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Biodiversity–ecosystem functioning relationships in long-term time series and palaeoecological records: deep sea as a test bed

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The link between biodiversity and ecosystem functioning (BEF) over long temporal scales is poorly understood. Here, we investigate biological monitoring and palaeoecological records on decadal, centennial and millennial time scales from a BEF framework by using deep sea, soft-sediment environments as a test bed. Results generally show positive BEF relationships, in agreement with BEF studies based on present-day spatial analyses and short-term manipulative experiments. However, the deep-sea BEF relationship is much noisier across longer time scales compared with modern observational studies. We also demonstrate with palaeoecological time-series data that a larger species pool does not enhance ecosystem stability through time, whereas higher abundance as an indicator of higher ecosystem functioning may enhance ecosystem stability. These results suggest that BEF relationships are potentially time scale-dependent. Environmental impacts on biodiversity and ecosystem functioning may be much stronger than biodiversity impacts on ecosystem functioning at long, decadal–millennial, time scales. Longer time scale perspectives, including palaeoecological and ecosystem monitoring data, are critical for predicting future BEF relationships on a rapidly changing planet.

1. Introduction

The relationship between biodiversity and ecosystem functioning (BEF) [1] has been a central topic of ecology since the 1990s [2,3]. A priority for ecosystem-based management, particularly in the context of global climate change and environmental degradation, is to understand how changes in species number and composition influence ecosystem functioning. Our understanding of various aspects of BEF relationships remains insufficient (see ref. [1] and other chapters [4–14] of this special volume), especially in marine systems, in spite of the growing body of information from experimental manipulations, modelling and observations.

Long-term BEF relationships relevant to the time scales of human-induced global climate change (e.g. decadal, centennial and millennial time scales) are a crucial but understudied field. Many BEF studies are based on short-term manipulative experiments and/or static spatial data [15–19]. Recent studies indicated

that BEF relationships change over time, and short-term experiments reveal only a subset of potential BEF mechanisms and may therefore be inadequate for understanding long-term changes [4,16,20,21]. However, continuing long-term ecological monitoring is logistically challenging (e.g. funding, staffing, researcher's career span), and it is difficult to obtain observational data spanning even decadal time scales, which is still exceedingly short compared with the pertinent time scales.

BEF relationships in fossil records are almost completely unexplored [22,23]. For example, BEF relationships during past biotic crises (e.g. mass extinction events) are not well understood (but see refs [9,24–26]). Palaeoecological records from microfossils can be a primary toolkit for understanding long-term (e.g. longer than several decades) changes in BEF relationships. Microfossils are microscopic organisms with high fossilization potential, such as ostracode and foraminifera [27]. These organisms are highly useful for palaeoecological reconstructions because of their high abundance, large spatial and temporal coverage, and good taxonomic and temporal resolution [27]. Microfossil records from the deep sea are particularly ideal because of the relatively continuous sedimentation and the potential for excellent preservation. Importantly, several exceptionally long-term biological monitoring datasets do exist for the deep sea, and provide a key opportunity to connect BEF relationships across disparate time scales [28–30].

Increasing attention is being placed on fossil records to reflect ecological signals [27,31–33], and on integration across ecological and palaeoecological sciences [27,34]. Decadal to millennial time scales are a blind spot between ecological and palaeoecological investigations, as they are longer than biological monitoring studies and are shorter than typical fossil records [35,36]. Critically, these time scales are exactly relevant to the immediate risks of anthropogenic climate change and the progression of climate-driven ecological disturbance. Therefore, it is timely to revisit exceptionally highly resolved fossil records from the BEF perspective to investigate how biodiversity has affected ecosystem functioning, and compare them with exceptionally long biological monitoring records.

Here, we use, for the first time in deep sea, palaeoecological and long-term monitoring data to investigate BEF relationships across decadal–millennial time scales. This investigation is structured to evaluate a suite of BEF questions, including: (i) are BEF relationships consistent between long-term studies and short-term manipulative experiments or spatial studies [2,3]?; (ii) does the relative importance of biotic (i.e. biodiversity) and abiotic (environmental) impacts on ecosystem functioning vary depending on time scales?; (iii) do richness and evenness affect ecosystem functioning differently over a long time scale?; and (iv) do higher ecosystem function or higher gamma diversity (or larger species pool over the long term) enhance the stability of biological communities?

2. Methods

Here, we investigated BEF relationships by using deep-sea nematode time-series and ostracode palaeoecological data. We used biomass, biovolume and abundance as proxies of ecosystem functioning. Alpha species diversity (as Hill numbers, see §2b) and functional diversity were calculated. First and second axes of multi-dimensional scaling (MDS) were considered as primal signals of faunal composition. Biodiversity measures (both alpha species diversity and functional diversity) were compared with ecosystem functioning proxies to investigate BEF relationships. In addition, biodiversity measures were compared with faunal composition to see if high- or low-diversity communities show some structural similarity (e.g. whether biodiversity correlates with MDS axis 1). Time window analyses were performed to evaluate possible impacts of regional species pool and ecosystem functioning on ecosystem stability over the long term. Detailed methodology is described below.

