke, K. and Gorley, R.: PRIMER v6: User Manual/tutorial, Primer-E Ltd, Plymouth, 2006.

Clarke, K. R. and Warwick, R. M.: A further biodiversity index applicable to species lists: variation in taxonomic distinctness, Mar. Ecol.-Prog. Ser., 216, 265–278, 2001.

Connell, J. H.: Diversity in tropical rain forests and coral reefs, Science, 199, 1302–1310, 1978.

Corliss, B. H., Brown, C. W., Sun, X., and Showers, W. J.: Deep-sea benthic diversity linked to seasonality of pelagic productivity, Deep-Sea Res. Pt. I, 56, 835–841, 2009.

Danovaro, R., Dell'Anno, A., Fabiano, M., Pusceddu, A., and Tselepides, A.: Deep-sea ecosystem response to climate changes: the eastern Mediterranean case study, Trends Ecol. Evol., 16, 505–510, 2001.

Danovaro, R., Gambi, C., Dell'Anno, A., Corinaldesi, C., Fraschetti, S., Vanreusel, A., Vincx, M., and Gooday, A. J.: Exponential decline of deep-sea ecosystem functioning linked to benthic biodiversity loss, Curr. Biol., 18, 1–8, 2008a.

Danovaro, R., Gambi, C., Lampadariou, N., and Tselepides, A.: Deep-sea nematode biodiversity in the Mediterranean basin: testing for longitudinal, bathymetric and energetic gradients, Ecography, 31, 231–244, 2008b.

Danovaro, R., Bianchelli, S., Gambi, C., Mea, M., and Zeppilli, D.: Alpha-, beta-, gamma-, delta- and epsilon-diversity of deep-sea nematodes in canyons and open slopes of Northeast Atlantic and Mediterranean margins, Mar. Ecol.-Prog. Ser., 396, 197–209, 2009a.

Danovaro, R., Canals, M., Gambi, C., Heussner, S., Lampadariou, N., and Vanreusel, A.: Exploring Benthic biodiversity patterns and hotspots on European margin slopes, Oceanography, 22, 16–25, 2009b.

Danovaro, R., Company, J. B., Corinaldesi, C., D'Onghia, G., Galil, B., Gambi, C., Gooday, A. J., Lampadariou, N., Luna, G. M., Morigi, C., Olu, K., Polymenakou, P., Ramirez-Llodra, E., Sabbatini, A., Sardà, F., Sibuet, M., and Tseleipides, A.: Deep-sea biodiversity in the Mediterranean Sea: the known, the unknown, and the unknowable, Plos One, 5, e11832, doi:10.1371/journal.pone.0011832, 2010.

De Bovee, F. and Labat, J.: A simulation model of a deep meiobenthic compartment: a preliminary approach, PSZNI Mar. Ecol., 14, 159–173, 1993.

De Ley, P., Decraemer, W., and Abebe, E.: Introduction: summary of present knowledge and research addressing the ecology and taxonomy of freshwater nematodes, in: Freshwater Nematodes: Ecology and Taxonomy, vol. 1, edited by: Abebe, E., Andrassy, I., and Traunspurger, W., CABI publishing, 2006.

Díaz, S. and Cabido, M.: Vive la différence: plant functional diversity matters to ecosystem processes, Trends Ecol. Evol., 16, 646–655, 2001.

Dormann, C. F., McPherson, J. M., Araújo, B. M., Bivand, R., Bolliger, J., Carl, G., Davies, G. R., Hirzel, A., Jetz, W., Kissling, D. W., Kühn, I., Ohlemüller, R., Peres-Neto, P. R., Reineking, B., Schröder, B., Schurr, F. M., and Wilson, R.: Methods to account for spatial autocorrelation in the analysis of species distributional data: a review, Ecography, 30, 609–628, 2007.

Etter, R. J. and Grassle, J. F.: Patterns of species-diversity in the deep-sea as a function of sediment particle-size diversity, Nature, 360, 576–578, 1992.

Fox, J. and Weisberg, S.: An R Companion to Applied Regression, Sage, 2011.

