

Exponential Decline of Deep-Sea Ecosystem Functioning Linked to Benthic Biodiversity Loss

Roberto Danovaro,^{1,*} Cristina Gambi,¹
Antonio Dell'Anno,¹ Cinzia Corinaldesi,¹
Simonetta Fraschetti,² Ann Vanreusel,³ Magda Vincx,³
and Andrew J. Gooday⁴

¹Department of Marine Science
Faculty of Science
Polytechnic University of Marche
Via Breccia Bianche
60131 Ancona
Italy

²Department of Biological and Environmental Science
and Technology
University of Salento
Provinciale Lecce-Monteroni
73100 Lecce
Italy

³Marine Biology Section
University of Ghent
Krijgslaan 281
S8 - Sterre Campus
B-9000 Ghent
Belgium

⁴National Oceanography Centre, Southampton
European Way
Southampton SO14 3ZH
United Kingdom

Summary

Background: Recent investigations suggest that biodiversity loss might impair the functioning and sustainability of ecosystems. Although deep-sea ecosystems are the most extensive on Earth, represent the largest reservoir of biomass, and host a large proportion of undiscovered biodiversity, the data needed to evaluate the consequences of biodiversity loss on the ocean floor are completely lacking.

Results: Here, we present a global-scale study based on 116 deep-sea sites that relates benthic biodiversity to several independent indicators of ecosystem functioning and efficiency. We show that deep-sea ecosystem functioning is exponentially related to deep-sea biodiversity and that ecosystem efficiency is also exponentially linked to functional biodiversity. These results suggest that a higher biodiversity supports higher rates of ecosystem processes and an increased efficiency with which these processes are performed. The exponential relationships presented here, being consistent across a wide range of deep-sea ecosystems, suggest that mutually positive functional interactions (ecological facilitation) can be common in the largest biome of our biosphere.

Conclusions: Our results suggest that a biodiversity loss in deep-sea ecosystems might be associated with

exponential reductions of their functions. Because the deep sea plays a key role in ecological and biogeochemical processes at a global scale, this study provides scientific evidence that the conservation of deep-sea biodiversity is a priority for a sustainable functioning of the worlds' oceans.

Introduction

The accelerating loss of biological diversity poses serious concerns, exemplified by recent predictions that species loss might impair the functioning and the sustainability of terrestrial ecosystems [1–3]. The global scale of the biodiversity crisis has stimulated investigations that explore the relationships between biodiversity (expressed as the number, identity, and relative abundance of species), productivity, stability, and services in different ecosystems of the world [1–5].

Deep-sea sediments cover 65% of the world's surface. The microbial processes occurring there provide essential services, driving the nutrient regeneration and global biogeochemical cycles that are essential to sustain primary and secondary production in the oceans [6]. Deep-sea habitats are also the largest reservoirs of biomass and nonrenewable resources (e.g., gas hydrates and minerals) [6], and although the census of deep-sea life is in its infancy, there is increasing evidence that they host a large proportion of undiscovered biodiversity on our planet (from 0.3 to 8.3×10^6 species) [5, 6]. Understanding the relationships between biodiversity and deep-sea ecosystem functioning is therefore crucial for understanding the functioning of our biosphere.

Benthic faunal diversity provides an ideal tool for exploring the relationships between biodiversity and ecosystem functioning [7], and among benthic faunal taxa, nematodes are ideal model organisms. Nematodes are, indeed, the most abundant metazoans on Earth; in terrestrial ecosystems, they account for 80% of the abundance of multicellular animals, and in the deep sea, this proportion rises to more than 90% [8]. This phylum is also characterized by (1) very high species richness (i.e., among the most diverse of marine Phyla), (2) distinct and easily recognizable feeding types, and (3) life strategies that make it possible to also identify functional diversity traits [9]. Moreover, although comparative studies are rare, deep-sea nematode diversity appears to be related to that of other benthic components, including Foraminifera [10], macrofauna [11], and the richness of higher meiofaunal taxa (a group which includes 22 of the 35 modern animal Phyla; [Figure S1](#) available online).

Ecosystem functioning involves several processes, which can be summarized as production, consumption and transfer of organic matter to higher trophic levels, organic matter decomposition, and nutrient regeneration. Terrestrial ecologists have related biodiversity to ecosystem functioning through analyses of ecosystem processes estimated by measuring the rates of energy and