(a) Dataset

We used two census datasets, including deep-sea nematode long-term monitoring data (1989–1998) from the Mediterranean Sea [28] and deep-sea ostracode palaeoecological data for the last 20 000 years from the North Atlantic Ocean [36].

For both nematode and ostracode analyses, we used raw census data. The high abundances of nematode and ostracode (in a small amount of sediment sample) are particularly well suited for quantitative diversity analyses. In the Mediterranean Sea, approximately 10 years of complete census and biomass datasets of meiobenthic nematodes are available [28], and this archive represents one of the longest biological time-series datasets available from the deep sea. Clear diversity–temperature relationships are described in this dataset [28], but BEF relationships are yet to be explored. In deep time, one of the best deep-sea palaeoecological datasets regarding time resolution and continuity of sedimentary record is available from Core 23GGC (61.67705° N, 21.738° W, 1695 m water depth) for the last 20 000 years, sampled at a 1 cm resolution, with an average sedimentation rate of approximately 26 cm kyr^{-1} [36]. This decadal–centennial scale ostracode record also indicates a diversity–temperature relationship [36]; however, BEF relationships are undescribed.

(b) Alpha species diversity indices of Hill number

We used Hill numbers [37], or the effective numbers of species, for species diversity. The Hill numbers, for $q \neq 1$, are defined as ${}^{q}D = \left(\sum_{i=1}^{S} p_i^q\right)^{1/(1-q)}$, where S is the number of species in a sample, and the ith species has relative abundance p_i. Three widely used Hill numbers, i.e. species richness ($q = 0$), exponential of Shannon diversity (q tends to 1; indicated as $q = 1$ thereafter) and inverse of Simpson diversity ($q = 2$), were calculated from the species abundance data. The order q in Hill numbers controls the index sensitivity to species relative abundance and thus a larger q gives more weight to common species (i.e. diversity considering only common species or evenness), and $q = 0$ gives equal weights to all species (i.e. species richness).

In order to standardize the sampling efforts, the Hill numbers were computed from m randomly selected individuals using individual-based sampling curves. The parameter m is thus limited to the minimum abundance among samples (the numbers of individual can be selected) when a traditional rarefaction method is used, which can lead to biased estimates of diversities (i.e. overestimating in depauperate but underestimating in abundant samples). Here, we adapted an interpolation (i.e. rarefaction) and extrapolation method developed by Chao *et al.* [27] to overcome this problem, so that when m was less than or equal to observed abundance, Hill numbers were extracted from the interpolated (i.e. rarefied) sampling curve. When m was greater than observed abundance, Hill numbers were extracted by extrapolating the sampling curves. Here the m selected was higher for nematodes ($m = 100$, 200 and 300 resampled individuals) than for ostracodes ($m = 10$, 50 and 100 resampled individuals), because the nematodes had higher abundance. The use of different levels of m was to ensure that diversity patterns were consistent across sample sizes (m) composed of different proportions of interpolated and extrapolated Hill numbers. Sampling curves for Hill numbers are shown in electronic supplementary material, figures S1 and S2 for nematode and ostracode datasets, respectively. Time series plots for Hill numbers are shown in electronic supplementary

material, figures S3 and S4 for nematode and ostracode datasets, respectively.

(c) Functional diversity

Functional diversity indices of the communities were determined from nematode and ostracode data. For nematodes, we used family richness as a proxy of functional diversity [38]. This approach captures phylogenetic diversity that is closely correlated to trophic diversity, a commonly used index of functional diversity in marine nematodes [38,39].

For ostracodes, functional traits and morphological traits that probably reflect function were used in the trait matrix for functional diversity calculations shown in electronic supplementary material, table S1. Most species (84 out of 91 species) were successfully coded and used in this study. Functional diversity measures included: functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), functional dispersion (FDis) [40] and Rao's quadratic entropy (RaoQ) [41]. Indices could not be calculated in some cases. For example, FEve, FRic and FDiv could not be calculated for communities with less than three functionally singular species; FDis equals 0 in communities with only one functionally singular species.

(d) Ecosystem functioning

Nematode biomass and ostracode abundance and biovolume (a stand-in for biomass) were used as proxies of ecosystem functioning in this study, as both abundance and biomass are widely recognized as ecosystem function proxies [42].

Nematode biomass was assessed by biovolumetric measurements of all retrieved specimens using the Andrassy [43] formula ($V = L \times W^2 \times 0.063 \times 10^{-5}$, where body length ($L$) and width ($W$) are expressed in µm). Body volume was multiplied by an average wet density (1.13 g cm^{-3}) to obtain biomass; the dry weight is calculated by using the ratio of dry to wet weight of 1 : 4 [44,45]; and the carbon content was considered to be 40% of the dry weight [46].