Glover, A., Smith, C., Paterson, G., Wilson, G., Hawkins, L., and Sheader, M.: Polychaete species diversity in the central Pacific abyss: local and regional patterns, and relationships with productivity, Mar. Ecol.-Prog. Ser., 240, 157–170, 2002.

Gooday, A., Bett, B., Jones, D., and Kitazato, H.: The influence of productivity on abyssal foraminiferal biodiversity, Mar. Biodiv., 1–17, 2012.

Grassle, J. F.: Species diversity in deep-sea communities, Trends Ecol. Evol., 4, 12–15, 1989.

Grassle, J. F. and Maciolek, N.: Deep-sea species richness: regional and local diversity estimates from quantitative bottom samples, Am. Nat., 139, 313–341, 1992.

Gravel, D., Bell, T., Barbera, C., Combe, M., Pommier, T., and Mouquet, N.: Phylogenetic constraints on ecosystem functioning, Nature, 3, 1117, doi:10.1038/ncomms2123, 2012.

Gray, J.: Species richness of marine soft sediments, Mar. Ecol.-Prog. Ser., 244, 285–297, 2002.

Heip, C., Vincx, M., and Vranken, G.: The ecology of marine nematodes, Oceanogr. Mar. Biol., 23, 399–489, 1985.

Heip, C. H. R., Herman, P. M. J., and Soetaert, K.: Data processing, evaluation, and analysis, in: Introduction to the Study of Meiofauna, edited by: Higgins, R. and Thiel, H., Smithsonian Institution Press, Washington and London, 197–231, 1988.

Hiddink, J. G., Wynter Davies, T., Perkins, M., Machairopoulou, M., and Neill, S. P.: Context dependency of relationships between biodiversity and ecosystem functioning is different for multiple ecosystem functions, Oikos, 118, 1892–1900, 2009.

Hooper, D., Solan, M., Symstad, A., Díaz, S., Gessner, M., Buchmann, N., Degrange, V., Grime, P., Hulot, F., and Mermillod-Blondin, F.: Species diversity, functional diversity and ecosystem functioning, in: Biodiversity and Ecosystem Functioning: Syntheses and Perspectives, vol. 17, edited by: Loreau, M., Naeem, S., and Inchausti, P., Oxford University Press, 195–208, 2002.

Huston, M.: A general hypothesis of species diversity, Am. Nat., 81–101, 1979.

Lambshead, P. J. D. and Boucher, G.: Marine nematode deep-sea biodiversity – hyperdiverse or hype?, J. Biogeogr., 30, 475–485, 2003.

Lambshead, P. J. D., Tietjen, J., Ferrero, T., and Jensen, P.: Latitudinal diversity gradients in the deep sea with special reference to North Atlantic nematodes, Mar. Ecol.-Prog. Ser., 194, 159–167, 2000.

Lambshead, P. J. D., Brown, C. J., Ferrero, T. J., Mitchell, N. J., Smith, C. R., Hawkins, L. E., and Tietjen, J.: Latitudinal diversity patterns of deep-sea marine nematodes and organic fluxes: a test from the central equatorial Pacific, Mar. Ecol.-Prog. Ser., 236, 129–135, 2002.

Lawton, J. H.: What do species do in ecosystems?, Oikos, 71, 367–374, 1994.

Leduc, D., Rowden, A. A., Probert, P. K., Pilditch, C. A., Nodder, S. D., Vanreusel, A., Duineveld, G. C. A., and Witbaard, R.: Further evidence for the effect of particle-size diversity on deep-sea benthic biodiversity, Deep-Sea Res. Pt. I, 63, 164–169, 2011.

Leduc, D., Rowden, A. A., Bowden, D. A., Probert, P. K., Pilditch, C. A., and Nodder, S. D.: Unimodal relationship between biomass and species richness of deep-sea nematodes: implications for the link between productivity and diversity, Mar. Ecol.-Prog. Ser., 454, 53–64, 2012a.

Leduc, D., Rowden, A., Bowden, D., Nodder, S., Probert, P., Pilditch, C., Duineveld, G., and Witbaard, R.: Nematode beta diversity on the continental slope of New Zealand: spatial patterns and environmental drivers, Mar. Ecol.-Prog. Ser., 454, 37–52, 2012b.