*Correspondence: r.danovaro@univpm.it

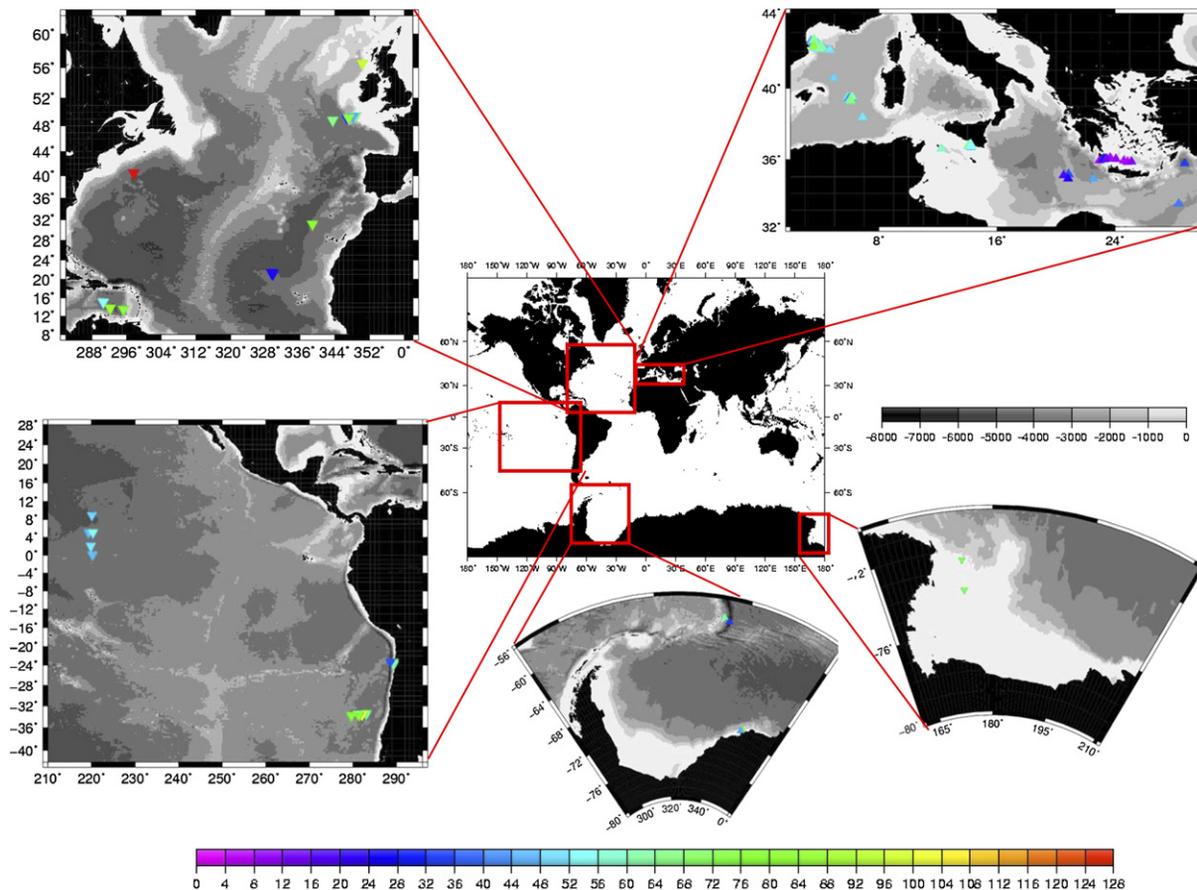


Figure 1. Sampling Areas and Deep-Sea Nematode Diversity

Maps of the sampling areas and the magnitude of deep-sea nematode species richness (a proxy for deep-sea benthic biodiversity) at the individual sampling points. Data from the Northeast and Central-East Atlantic are based on nematode genera. Nematode species richness from the deep anoxic Black Sea is not reported. Colored bars and symbols refer to species richness (and to genus richness only for the Porcupine Abyssal Plain); the black-and-white bar refers to sampling depths.

material flow between biotic and abiotic compartments (e.g., biomass production, organic matter decomposition, nutrient regeneration, or other measures of material production, transport, or loss) [2]. Applying the same approach through a series of independent and synoptic measures, we investigated the relationships between deep-sea biodiversity and ecosystem functioning. Deep-sea ecosystems lack photosynthetic primary production, and their functioning reflects the collective activities of animals, protists, and prokaryotes in exploiting and recycling the inputs of material from the photic zone. We therefore identified the following key processes: (1) benthic prokaryote production, (2) total meiofaunal biomass (a measure of the production of renewable resources by ecosystems), and (3) the rates at which organic matter is decomposed and recycled. The three independent indicators of ecosystem functioning represent key variables of deep-sea ecosystems as they regulate (1) the transfer of mobilized organic matter to higher trophic levels, (2) the ability of the ecosystem to transfer energy and material to higher trophic levels, thus providing indications of the heterotrophic production of the ecosystem, and (3) nutrient regeneration processes, which reflect the ability of ecosystems to sustain their functions over time.

Results

We report here the results of largest data set produced so far for investigating the interaction between deep-sea biodiversity and ecosystem processes. From 116 deep-sea sites, we compiled an inventory of 270 data sets, each comprising benthic faunal (nematode) biodiversity and other variables reflecting ecosystem functioning (Figure 1). This inventory integrated all relevant information from the literature with data from 83 new sites obtained with the same protocols and taxonomic references. Our database covers latitudes from 55° N to 75° S and depths from approximately 200 m to 8200 m (information for each data set is provided in Table S1) and includes quantitative data from deep-water sites spanning a bottom water temperature ranges from approximately -1.9°C (Southern Ocean) to 13.0°C (Mediterranean Sea). In total, approximately 61,000 individuals were counted, and about 25,000 of these were classified to the species level (in five data sets, nematodes were identified only to genus level).