Ostracode abundance and biovolume were calculated as benthic ostracode accumulation rate (BOAR) and ostracode biovolume accumulation rate (OBVAR), respectively. These ecosystem function proxies are highly correlated (electronic supplementary material, figure S5, $R^2 = 0.7323$, $p < 0.001$). BOAR measures the number of individuals deposited per cm^2 of ocean floor per thousand years (N cm^{-2} kyr^{-1}), and is calculated as the product of the number of specimens per g of sediment, the sediment bulk dry density, and the linear sedimentation rate. Benthic microfossil accumulation rates were originally developed with benthic foraminifera as benthic foraminiferal accumulation rate (BFAR) [47,48]. OBVAR is similarly calculated as the product of the approximate biovolume of each genus, the number of specimens per g of sediment of each genus, the sediment bulk dry density, and the linear sedimentation rate, and measures the total biovolume of ostracodes deposited per cm^2 of ocean floor per thousand years (mm^3 cm^{-2} kyr^{-1}). For the approximate biovolume of each genus, we assumed an ellipsoid shape for all ostracodes, using the formulae

$$\mathrm{OBA} = \left(\frac{4}{3}\right) * 3.14 * \left(\frac{L}{2}\right) * \left(\frac{H}{2}\right) * W.$$

$$\mathrm{OBJ} = \frac{\mathrm{OBA}}{2},$$

where OBA, ostracode biovolume of adult; OBJ, ostracode biovolume of A-1 (adult minus 1) juvenile; L, length (mm); H, height (mm); W, width (mm) of a valve or 50% value of width of a carapace (i.e. we assumed ostracode carapace is symmetrical, ignoring minor difference between left and right valves). The OBJ can be calculated as 50% of the OBA, because ostracodes are known to grow double by volume in every moult [49–51]. The OBJ was used for this study, because A-1 juveniles are usually most abundant (i.e. more abundant than adults and most abundant among all juvenile stages) [52], especially in Pliestocene–Holocene deep-sea fossil ostracode assemblages. The size information (height, length and width) is based on taxonomic literature. Genus size was approximated from the size of individual species for which the width data are reported, as the width of ostracodes is rarely reported compared with length and height. If width information was not available for a genus, we used the length : width ratio of similar genus to calculate the width. Selection criteria representative species included (i) that the species could be representative of the deep-sea species of the genus; (ii) North Atlantic deep-sea species in the genus (i.e. species from the same oceanographic region as the studied site); (iii) shallow-marine species morphologically similar to deep-sea species in the genus when the size information was not available for any deep-sea species. Biovolume was successfully calculated for almost all genera (36 out of 37 genera; see Dryad (http://dx.doi.org/10.5061/dryad.23gq5) for further details).

(e) Statistical analyses

(i) Multi-dimensional scaling

Multivariate species abundance composition was decomposed by multi-dimensional scaling (MDS) to MDS1 and MDS2 axes based on Bray–Curtis dissimilarities calculated from raw census data. The distances between samples in MDS ordination represent their relative dissimilarities in species abundance composition. We interpreted the MDS1 and MDS2 axes as capturing primary variation in faunal composition. The MDS1 and MDS2 plots for both datasets are shown in electronic supplementary material, figures S6 and S7.

(ii) Window analyses

A gamma diversity-type approach was applied to time series data in this study. Total species richness was calculated for (i) 1 kyr moving window starting from present time; (ii) 50 cm moving window starting from core surface; and (iii) 10 sample moving window starting from core surface. Such total species richness in a large time window reflects a regional species pool similar to gamma diversity. In addition, multivariate dispersion, the average distance of each sample to the sample centroid in the same sliding window, was also calculated based on Bray–Curtis dissimilarities converted from species abundance data (method according to Anderson *et al*. [53]). The multivariate dispersion measures the variability of species composition in a long time window, which is considered as the indicator of ecosystem instability in this study. Total BOAR and OBVAR were also calculated for these sliding windows.

(iii) Linear model

We performed the simple linear models for analysis of relationships between variables (electronic supplementary material, tables S2–S4). In the models, we accounted for the temporal autocorrelation of model residuals using generalized least squares by following the method of Hunt *et al*. [54]. As such, α-values were set as 0.05 for deciding the significance. Graphics were performed by R software v. 3.2.2 [55]. For Hill numbers, linear model and MDS, we used the packages iNEXT v. 2.0.5 [56], nlme v. 3.1–12 [57] and vegan v. 2.3.1 [58].