Levin, L. A., Etter, R. J., Rex, M. A., Gooday, A. J., Smith, C. R., Pineda, J., Stuart, C. T., Hessler, R. R., and Pawson, D.: Environmental influences on regional deep-sea species diversity, Annu. Rev. Ecol. Syst., 32, 51–93, 2001.

Loreau, M.: Biodiversity and ecosystem functioning: recent theoretical advances, Oikos, 91, 3–17, 2000.

Lutz, M. J., Caldeira, K., Dunbar, R. B., and Behrenfeld, M. J.: Seasonal rhythms of net primary production and particulate organic carbon flux to depth describe the efficiency of biological pump in the global ocean, J. Geophys. Res., 112, doi:10.1029/2006JC003706, 2007.

Mason, N. W. H., Mouillot, D., Lee, W. G., and Wilson, J. B.: Functional richness, functional evenness and functional divergence: the primary components of functional diversity, Oikos, 111, 112–118, 2005.

McClain, C. R., Allen, A. P., Tittensor, D. P., and Rex, M. A.: Energetics of life on the deep seafloor, P. Natl. Acad. Sci. USA, 109, 15366–15371, 2012.

Menot, L., Sibuet, M., Carney, R. S., Levin, L. A., Rowe, G. T., Billett, D. S. M., Poore, G., Kitazato, H., Vanreusel, A., Galéron, J., Lavrado, H. P., Sellanes, J., Ingole, B., and Krylova, E.: New perceptions of continental margin biodiversity, in: Life in the World's Oceans, edited by: McIntyre, A. D., Wiley-Blackwell, 79–102, 2010.

De Mesel, I., Derycke, S., Swings, J., Vincx, M., and Moens, T.: Influence of bacterivorous nematodes on the decomposition of cordgrass, J. Exp. Mar. Biol. Ecol., 296, 227–242, 2003.

Messier, J., McGill, B. J., and Lechowicz, M. J.: How do traits vary across ecological scales? A case for trait-based ecology, Ecol. Lett., 13, 838–848, 2010.

Miljutin, D. M., Gad, G., Miljutina, M. M., Mokievsky, V. O., Fonseca-Genevois, V., and Esteves, A. M.: The state of knowledge on deep-sea nematode taxonomy: how many valid species are known down there?, Mar. Biodiv., 1–17, 2010.

Mokievsky, V. and Azovsky, A.: Re-evaluation of species diversity patterns of free-living marine nematodes, Mar. Ecol.-Prog. Ser., 238, 101–108, 2002.

Mora, C., Tittensor, D. P., Adl, S., Simpson, A. G. B., and Worm, B.: How many species are there on Earth and in the ocean?, Plos Biol., 9, e1001127, doi:10.1371/journal.pbio.1001127, 2011.

Moya-Laraño, J. and Corcobado, G.: Plotting partial correlation and regression in ecological studies, Web Ecology, 8, 35–46, 2008.

Muthumbi, A., Vanreusel, A., and Vincx, M.: Taxon-related diversity patterns from the continental shelf to the slope: a case study on nematodes from the Western Indian Ocean, Mar. Ecol.-Evol. Persp., 32, 453–467, 2011.

Naeem, S. and Wright, J. P.: Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem, Ecol. Lett., 6, 567–579, 2003.

Naeem, S., Thompson, L. J., Lawler, S. P., Lawton, J. H., and Woodfin, R. M.: Empirical evidence that declining species diversity may alter the performance of terrestrial ecosystems, Philos. T. Roy. Soc. B, 347, 249–262, 1995.

Pape, E., Jones, D. O. B., Manini, E., Bezerra, T. N., and Vanreusel, A.: Benthic–pelagic coupling: effects on nematode communities along southern European continental margins, Plos One, in review, 2012.