Our analyses have revealed for the first time that ecosystem functioning is positively and exponentially related to biodiversity in all of the deep-sea regions investigated (Figure 2). This relationship applies also when

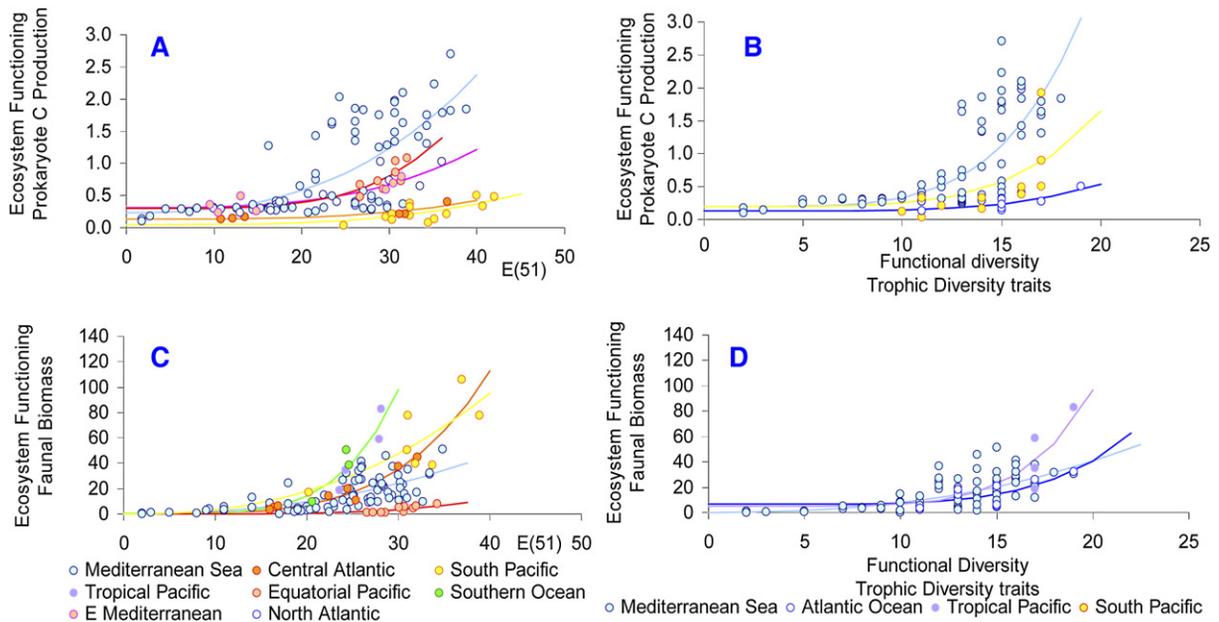


Figure 2. Relationship between Biodiversity and Ecosystem Functioning

(A) The relationship between expected species number [ES(51)] and ecosystem functioning (as prokaryote C production, expressed as $\mu\text{g C g}^{-1} \text{d}^{-1}$). The equations of the fitting lines are (1) $Y = 0.24 + 1.2 \times 10^{-4} \times (X^{2.6})$ for the Mediterranean Sea ($n = 75$, $R^2 = 0.52$, $p < 0.01$), (2) $Y = 0.31 + 6.7 \times 10^{-6} \times (X^{3.2})$ for the Eastern Mediterranean Sea ($n = 7$, $R^2 = 0.82$, $p < 0.05$), (3) $Y = 0.08 + 2.3 \times 10^{-3} \times (X^{1.7})$ for the North Atlantic ($n = 10$, $R^2 = 0.77$, $p < 0.05$), (4) $Y = 0.30 + 2.2 \times 10^{-7} \times (X^{4.3})$ for the Equatorial Pacific ($n = 8$, $R^2 = 0.59$, $p < 0.05$), (5) $Y = 0.05 + 1.5 \times 10^{-6} \times (X^{3.3})$ for the South Pacific ($n = 13$, $R^2 = 0.67$, $p < 0.01$), and (6) $Y = 0.1 + 9.7 \times 10^{-7} \times (X^{3.2})$ for the Central Atlantic ($n = 6$, $R^2 = 0.81$, $p < 0.05$).

(B) The relationship between functional diversity (number of trophic traits) and ecosystem functioning (as prokaryote C production, expressed as $\mu\text{g C g}^{-1} \text{d}^{-1}$). The equations of the fitting lines are (1) $Y = 0.41 + 9.3 \times 10^{-3} \times (X^{2.3})$ for the Mediterranean Sea ($n = 80$, $R^2 = 0.45$, $p < 0.01$), (2) $Y = 0.50 + 3.1 \times 10^{-5} \times (X^{4.1})$ for the Central Atlantic ($n = 8$, $R^2 = 0.94$, $p < 0.01$), (3) $Y = 2.1 \times 10^{-6} \times (X^{4.2})$ for the Equatorial Pacific ($n = 10$, $R^2 = 0.60$, $p < 0.05$), and (4) $Y = 1.3 \times 10^{-2} \times (X^{2.4})$ for the South Pacific ($n = 7$, $R^2 = 0.66$, $p < 0.05$).

(C) The relationship between expected species number (ES(51)) and ecosystem functioning (as faunal biomass, expressed as mg C m^{-2}). The equations of the fitting lines are (1) $Y = 0.19 + 2.3 \times 10^{-6} \times (X^{4.8})$ for the Mediterranean Sea ($n = 75$, $R^2 = 0.80$, $p < 0.01$), (2) $Y = 0.13 + 2.4 \times 10^{-7} \times (X^{4.8})$ for the Atlantic Ocean ($n = 7$, $R^2 = 0.80$, $p < 0.05$), and (3) $Y = 0.22 + 8.8 \times 10^{-7} \times (X^{4.8})$ for the South Pacific ($n = 11$, $R^2 = 0.43$, $p < 0.05$).

(D) The relationship between functional diversity (number of trophic traits) and ecosystem functioning (as faunal biomass expressed as mgC m^{-2}). The equations of the fitting lines are (1) $Y = 3.2 \times 10^{-2} \times (X^{2.4})$ for the Mediterranean Sea ($n = 79$, $R^2 = 0.41$, $p < 0.01$), (2) $Y = 6.6 + 6.3 \times 10^{-6} \times (X^{5.2})$ for the Atlantic Ocean ($n = 8$, $R^2 = 0.58$, $p < 0.05$), and (3) $Y = 5.0 + 2.3 \times 10^{-6} \times (X^{5.8})$ for the Tropical Pacific ($n = 4$, $R^2 = 0.60$, not significant [ns]).