3. Results

(a) Mediterranean nematode time series

Nematode alpha species diversity shows a weak positive relationship with biomass (figure 1, electronic supplementary material, figure S8; table 1, electronic supplementary material, table S2), probably because of insufficient number of sample

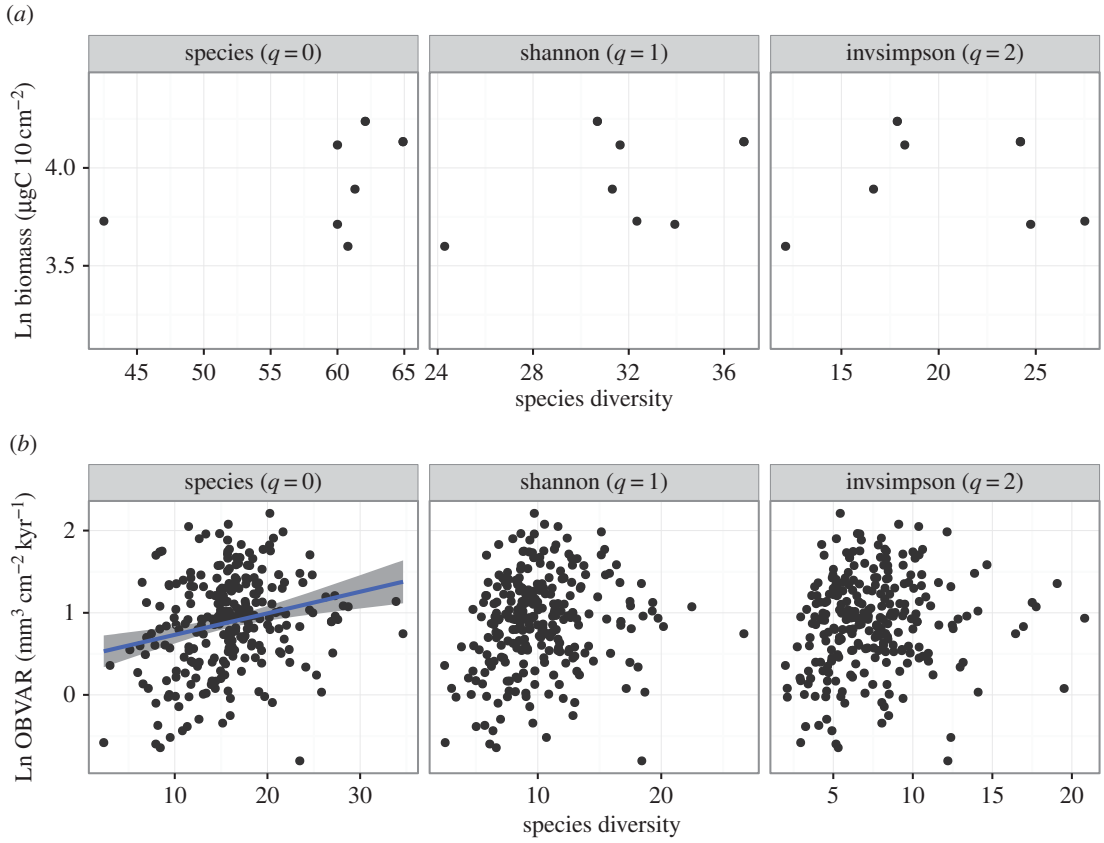

Figure 1. The relationships between species diversity (Hill numbers: species richness [species], exponential of Shannon diversity [shannon] and inversed Simpson diversity [invsimpson]) and ecosystem functioning (log-transformed nematode biomass and ostracode biovolume [OBVAR]). The Hill diversity measures were calculated at $m = 300$ and 100 resampled individuals for nematode and ostracodes, respectively. The line and grey area (linear regression model and standard error of regression slope, respectively) are shown for the significant relationship. Full results are shown in electronic supplementary material, figures S8 and S12. See table 1 and electronic supplementary material, table S2 for the statistical results. (*a*) Nematoda time series, (*b*) ostracode palaeoecological record. (Online version in colour.)

points (=7). Only species richness at $m = 100$ did resampled individuals show significant positive relationship with biomass (electronic supplementary material, figure S8 and table S2). Functional diversity shows a significant positive relationship with biomass (figure 2, electronic supplementary material, table S3). In addition, species diversity measures generally show significant relationships with functional diversity, with the exception of inversed Simpson at $m = 300$ resampled individuals (electronic supplementary material, figure S9 and table S2). Diverse communities exhibit some structural similarity, as captured by MDS2. Species richness shows significant correlation with MDS2 at $m = 200$ and 300 resampled individuals (figure 3, electronic supplementary material, table S2). However, all other relationships between MDS axes and diversity measures are insignificant (electronic supplementary material, figures S10 and S11 and table S2).

(b) North Atlantic ostracode palaeoecological record

Deep-sea ostracode data from Core 23GGC show noisy but significant positive BEF relationships both for species and functional diversity. Alpha species richness shows significant positive relationship with BOAR and OBVAR at all resampled individuals of $m = 10$, 50 and 100 (figure 1, electronic supplementary material, figure S12 and table S2). Other diversity measures (Shannon and inversed Simpson) do not show any significant relationship with BOAR or OBVAR, except Shannon at $m = 10$ resampled individuals. Four out of five functional diversity measures show significant positive relationships with BOAR (electronic supplementary material, figure S13 and table S3). One (FEve) shows significant negative relationship. Similarly, three out of five functional diversity measures show significant positive relationships with OBVAR (figure 2, electronic supplementary material, table S3). Two (FEve, FDiv) show no significant relationships with OBVAR. In addition, species diversity measures generally show significant relationships with functional diversity measures, except FDiv (electronic supplementary material, figure S14 and table S2).