Pereira, H. M., Leadley, P. W., Proença, V., Alkemade, R., Scharlemann, J. P. W., Fernandez-Manjarrés, J. F., Araújo, M. B., Balvanera, P., Biggs, R., Cheung, W. W. L., Chini, L., Cooper, D. H., Gilman, E. L., Guénette, S., Hurtt, G. C., Huntington, H. P., Mace, G. M., Oberdorff, T., Revenga, C., Rodrigues, P., Scholes, R. J., Sumaila, U. R., and Walpole, M.: Scenarios for global biodiversity in the 21st century, Science, 330, 1496–1501, 2010.

Petchey, O. L., Hector, A., and Gaston, K. J.: How do different measures of functional diversity perform?, Ecology, 85, 847–857, 2004.

Pike, J., Bernhard, J. M., Moreton, S. G., and Butler, I. B.: Microbioirrigation of marine sediments in dysoxic environments: Implications for early sediment fabric formation and diagenetic processes, Geology, 29, 923–926, 2001.

Pinheiro, J. and Bates, D.: Mixed-Effects Models in S and S-PLUS, Springer, 2000.

Pinheiro, J., Bates, D., and DebRoy, S.: nlme: Linear and Nonlinear Mixed Effects Models, R package version 3.1-105, 2012.

Plant, R. E.: Spatial Data Analysis in Ecology and Agriculture Using R, CRC Press, 2012.

Quintana, X. D., Brucet, S., Boix, D., López-Flores, R., Gascón, S., Badosa, A., Sala, J., Moreno-Amich, R., and Egozcue, J. J.: A non-parametric method for the measurement of size diversity, with emphasis on data standardisation, Limnol. Oceanogr.-Meth., 6, 75–86, 2008.

R Core Team R: A language and environment for statistical computing, R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, http://www.R-project.org/, 2012.

Reiss, J., Bridle, J. R., Montoya, J. M., and Woodward, G.: Emerging horizons in biodiversity and ecosystem functioning research, Trends Ecol. Evol., 24, 505–514, 2009.

Revelle, W.: psych: procedures for Psychological, Psychometric, and Personality Research, R package version 1.2.8, 2012.

Rex, M. A. and Etter, R. J.: Deep-Sea Biodiversity: Pattern and Scale, Harvard University Press, 2010.

Ruhl, H. A., Ellena, J. A., and Smith, K. L.: Connections between climate, food limitation, and carbon cycling in abyssal sediment communities, P. Natl. Acad. Sci. USA, 105, 17006–17011, 2008.

Sanders, H.: Marine benthic diversity: a comparative study, Am. Nat., 102, 243–282, 1968.

Smith, C. R., De Leo, F. C., Bernardino, A. F., Sweetman, A. K., and Arbizu, P. M.: Abyssal food limitation, ecosystem structure and climate change, Trends Ecol. Evol., 23, 518–528, 2008.

Snelgrove, P. V. R. and Butman, C. A.: Animal sediment relationships revisited – cause versus effect, Oceanogr. Mar. Biol., 32, 111–177, 1994.

Soetaert, K. and Heip, C.: Sample-size dependence of diversity indexes and the determination of sufficient sample size in a high-diversity deep-sea environment, Mar. Ecol.-Prog. Ser., 59, 305–307, 1990.

Srivastava, D. S., Cadotte, M. W., MacDonald, A. A. M., Marushia, R. G., and Mirotchnick, N.: Phylogenetic diversity and the functioning of ecosystems, edited by: Mooers, A., Ecol. Lett., 15, 637–648, 2012.

Stachowicz, J., Bruno, J., and Duffy, J.: Understanding the effects of marine biodiversity on communities and ecosystems, Annu. Rev. Ecol. Syst., 38, 739–766, 2007.

Stuart, C. T., Rex, M., and Etter, R. J.: Large-scale spatial and temporal patterns of deep-sea benthic species diversity, in: Ecosystems of the Deep Oceans, edited by: Tyler, P., 295–311, 2003.

Tecchio, S., Ramirez-Llodra, E., Sarda, F., Company, J. B., Palomera, I., Mecho, A., Pedrosa-Pamies, R., and Sanchez-Vidal, A.: Drivers of deep Mediterranean megabenthos communities along longitudinal and bathymetric gradients, Mar. Ecol.-Prog. Ser., 439, 181–219, 2011.