Data originate from the Equatorial Pacific (bathymetric range: 4305–4994 m, mean \pm standard deviation [SD]: 4606 ± 283 m), Tropical Pacific (bathymetric range: 1140–1355 m, mean \pm SD: 1248 ± 152 m), South Pacific Ocean (bathymetric range: 2040–3070 m, mean \pm SD: 2629 ± 440 m), Central Atlantic (bathymetric range: 3858–5411 m, mean \pm SD: 4460 ± 914 m), North Atlantic (bathymetric range: 1034–4850 m, mean \pm SD: 2720 ± 1547 m), Western Mediterranean (bathymetric range: 2755–3870 m, mean \pm SD: 2912 ± 256 m), Eastern Mediterranean Sea (bathymetric range: 1078–1840 m, mean \pm SD: 1350 ± 286 m), and Southern Ocean (bathymetric range: 228–588 m, mean \pm SD: 462 ± 166 m). Data from the North Atlantic are based on nematode genera; all other data are based on nematode species.

different biodiversity measures (including the richness of all higher meiofaunal taxa) and independent measures of ecosystem functioning are used (Table S2, Figures S2 and S3). The analysis of descriptive data represents, at present, the most convenient approach for investigating the relationships between biodiversity and ecosystem functioning in remote habitats, such as the deep-sea ecosystems, at large spatial scales. However, because measures of biodiversity and ecosystem functioning can change in response to different environmental factors, these relationships could reflect the covariation of different variables rather than a causal relationship. Previous studies have related patterns of deep-sea biodiversity to a variety of factors, including (1) temperature, (2) water depth, and (3) the export of primary organic matter from the photic zone and oxygen availability [11, 12]. Although differences of temperature among different deep-sea systems can be relevant, the relationships reported in Figure 2 are presumably not affected by temperature because they were obtained by the plotting of

values of biodiversity and ecosystem functioning within deep-sea regions in which temperatures were highly homogeneous (e.g., all of the deep-Mediterranean samples displayed temperatures of $13.0 \pm 0.2^\circ\text{C}$), and the same applies to all deep-sea regions within the bathymetric ranges considered (Table S1).

We also investigated the relationships between benthic biodiversity and deep-sea ecosystem efficiency [2], which reflects the ability of an ecosystem to exploit the available energy (food sources) and thereby maximize the biomass and its production [1, 2]. Given the specificity of deep-sea ecosystem functioning, we used three independent indicators of ecosystem efficiency: (1) the ratio of meiofaunal biomass to organic C fluxes, reflecting the ability of the system to exploit the input of primary production from the photic zone, (2) the ratio of prokaryote C production to organic C flux, representing a basic estimate of the ability of the system to convert organic detritus into bacterial biomass and thus to recycle organic matter deposited on

the sea floor, and (3) the ratio of total benthic meiofaunal biomass to biopolymeric C content in the sediment as an estimate of the ability of the system to channel detritus to higher trophic levels.

We found significant and exponential relationships between benthic biodiversity and different independent measures of ecosystem efficiency (Figure 3) (Table S2, Figure S4). Moreover, species number and the diversity of functional traits were directly and positively related (Figure 4). We also carried out statistical analyses revealing that the relationships between biodiversity and ecosystem functioning are highly significant even when the effects of depth and C flux are discounted (i.e., considering depth and C fluxes as covariates), both independently and simultaneously (Table 1, Figure S5).

Biodiversity and ecosystem functioning can be affected by hypoxic or anoxic conditions. In deep-water hypoxic settings, sedimentary carbon cycling is depressed at depths where oxygen depletion is most severe and metazoan abundance and diversity are lowest. ^{13}C tracer experiments conducted in the Arabian Sea oxygen minimum zone (OMZ) suggest that Foraminifera are responsible for most organic matter processing in these stressed, but food-rich, environments [13]. At slightly higher bottom-water oxygen concentration within the OMZ, high-density, virtually monospecific populations of macrofaunal metazoans (polychaetes) are active in the short-term uptake of organic matter [13]. Moreover, in the permanently anoxic and sulphidic deep Black Sea, where conditions are even more extreme and the sediments are devoid of eukaryotic life, rates of prokaryote C production and C cycling are extremely low (Figure S6). However, all of the deep-sea sites investigated (except the deep Black Sea) display constantly high oxygen concentrations (typically $> 5.0 \text{ ml O}_2 \text{ L}^{-1}$), which are ten times higher than those potentially limiting deep-sea metazoan life [11]. As such, the effect of oxygen concentration on biodiversity is negligible in the deep-sea systems considered here.

The spatial scales at which biodiversity interacts with ecosystem functioning are also crucial for understanding the significance of these relationships. Data presented here (Figure S7) reveal that patterns of benthic biodiversity are consistent at local and larger scales (hundreds of km) and congruent over time (within ecological time scales; Figure S8, Table S3).

Discussion

Overall, our findings indicate that the exponential relationships between deep-sea biodiversity and ecosystem functioning are consistent across a wide range of bottom-water temperatures (including the warm, deep-water regime of the Mediterranean) and trophic conditions and therefore reflect interactions between organismal life and deep-sea ecosystem processes occurring on a global scale.