Species richness shows significant correlation with MDS2 (at $m = 50$ and 100 resampled individuals), and Shannon or inversed Simpson does not show significant relationship with MDS2 (figure 3, electronic supplementary material, figure S10 and table S2). Inversely, Shannon and Inversed Simpson show significant correlations with MDS1 at all resampled individuals of $m = 10$, 50 and 100, and species richness does not show significant relationship with MDS1, except at $m = 10$ resampled individuals (electronic supplementary material, figure S11 and table S2).

Total OBVAR does not show any significant relationship with multivariate dispersion in all of 1 kyr, 50 cm depth and 10 sample window analyses (electronic supplementary material, figure S15), whereas total BOAR shows negative significant relationships with multivariate dispersion in 50 cm depth and 10 sample window analyses (figure 4, electronic supplementary material, table S4). Gamma-type time window diversity and multivariate dispersion do not show any significant relationship in any window analyses (figure 4, electronic supplementary material, table S4).

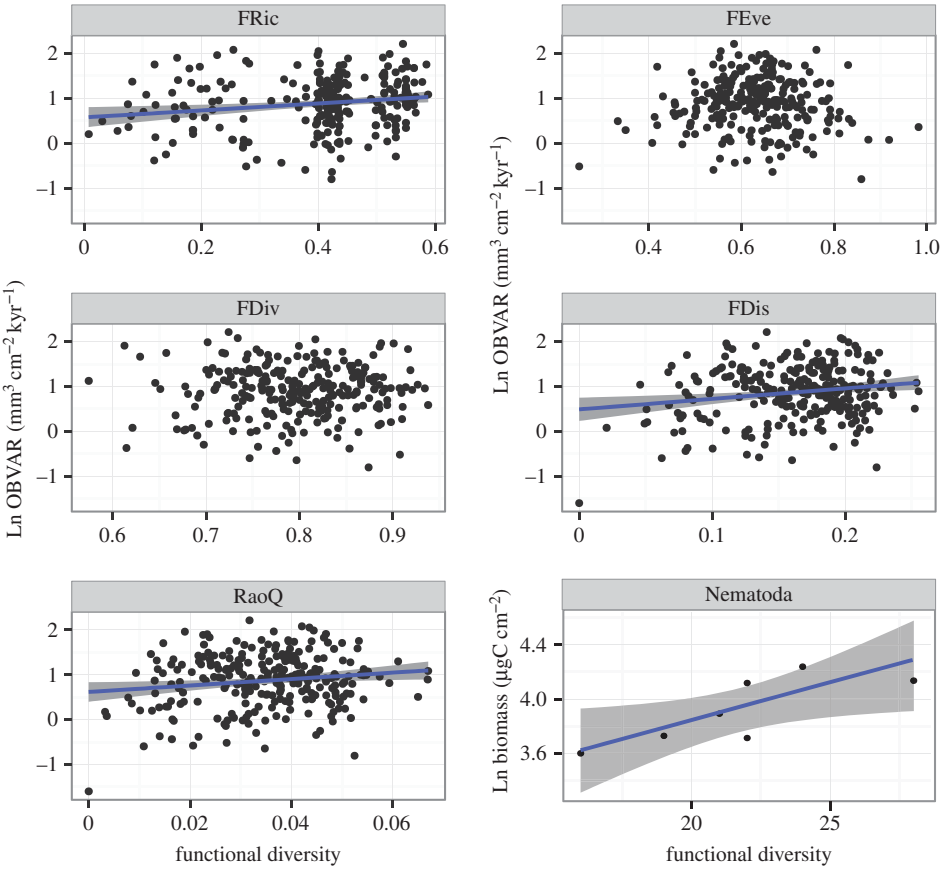

Figure 2. The relationships between functional diversity (ostracode: functional richness [FRic], functional evenness [FEve], functional divergence [FDiv], functional dispersion [FDis], Rao's quadratic entropy [RaoQ]; nematode: family richness) and ecosystem functioning (ostracode: log-transformed biovolume [OBVAR]; nematode log-transformed biomass). The line and grey area (linear regression model and standard error of regression slope, respectively) are shown for the significant relationships. The results with another ecosystem function proxy, BOAR, are shown in electronic supplementary material, figure S13. See electronic supplementary material, table S3 for the statistical results. (Online version in colour.)

Table 1. Coefficients and statistics for linear models using generalized least squares for the relationships between species diversity ($q = 0$: species richness) and ecosystem functioning (biomass, OBVAR, BOAR). Italicized characters indicate significant coefficient. s.e.m.: standard error of the mean. Full results are shown in electronic supplementary material, table S2.

dataset	equation	*M*	coefficient ± s.e.m.	*t*-value	*p*-value
Nematoda	Ln biomass ~ diversity	300	0.019 ± 0.012	1.611	0.151
Ostracoda	Ln OBVAR ~ diversity	100	*0.014 ± 0.005*	*2.623*	*0.009*
Ostracoda	Ln BOAR ~ diversity	100	*0.017 ± 0.005*	*3.673*	*<0000.1*

4. Discussion

Deep-sea nematode long-term time series and ostracode palaeoecological records generally show positive BEF relationships, between both species diversity and ecosystem functioning (figure 1, electronic supplementary material, figures S8 and S12; table 1, electronic supplementary material, table S2) and between functional diversity and ecosystem functioning (figure 2, electronic supplementary material, figure S13 and table S3). Although the nematode and ostracode datasets are different in terms of robustness (e.g. number of data points: approx. 10 versus approx. 250) and temporal coverage (10 years versus 20 kyr), our long-term results support the conclusions from short-term manipulative experiments [2,3].