Tittensor, D. P., Rex, M. A., Stuart, C. T., McClain, C. R., and Smith, C. R.: Species–energy relationships in deep-sea molluscs, Biol. Lett., doi:10.1098/rsbl.2010.1174, 2011.

Tselepides, A., Papadopoulou, K.-N., Podaras, D., Plaiti, W., and Koutsoubas, D.: Macrobenthic community structure over the continental margin of Crete (South Aegean Sea, NE Mediterranean), Prog. Oceanogr., 46, 401–428, 2000.

Tyler, P. A.: The peripheral deep seas, in: Ecosystems of the World, edited by: Tyler, P. A., Elsevier, Amsterdam, 261–293, 2003.

Vellend, M., Cornwell, W., Magnuson-Ford, K., and Mooers, A. Ø.: Measuring phylogenetic biodiversity, in: Biological Diversity: Frontiers in Measurement and Assessment, vol. 14, Oxford University Press, Oxford, UK, 2010.

Warwick, R. M. and Clarke, K. R.: Taxonomic distinctness and environmental assessment, J. Appl. Ecol., 35, 532–543, 1998.

Weiher, E.: A primer of trait and functional diversity, in: Biological Diversity: Frontiers in Measurement and Assessment, vol. 13, edited by: Magurran, A. and McGill, B., Oxford University Press, Oxford, 175–193, 2011.

Wickham, H.: ggplot2: Elegant Graphics for Data Analysis, Springer, New York, 2009.

Wieser, W.: Die Beziehung zwischen Mundhöhlengestalt, Ernährungsweise und Vorkommen bei freilebenden marinen Nematoden. Eine ökologisch-morphologische Studie, Ark. Zool., 4, 439–483, 1953.

Zar, J. H.: Biostatistical Analysis, 5th edn., Prentice Hall, New Jersey, 2010.

Zuur, A. F., Ieno, E. N., and Elphick, C. S.: A protocol for data exploration to avoid common statistical problems, Meth. Ecol. Evol., 1, 3–14, 2010.

Table 1. Sampling details. Indicated are the region where samples were collected in (GB: Galicia Bank region, A: Algerian basin, AP: Algero-Provençal basin, I: Ionian basin and L: Levantine basin), station code (representing region and approximate water depth), latitude and longitude (in decimal degrees; where rounded coordinates of replicates differed, a range is given), range of water depths over replicates, number of replicate samples, surface area of the core, and the research vessel (R/V) aboard which samples were taken (SDG: *Sarmiento de Gamboa*).

Region	Period	Station	Lat	Long	Depth (m)	Nr of replicates	Core area (cm^2)	R/V
GB	Jun 2008	GB1200	42.9	−11.8	1139–1141	3	78.54	*Belgica*
GB	Oct 2008	GB1900	42.4–42.5	−10.7	1770–1896	3	70.88	*Pelagia*
GB	Oct 2008	GB3000	41.7	−10.7	3066–3072	3	70.88	*Pelagia*
A	Jun 2009	A1200	38.4	1.8	1211–1214	3	69.40	*SDG*
A	Jun 2009	A1900	38.0	1.9	2004, 2016	2	69.40	*SDG*
AP	Nov 2009	AP1900	39.4	4.3	1582	3	56.45	*Pelagia*
AP	Jun 2009	AP3000	38.7	5.5–5.7	2841–2846	3	69.40	*SDG*
I	Jun 2008	I3000	34.9–35.1	20.5–20.8	2770–2807	7	10.18	*Urania*
L	Jun 2008	L1200	35.0	24.6	1026–1143	3	10.18	*Urania*
L	Jun 2008	L3000	34.9	24.5	2647	1	10.18	*Urania*