Taken together, the relationships between biodiversity and ecosystem functioning and efficiency suggest that a higher biodiversity supports higher rates of ecosystem processes and an increased efficiency with which these processes are performed. The exponential relationship between biodiversity and ecosystem efficiency supports previous studies that hypothesized

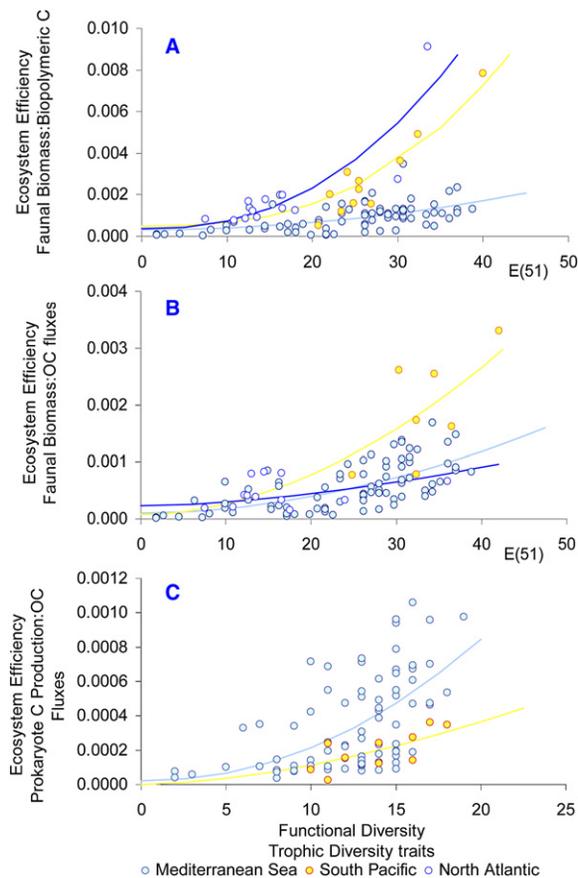


Figure 3. Relationships between Biodiversity and Ecosystem Efficiency and between Functional Diversity and Ecosystem Functioning Relationships between biodiversity and ecosystem efficiency and between structural and functional diversity. Three independent indicators of ecosystem efficiency are plotted against expected species number [ES(51)] and functional diversity. Data origins and bathymetric ranges as detailed for Figure 2.

(A) The ratio of faunal biomass to biopolymeric C (as a measure of the bioavailable organic detritus). The y axis is dimensional. The equations of the fitting lines are (1) $Y = 3.1 \times 10^{-4} + 8.7 \times 10^{-7} \times (X^{2.0})$ for the Mediterranean Sea ($n = 78$, $R^2 = 0.29$, $p < 0.01$), (2) $Y = 3.6 \times 10^{-4} + 1.7 \times 10^{-6} \times (X^{2.4})$ for the Atlantic Ocean ($n = 11$, $R^2 = 0.77$, $p < 0.01$), and (3) $Y = 5.0 \times 10^{-4} + 3.4 \times 10^{-7} \times (X^{2.7})$ for the South Pacific ($n = 11$, $R^2 = 0.86$, $p < 0.01$).

(B) The ratio of faunal biomass to organic carbon (OC) fluxes. The unit of the y axis is d^{-1} . The equations of the fitting lines are (1) $Y = 1.0 \times 10^{-4} + 1.1 \times 10^{-6} \times (X^{1.9})$ for the Mediterranean Sea ($n = 81$, $R^2 = 0.39$, $p < 0.01$), (2) $Y = 2.3 \times 10^{-4} + 1.6 \times 10^{-6} \times (X^{1.6})$ for the Atlantic Ocean ($n = 12$, $R^2 = 0.58$, $p < 0.05$), and (3) $Y = 7.3 \times 10^{-5} + 2.5 \times 10^{-6} \times (X^{1.9})$ for the South Pacific ($n = 7$, $R^2 = 0.45$, ns).

(C) The ratio of prokaryote C production to OC fluxes. The y axis is dimensional. The equations of the fitting lines are (1) $Y = 2.2 \times 10^{-5} + 1.5 \times 10^{-6} \times (X^{2.1})$ for the Mediterranean Sea ($n = 82$, $R^2 = 0.31$, $p < 0.01$) and (2) $Y = 1.0 \times 10^{-7} + 2.3 \times 10^{-6} \times (X^{1.7})$ for the South Pacific ($n = 10$, $R^2 = 0.52$, $p < 0.05$).

the existence of mutually positive functional interactions (ecological facilitation) [14]. In addition, results reported here from all latitudes and depths suggest that interactions of this kind among species are common in the largest biome of our biosphere.

It is generally accepted that changes in species diversity are associated with changes in functional diversity [2], but the relationship between these two community