However, the relationships reported in this study are noisy, perhaps because deep sea is subjected to certain degrees of change in some crucial variables such as food inputs [29,59]. Food inputs from ocean surface (i.e. particulate organic carbon (POC) flux) is limited and the only food source for deep-sea benthic organisms, except those in chemosynthetic systems, because of general absence of light and primary production in deep-sea environments. Thus, the noisiness of the BEF relationships described here for the deep sea indicates that ecosystem functioning (i.e. biomass) may be influenced more by food availability (POC flux) than by biodiversity. Environmental factors may be more important than BEF relationships (i.e. biodiversity impact) in deep-sea environments.

Stronger environmental, and weaker biodiversity, control may be especially characteristic at longer time scales. Here, we find BEF relationships to be noisier in long-term nematode and fossil ostracode data, when compared with modern observations [38,60]. Temperature is almost always

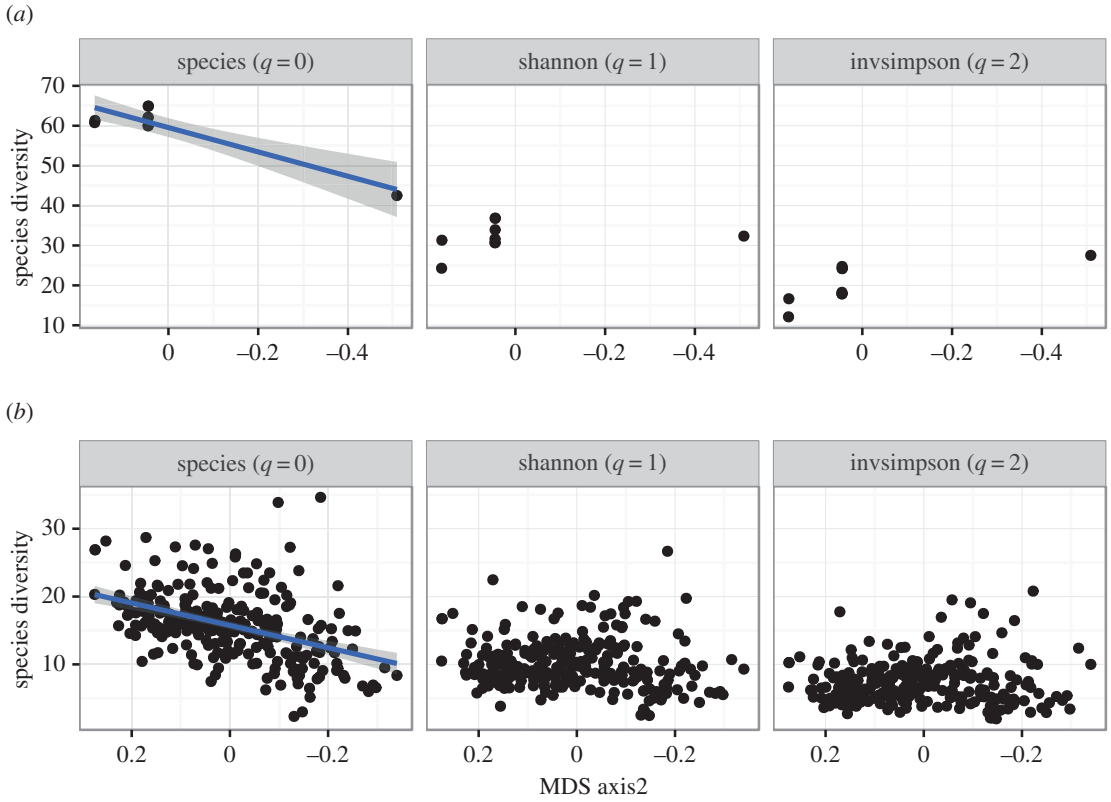

Figure 3. The relationships between species diversity (Hill numbers: species richness [species], exponential of Shannon diversity [Shannon] and inversed Simpson diversity [invsimpson]) and faunal composition (MDS2). The Hill diversity measures were calculated at $m = 300$ and 100 resampled individuals for nematode and ostracodes, respectively. The line and grey area (linear regression model and standard error of regression slope, respectively) are shown for the significant relationships. The MDS stress value is (nearly) zero for nematodes and is 0.23 for ostracodes. Full results are shown in electronic supplementary material, figure S10, and the results for MDS1 are shown in electronic supplementary material, figure S11. See electronic supplementary material, table S2 for the statistical results. (*a*) Nematoda time series, (*b*) ostracode palaeoecological record. (Online version in colour.)