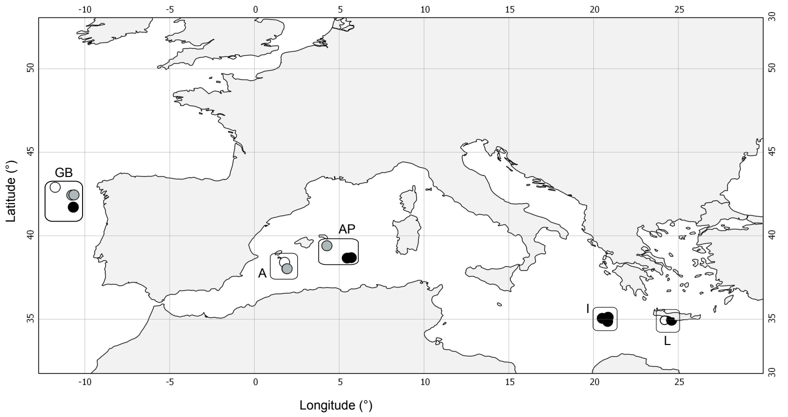

Fig. 1. Map with sampling locations. Colours indicate approximate water depth (white: 1200 m, grey: 1900 m, black: 3000 m). The rectangles enclose samples that were collected within the same region (GB: Galicia Bank region, A: Algerian basin, AP: Algero-Provençal basin, I: Ionian basin and L: Levantine basin).

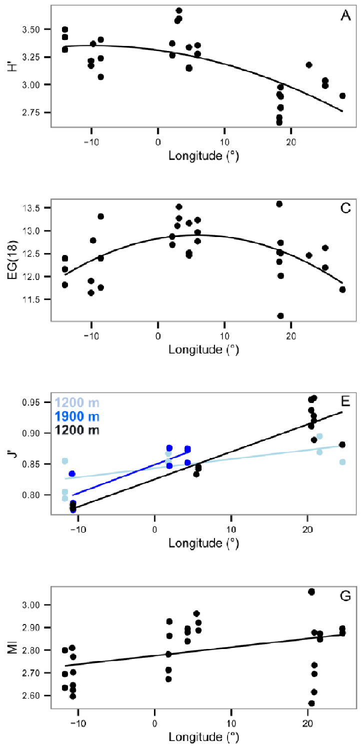

Fig. 2. Bathymetric and longitudinal trends in nematode diversity. For *H'* and EG(18) which related to depth and longitude, partial regression plots were constructed to show the isolated effects of these variables. *H'*: Shannon-Wiener diversity, EG(18): expected genus richness for a sample of 18 individuals, *J'*, TD: trophic diversity, MI: maturity index.

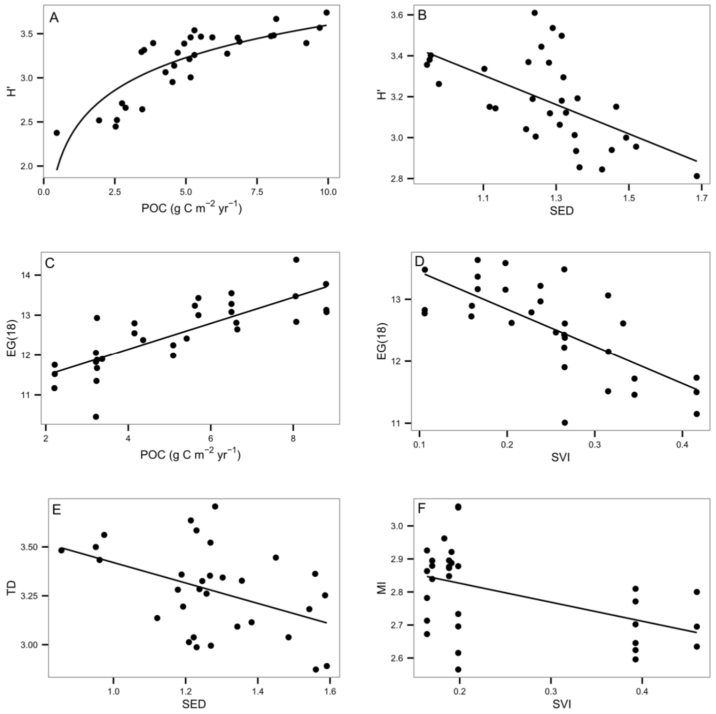

Fig. 3. Environmental drivers of nematode diversity. For *H'* and EG(18) which related with two environmental variables, partial regression plots were constructed to show the isolated effects of these variables. *H'*: Shannon–Wiener diversity, EG(18): expected genus richness for a sample of 18 individuals, *J'*: Pielou's evenness index, TD: trophic diversity, MI: maturity index, POC: seafloor POC flux, SVI: seasonal variability in primary productivity, SED: sediment particle size diversity.