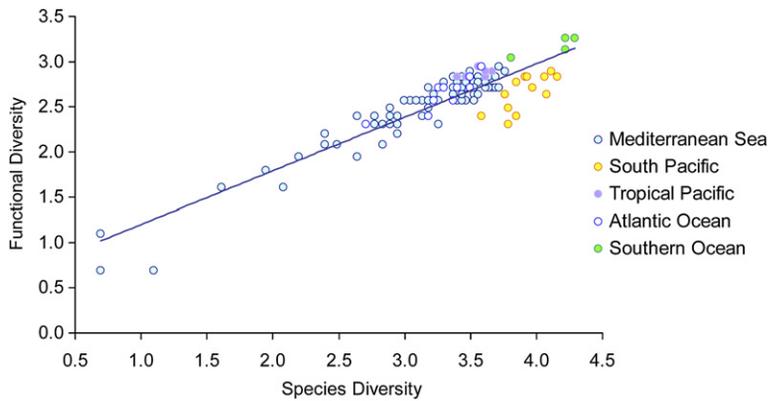


Figure 4. Relationship between Biodiversity and Functional Diversity

Relationship between species diversity (as SR) and functional diversity (as total number of trophic traits). The equation for the line fits for the full data set (log transformed) is $Y = 0.59X + 0.61$ ($n = 115$, $R^2 = 0.83$, $p < 0.01$) (Mediterranean Sea: $R^2 = 0.91$, Atlantic Ocean: $R^2 = 0.77$, Southern Ocean: $R^2 = 0.75$, and South Pacific: $R^2 = 0.47$). Data origins and bathymetric ranges as detailed for Figure 2.

properties remains largely unknown, especially in deep-sea ecosystems. A low functional redundancy has been observed in coastal marine assemblages [15]. Similarly, in deep-sea sediments, species number and the diversity of functional traits are directly and positively related (Figure 4), so that a higher structural biodiversity (species richness) has a direct and positive effect on functional diversity and related ecological processes.

Recent studies have emphasized the importance of functional diversity traits that influence ecosystem functioning [1, 16] and agree that such measures require validation [17]. Understanding how species interactions influence the relationship between biodiversity and ecosystem functioning or efficiency implies a thorough knowledge of the processes regulating deep-sea benthic food webs and the ecological role of each species. In benthic ecosystems, a higher functional diversity can promote ecosystem processes in different ways [18, 19]. (1) A higher benthic diversity might increase bioturbation, with a consequent increase of benthic fluxes [20, 21] and the redistribution of food within the sediment; nematodes, together with Foraminifera, are mainly responsible for cryptobioturbation [22, 23]. (2) A higher number of nematode species stimulates prokaryote C production to a greater extent than selective grazing by a few species [24]. (3) Higher benthic species richness can also promote higher rates of detritus processing, digestion, and reworking, thus resulting in faster rates of organic matter remineralization. (4) Predatory nematodes might influence the structural and functional diversity of meio-, macro- and megafaunal assemblages by preying selectively on the larvae of organisms displaying lower mobility [23].

One case study from the deep Eastern Mediterranean enabled us to identify a clear linkage between ecosystem functioning and functional diversity. Here, an extreme climate event determined the cascading of dense and cold waters down to bathyal depths, profoundly modifying the physical and chemical characteristics of the entire water column and determining a remarkable drop of deep-water temperature. Such changes had a major impact on deep-sea fauna because nematode functional diversity decreased by approximately 35%. Such a loss in functional diversity was associated with an exponential decrease in ecosystem functioning because benthic faunal biomass decreased by 40% and prokaryote biomass decreased by more than 80% (Figure 5). Although the mechanisms causing changes in nematode biodiversity have not been completely clarified, it has been hypothesized that temperature changes had direct effects on nematode abundance and biodiversity by reducing metabolic rates and reproduction potential and favoring the nematode species with higher tolerance to the new temperature settings [19]. These results support the evidence of a linkage between deep-sea ecosystem functioning and functional biodiversity and suggest that a reduction in functional biodiversity might be associated with an exponential decline of ecosystem processes. Overall, our results suggest that a higher biodiversity can enhance the ability of deep-sea benthic systems to perform the key biological and biogeochemical processes that are crucial for their sustainable functioning.

Our findings suggest that the shape of the relationship between biodiversity and the functioning of natural deep-sea ecosystems is different from that typically

Table 1. Species Diversity

	Prokaryote C Production ^a			Faunal Biomass ^b		
	df	SS	MS	df	SS	MS
Covariables	2	0.00077		2	635132.88	
Regression	1	0.00087	0.00087	1	1536282.84	1536282.84
Residual	87	0.01212	0.00014	131	5247823.93	40059.72
Total	90	0.01376		134	7419239.65	

Effects of biodiversity, measured as ES(51), on ecosystem functioning. In the regression analyses, all tests were based on Euclidean distances calculated among observations from untransformed data. The following abbreviations are used: degrees of freedom (df), sum of squares (SS), and mean squares (MS). Regression SS, residual SS, and residual df were calculated after the removal of SS and df because of covariables: depth and organic carbon fluxes.

^a Pseudo-F = 6.25. Permutation $p = 0.01$.

^b Pseudo-F = 38.35. Permutation $p = 0.00020$.

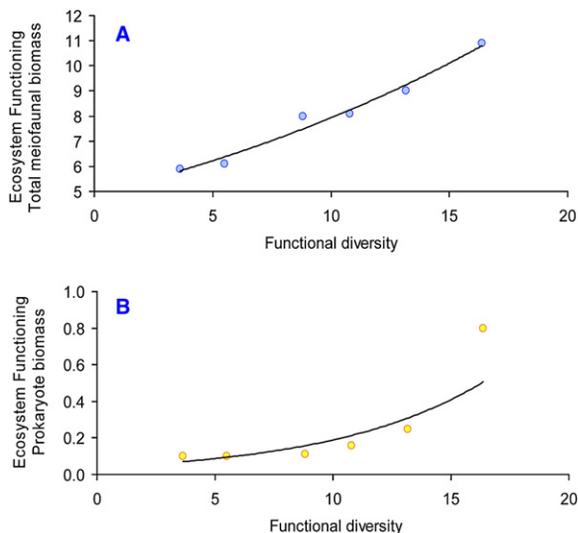


Figure 5. Relationship between Functional Diversity and Ecosystem Functioning

Relationship between functional biodiversity and ecosystem functioning based on a study carried out in the deep Eastern Mediterranean before and after an extreme climate event, which changed the deep-sea water characteristics. Data referred to sediment samples collected at approximately 1600 m depth before the event in 1989 and after the event in 1995 (twice a year), 1996 (twice a year), and 1998.