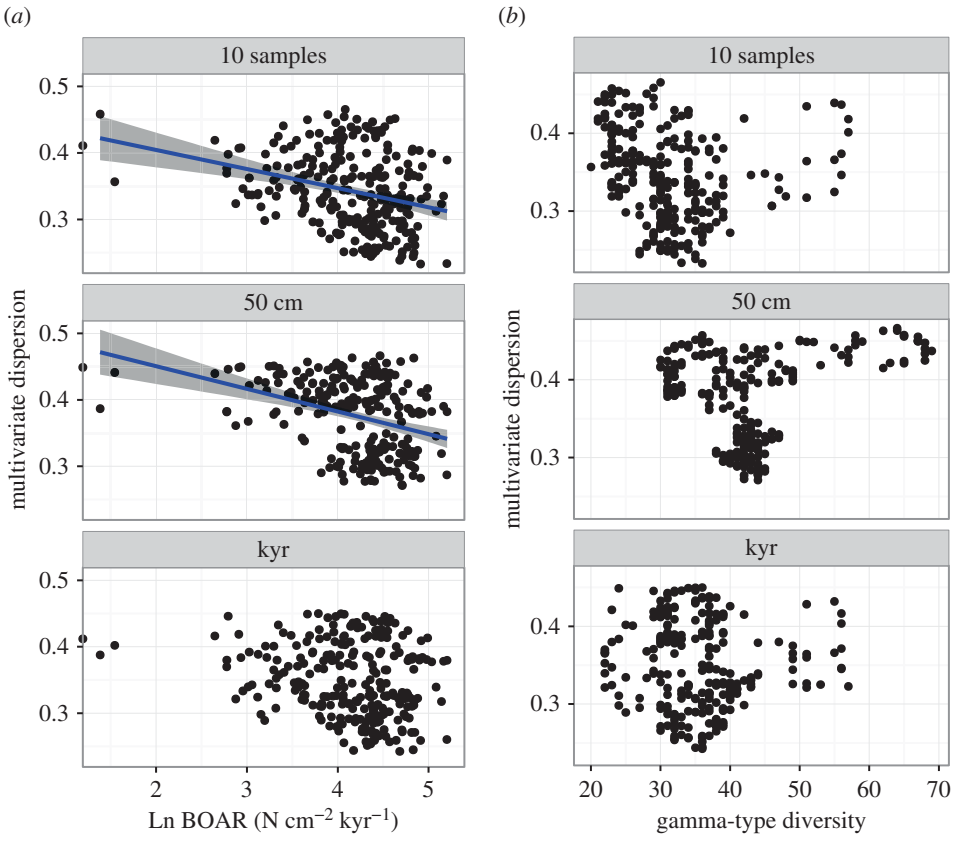

Figure 4. The relationships between (*a*) multivariate dispersion (=ecosystem instability) and ecosystem functioning (total BOAR), and (*b*) multivariate dispersion and gamma-type diversity in a time window, for ostracode palaeoecological record. The line and grey area (linear regression model and standard error of regression slope, respectively) are shown for the significant relationships. The results with another ecosystem function proxy, OBVAR, are shown in electronic supplementary material, figure S15. The statistical results are shown in electronic supplementary material, table S4. (Online version in colour.)

a significant predictor of deep-sea species diversity in palaeoecological and long-term time series datasets, but less so in modern observational datasets [28,36,61–65]. Instead, POC flux tends to be a significant predictor of deep-sea biodiversity in modern observational datasets [66,67], and indeed, POC flux can vary more greatly across short (e.g. seasonal) time scales [29,30] than temperature [65]. These data suggest time scale dependency of deep-sea BEF and environment–diversity relationships, although this idea must be tested by manipulative experiments and other means. Manipulative experiments, either *in situ* or in the laboratory, are difficult for deep-sea organisms, because of the remote and extreme nature of the deep sea. This difficulty is potentially the reason why deep-sea ecology has focused on POC flux control of biodiversity (perhaps through metabolic rate-related mechanisms) [66] rather than the BEF relationship [60]. However, recent technical advances [68] may make complex deep-sea manipulative experiments for BEF study possible.

The BEF relationship is much stronger with species richness than with evenness (i.e. inversed Simpson) for which the relationship is never significant (figure 1, electronic supplementary material, table S2). This is also similarly true for functional diversity: FRic shows a significant positive BEF relationship, whereas FEve shows an insignificant or even negative BEF relationship (figure 2, electronic supplementary material, table S3). This result is consistent with a study (in this special issue) showing that richness and evenness components of biodiversity affect ecosystem functioning differently, more specifically richness and evenness have positive and negative impacts on ecosystem functioning, respectively [10]. Indeed, species richness tends to show a significant relationship with MDS2 but not with MDS1 (figure 3, electronic supplementary material, figures S10 and S11 and table S2). In contrast, diversity measure including evenness component (i.e. inversed Simpson) tends to show a significant relationship with MDS1 but not with MDS2 (figure 3, electronic supplementary material, figures S10 and S11 and table S2). These results indicate that richness and evenness are related to different components of faunal community structure. This is reasonable, because evenness should be controlled by a few dominant species, and richness is the total number of species that should be controlled more by rare or less-abundant species.