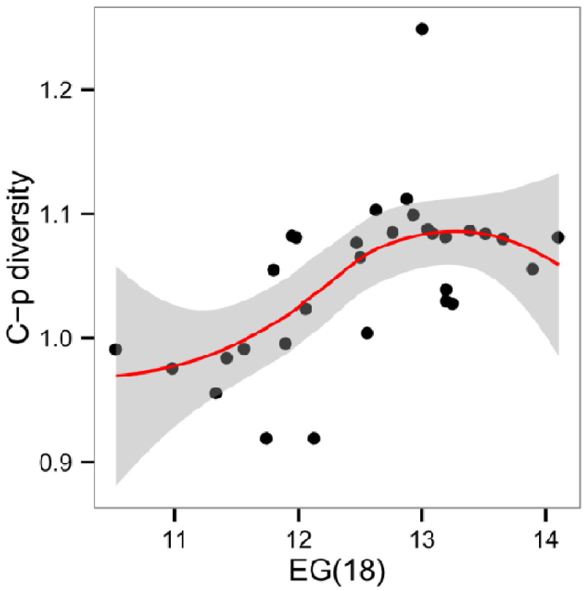

Fig. 4. Significant Spearman rank correlation between taxon diversity (EG(18)) and functional diversity (c–p diversity) of nematodes. The red line and associated grey zone represents a LOESS smoother and the 95 % confidence interval, respectively. EG(18): expected genus richness for a sample of 18 individuals, c–p diversity: diversity of c–p (life history) classes.

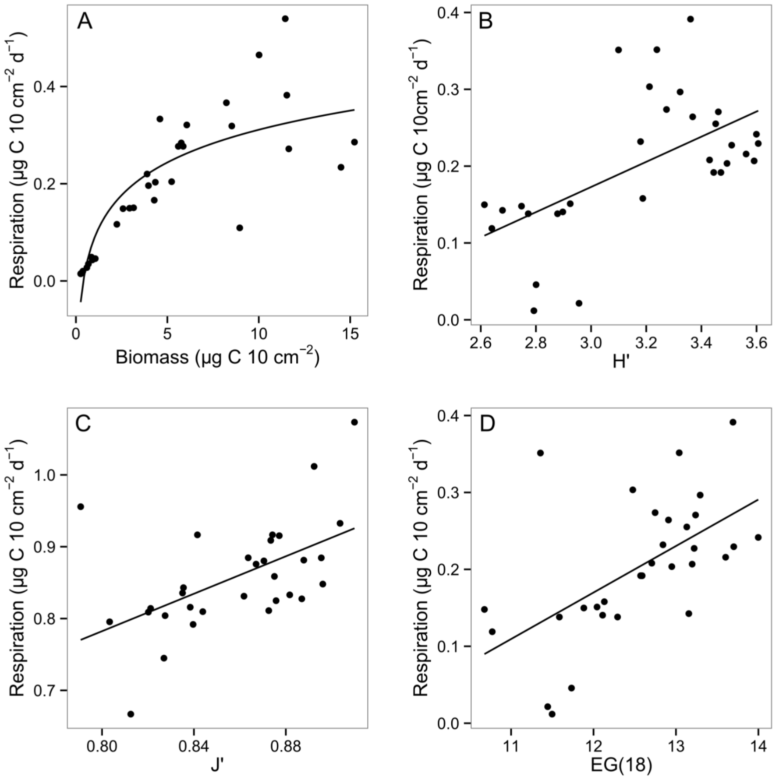

Fig. 5. Relationship between **(A)** biomass and respiration and **(B–D)** between diversity and respiration of nematode communities. *H′*: Shannon-Wiener diversity index, *J′*: Pielou's evenness index, EG(18): expected genus richness for a sample of 18 individuals.