(A) Relationship between functional diversity (number of trophic traits) and ecosystem functioning (as total meiofaunal biomass, mg C m⁻²; $R^2 = 0.939$, $p < 0.01$).

(B) Relationship between functional diversity (number of trophic traits) and ecosystem functioning (as prokaryote biomass, μg C g⁻¹; $R^2 = 0.898$, $p < 0.01$).

observed in manipulative experiments conducted in other ecosystems (i.e., null, positive, or idiosyncratic, [25–27]). An exponential relationship might reflect several factors, including the characteristics of deep-sea ecosystems and the nature of the relationship between structural and functional biodiversity, as well as the functional role and identity of the species involved [28]. Notably, our results suggest that the effect of deep-sea benthic biodiversity on ecosystem functioning becomes more evident when biodiversity values are high. Results presented here, demonstrating exponential relationships in all deep-sea ecosystems, provide valuable pointers to the mechanisms that might cause the observed patterns and point to the need for new experiments capable of reflecting conditions occurring in deep-sea ecosystems.

Over the geological past, the fossil record preserved in deep-sea sediments reveals substantial fluctuations in the diversity of important benthic taxa, notably the Foraminifera [29] and Ostracoda [30]. Changes in deep-sea foraminiferal diversity are often accompanied by changes in functional types (e.g., infaunal versus epifaunal). Some periods—for example, the Paleocene-Eocene Thermal Maximum—witnessed a sharp decrease in deep-sea benthic foraminiferal diversity [31]. If such shifts are representative of the wider benthic community, then these events must have had a profound effect on ecosystem functioning.

Deep-sea ecosystems are highly vulnerable and susceptible to biodiversity losses [5, 6, 11]. In modern

oceans, deep-sea ecosystems are already being threatened by man through trawling, dumping, oil, gas and mineral extraction, and other pollution sources [32]. Moreover, impacts due to changes in thermohaline circulation linked to global climate change [33] are expected to be extremely severe [19]. Empirical and theoretical studies increasingly argue that biodiversity regulates the ecosystem functions that are responsible for the production of these goods and services [2, 4, 16, 17, 28]. If the mechanisms that have been widely demonstrated in a number of studies [2, 4, 12, 16] can be applied in the deep sea, then reductions of biodiversity might be associated with exponential reductions of ecosystem functions. Deep-sea ecosystems provide goods (including biomass, bioactive molecules, oil, gas, and minerals) and services (climate regulation, nutrient regeneration and supply to the photic zone, and food) and, for their profound involvement in global biogeochemical and ecological processes, are essential for the sustainable functioning of our biosphere and for human wellbeing. Our results suggest that the conservation of deep-sea biodiversity can be crucial for the sustainability of the functions of the largest ecosystem of our biosphere.

Experimental Procedures

Sampling Sites

Sampling was carried out in the North and Central Atlantic Ocean (20 sites), the Equatorial and South Pacific (26 sites), the Western and Eastern Mediterranean Sea (57 sites), the Southern Ocean (the Ross and Weddell Seas; five sites), and the Black Sea (eight sites). The investigated areas included only open-ocean sites and continental-margin systems and excluded specific hot-spot ecosystems (i.e., deep-water coral sites, canyons, cold seeps, and hydrothermal vents) and minimum oxygen zones, with the exception of the permanently anoxic deep Black Sea, an area with extremely low biodiversity. Except for those in the deep Black Sea, all sites are overlain by fully oxic bottom water. The sampling design allowed for the comparison of similar systems covering more than 96% of the deep-sea surface. Overall, approximately 30% of the sampling sites were located at depths between 200 m and 1000 m, approximately 15% between 1000 m and 2000 m, approximately 30% between 2000 m and 3000 m, and approximately 25% from 3000 m to over 8000 m.

Benthic Biodiversity

At all of the sites, samples were collected for the analysis of richness of higher meiofaunal taxa and nematode diversity. Synoptic samples for macrofaunal diversity were collected at 18 selected sites (Western, Central, and Eastern Mediterranean) (Figures S1A and S1B); the biodiversity values from the Equatorial Pacific and Atlantic Ocean were obtained from literature (see References for Data Sources in the Supplemental Data). All meiofaunal taxa were counted and identified under a stereomicroscope. All of the nematodes have been identified to the species level, except in the Northeast and Central-East Atlantic, where identification was conducted to genus level (see Table S1). Macrofaunal samples were identified to the species level.

Because most indices of species diversity are sample-size dependent, the rarefaction method was applied so that all samples could be reduced to the same size, with ES(51) as the expected number of species in a hypothetical random sample of 51 individuals. Previous studies have shown that this approach enables the provision of robust data on species richness in the deep sea and the expected species number is the best density-independent index for the comparison of areas with a nonstandardized sample size [34].

All indexes of biodiversity were calculated with the PRIMER 6 statistical package (www.primers.com). The results are also presented as the number of species present in a sample (species richness [SR]) or with widely accepted biodiversity indices. Shannon-Wiener diversity (H') was calculated as $H' = -\sum p_i \log_2 p_i$, where $p_i = n_i/N$, n_i is the

number of individuals of the i species, and N is the total number of individuals.