In the time window analyses, total BOAR shows a negative relationship with the multivariate dispersion (i.e. ecosystem instability; figure 4, electronic supplementary material, table S4), suggesting that higher ecosystem functioning (in the form of abundance) may enhance ecosystem stability. Higher abundance may favour stronger competitors, resulting in a more uniform community, and therefore higher ecosystem stability (lower multivariate dispersion). Gamma-type diversity (total number of species in a time window) does not show any significant relationship with multivariate dispersion (figure 4, electronic supplementary material, table S4). As such, these data do not support the hypothesis that higher gamma-type diversity (i.e. species pool in a time window) enhances ecosystem stability in the deep sea. This finding is in contrast with a previously reported relationship in fossil records from shallow reef systems [23]. The conflicting results across these two case studies indicate that further investigations using palaeoecological data across time scales and oceanographic provinces are needed.

5. Conclusion and future outlook

This study shows the presence of positive BEF relationships over decadal–millennial time scales, beyond the time scale of ordinary manipulative experiments. However, the relationship is much noisier in these long time scales than in modern observational studies, suggesting that BEF relationships may be time scale-dependent. Environmental factors may independently affect species diversity and biomass, and such effects may be much stronger than biodiversity impacts on ecosystem functioning at longer, i.e. decadal–millennial, time scales. Indeed, environmental (temperature and POC flux) impacts on deep-sea species diversity and microfossil accumulation rate (here we used this as a proxy for biomass, i.e. ecosystem functioning) are well described [36,62,65,67,69]. Microfossil accumulation rate is a proxy for POC flux [47,69] and here we used it as a proxy for ecosystem function. Manipulative BEF experiments usually look into biodiversity effects on ecosystem function, whereas this palaeo-observational study investigated correlations between these effects, which are usually interpreted as POC-flux impact on biodiversity. In other words, manipulative and palaeo-observational studies may look at 'opposite' causality (as indicated by [2]).

Analysing BEF relationships over long temporal scales has some critical associated caveats. For example, biomass estimation from micropalaeontological data requires robust age controls, which may be difficult to achieve. In the deep sea, very accurate age control is possible, because many sediment cores (e.g. 23GGC in this study) have excellent radiocarbon and/or oxygen isotope geochronology. In turn, biomass estimation from micropalaeontological data also requires assumptions for size and shape measurements (e.g. usage of standard size of a genus for all individuals of that genus, and assumption of ellipsoid shape for all ostracodes) and estimation of body density [70–72], because direct size and shape measurements of tens of thousands of individuals under microscope is almost impossible, and body density of microfossil taxa is seldom known (e.g. body density of living ostracode is unknown [70]). These biometric measurement issues may be resolved by developments in automation techniques (http://people.earth.yale.edu/automorph/pincelli-hull) [73,74]. There are several excellent functional morphology studies in microfossils: for example, general habitats of ostracodes can be estimated by morphology of shells (i.e. hard parts preserved as fossils) [75]. However, the number of functional trait studies in microfossils is limited and functional traits in microfossils remain a principle knowledge gap.

In addition, it is important to note that we used biomass of nematodes and biovolume, and abundance (as stand-ins for biomass) of ostracodes as ecosystem-functioning proxies in this study. They are not direct measures of ecosystem functioning (i.e. ecosystem process rates such as primary production, respiration and growth), although direct assessment of ecosystem functions is difficult in palaeoecological records, and biomass and abundance are widely used proxies for ecosystem functioning [2,42]. It is also uncertain whether biomass and abundance of a clade (or a taxonomic group, like ostracode) work as appropriate ecosystem-functioning proxies just like those of a trophic group [42]; although nematode is the dominant metazoan meiofauna and ostracode is one of few organisms that have excellent fossil record in deep sea, potentially reflecting broader benthic community [35,63].

Benton [76], in a discussion on regional-to-global diversities and macroevolutionary time scales of speciation and extinction, argued that abiotic factors (aka Court Jester) are more important in shaping large-scale diversity patterns in long time scales (above 10^5 years) than biotic factors (aka Red Queen). Our study strongly suggests that the same is true for alpha (local-scale) diversity and ecological (i.e. decadal–millennial) time scales, which are much shorter than a species' approximate lifespan (1–2 million years), and rarely involve speciation or extinction [27,76]. In conclusion, long-term and palaeoecological records allow us to address questions that cannot properly be addressed by field observations, macroecological data or manipulative experiments. Despite intrinsic limitations, the approach used here remains the best available tool to understand how biodiversity influences ecosystem function over time.

Data accessibility. Data are available at Dryad (http://dx.doi.org/10.5061/dryad.23gq5).

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