Functional Diversity

Functional diversity is the range of functions that are performed by organisms in a system [18]. In the present study, we used the number of different functional (trophic) traits based on the analysis of the feeding types according to the classical literature [35] and updated to the most recent approaches [36]. The diversity of morphofunctional traits has been measured with the assumption that different morphologies, buccal sizes, and other traits reflect a diverse ecological role (e.g., selection of food items within the same feeding guild). The number of predator species is another measure of functional diversity that depends upon the assumption that the number of species at the top of the benthic food web reflects a higher functional diversity of the entire benthic assemblage [37] (Table S4).

Ecosystem Functioning

Three independent indicators of ecosystem functioning were considered: (1) prokaryote biomass and production, (2) total faunal biomass, and (3) organic-matter decomposition. Prokaryotic biomass was estimated after cell counting, carried out by epifluorescence microscopy (EM).

Biovolumes were calculated after intercalibration with measurements conducted with EM and scanning electron microscopy (SEM) and converted into C content, with $310 \text{ fg C } \mu\text{m}^{-3}$ assumed as a conversion factor. Benthic prokaryotic production was measured by [^3H]-leucine incorporation [38]. So that the effect of decomposition on prokaryotic production could be determined, additional experiments were conducted under in situ pressure and at 1 atmosphere on samples collected at the sediment-water interface at approximately 2500 and 3500 m depth. Our results indicated that there were no significant differences between samples collected under in situ pressure and samples analyzed at 1 atmosphere (at approximately 2500 m depth: $0.068 \pm 0.02 \text{ ngC ml}^{-1} \text{ h}^{-1}$ both at in situ pressure and at 1 atmosphere; at 3500 m depth: 0.056 ± 0.03 and $0.048 \pm 0.01 \text{ ngC ml}^{-1} \text{ h}^{-1}$ in situ pressure and at 1 atmosphere, respectively). These results apply to all the samples collected above 3500 m depth (i.e., more than 70% of all samples).

For the determination of faunal biomass, we calculated the individual biomass of all animals belonging to different taxa. Nematode biomass was calculated from biovolume ($n = 100$ per replicate) with Andrassy's formula ($V = L \times W^2 \times 0.063 \times 10^{-3}$; body length L in μm and width W in μm). For all of the other taxa, the biovolume was measured for all of the specimens encountered. Body volume was derived from measurements of body length (L ; in mm) and width (W ; in mm) with the formula $V = L \times W^2 \times C$, where C is the approximate conversion factor for each meiofaunal taxon [39]. The body volume was multiplied by an average density (1.13 g cm^{-3}) to obtain the biomass ($\mu\text{g DW}$) assuming that the dry:wet weight ratio was 20%–25%, and the C content was considered as 40% of the dry weight.

For the measurement of organic matter decomposition, we determined extracellular enzymatic activities (as aminopeptidase) on surface sediments in triplicate by adding L-leucine-4-methylcoumarinyl-7-amide. This method has been widely used on sediments, including deep-sea systems [40].

Ecosystem Efficiency

Three independent indicators of ecosystem efficiency have been utilized: (1) the ratio of benthic faunal biomass to organic C fluxes, (2) the ratio of prokaryote C production to organic C flux, and (3) the ratio of benthic faunal biomass to biopolymeric C content in the sediment. For the determination of organic C fluxes data, originated from sediment traps deployed in the Equatorial Pacific, North Atlantic, and the Mediterranean at 50–150 mab (see Supplemental Data). Organic C concentrations were determined via standard protocols with a carbon hydrogen nitrogen (CHN) analyzer. The determination of the biopolymeric C in the sediment was estimated through the analysis of the biochemical composition of sediment organic matter [9].

Spatial and Temporal Variability of Deep-Sea Biodiversity

Analyses for the effect of spatial variability were conducted in the Western and Eastern Mediterranean Sea with samples collected in two bathyal plains within an extremely narrow bathymetric range

at 3000 m depth (approximately 1%). Spatial patterns were investigated with a hierarchical sampling design, as illustrated in Figure S7B (Table S1). The two regions are at a distance of more than 1000 km, allowing a comparison a large spatial scale. Within each of the two regions, a triangle of approximately 30 km along each side was identified. Three stations were located at approximately 7 km apart at the corner of each triangle. Finally, at each station, three independent deployments were performed. For the analysis of temporal variability, sediment samples were collected in three main areas: (1) the Porcupine Abyssal Plain (seasonal sediment sampling conducted at depth of 4850 m), (2) the Western Mediterranean, and (3) the Eastern Mediterranean (in both cases, biannual sampling conducted at 3000 m depth).

Statistical Analyses

The relationships between biodiversity and ecosystem functioning and ecosystem efficiency in the different deep-sea sites were assessed by nonlinear-regression analyses. The following equation was used for the fitting of the experimental data: $Y = a + m \times (X^b)$. A multivariate multiple regression analysis was also used for the investigation of the relationships between individual indexes of biodiversity and measures of ecosystem functioning and efficiency. All the analyses were done with the routine distance-based multivariate analysis for a linear model (DISTLM) forward [41], and the effects of depth and C fluxes were included as covariates in the analyses. p values were obtained with 4999 permutations of residuals under the reduced model [42].

Supplemental Data

Experimental Procedures, eight figures, four tables, and references for data sources are available at <http://www.current-biology.com/cgi/content/full/18/1/1/DC1/>.

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