Toward a Conceptual Understanding of β-Diversity in the Deep-Sea Benthos

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Keywords

Abstract

We review patterns and causes of β-diversity in the deep-sea benthos at different spatial scales and for different body sizes. Changes in species composition occurring with depth are generally gradual, the rate of change being a function of the rate of descent. This gradual change can be interrupted by abrupt environmental shifts, such as oxygen minimum zones, and by major topographic features that alter oceanographic conditions. Changes in species composition with depth can involve both species replacement and species loss, leading to nestedness. Horizontal β-diversity is more moderate than that occurring with depth, except at upper bathyal zones impacted by coastal influences. At very large oceanic scales, both environmental filtering and dispersal limitation influence β-diversity. Although many ecological and evolutionary–historical factors must shape β-diversity in the deep sea, energy availability appears to structure community makeup at all scales examined. We recommend that standardized sampling protocols, statistical methods, and data archiving be used to direct future research.

It is in the exploration of this vast deep-sea region that the finest field for submarine discovery yet remains.

—Forbes & Godwin-Austen (1859)

The occurrence of "guests" in the abyssal zone is a well-known phenomenon . . . . A population which has descended into the abyssal may be unable to reproduce (although, as far as I know, this has actually never been investigated), being dependent on the bathyal population for its replenishment.

—Knudsen (1970)

1. INTRODUCTION

Recently, there has been a resurgence of interest in β-diversity among ecologists as new analytical tools have become available to measure species turnover (Soininen et al. 2007a,b; Legendre 2008; Swenson 2011), decompose it into fundamentally different processes (Baselga 2010, 2012), and attribute compositional change to potential drivers, including environmental filtering, dispersal (McClain et al. 2012a), past climate change (Leprieur et al. 2011), and source–sink dynamics (Brault et al. 2013a,b). Quantitative sampling studies of changes in species composition along gradients in the deep-sea benthos began only in the late 1960s (reviewed by Gage & Tyler 1991, Carney 2005). Until quite recently, these studies were almost entirely inductive and descriptive. They have been primarily concerned with grouping assemblages of species into depth zones, regions of relatively little change separated by more pronounced transitions called boundaries. Speculation about causality has centered on which physical and oceanographic conditions coincided with, and might form, the boundaries. There have been few attempts to place patterns of faunal change into the modern theoretical contexts of ecology and biogeography. With more intensive sampling, it has become apparent that faunal change occurring with depth is mostly gradual, with few abrupt transitions, and the problem of β-diversity became one of explaining the relative rates of faunal change. Only during the past 10 years have large survey studies simultaneously sampled fauna along with biological and physical-environmental variables at the seabed, making it possible to statistically partition the variation in β-diversity among potential ecological causes, and develop a more general conceptual model of faunal change.

We review recent studies of β-diversity in the deep-sea benthos, attempt to infer common patterns and causes, and suggest an agenda for future research. We include large-scale descriptive studies because they permit us to establish accurate and consistent patterns of faunal change, without which we cannot begin to formulate causal explanations. We focus on similarities and differences among body sizes and spatial scales across both vertical (i.e., depth) and horizontal gradients. We hope this synthesis will make it possible to integrate β-diversity in the deep sea with patterns and causes in terrestrial and coastal systems to develop a unified theory of β-diversity.

2. PATTERNS OF β-DIVERSITY IN THE DEEP SEA

2.1. Local Scales

Most studies of variation in species composition at local scales have centered on meio- and macrofauna. Species richness in some localities can reach more than 300 species of macrofauna within a square meter (Grassle 1989, Etter & Mullineaux 2001). The reason for this high level of coexistence of species remains one of the most intriguing paradoxes in deep-sea ecology, and has received considerable theoretical attention. This high level of species coexistence is often linked to microhabitat variation. The creation of a spatial mosaic of patches is thought to reflect variability

in food parcels sinking from surface waters, bioturbation by megafauna, or biogenic structures created by other organisms (Jumars 1975, Jumars & Eckman 1983, Thistle 1983, Smith 1985, Jumars & Wheatcroft 1989, McClain & Barry 2010). Grassle & Sanders (1973) envisioned carbon flux and bioturbation as small-scale disturbances producing successional sequences that were temporally out of phase and varied across the landscape. In their model, local coexistence is achieved through the differential adaptation of species to successional stages. However, disturbance models or the temporal sequencing of successional changes need not be invoked. Food, biogenic structures, and bioturbation produce spatial variation in environmental regimes, leading to different suites of species adapted for each regime.

The empirical studies documenting high local turnover in macrofauna and meiofauna are limited. Sampling often yields species-accumulation curves that rarely reach an asymptote (reviewed in Etter & Mullineaux 2001, Snelgrove & Smith 2002), and are frequently interpreted as evidence of high turnover of local species. Initial work centered on species occurrences among subcores of boxcores. Contrary to the expected species patchiness proposed under the patch-mosaic hypothesis, the spatial distributions of individual species are often no different than the null expectation of randomness, suggesting there is a low response to environmental patchiness (Jumars 1975, 1976, 1978; Thistle 1978; Jumars & Eckman 1983; Lamont et al. 1995; reviewed in Rex & Etter 2010). As demonstrated in subsequent work, however, the variance-to-mean ratios utilized by some of these studies can be ineffective as measures of aggregation as departures from randomness (Hurlbert 1990, McClain et al. 2011). Experimental work creating artificial mounds or enriching nutrients has found assemblage shifts in only a small minority of species that are often opportunistic species and not found in background assemblages (Smith et al. 1986, Snelgrove et al. 1992). These limited responses led Rex & Etter (2010) to conclude that evidence suggests that patchy phenomena cannot account for high diversity in local species.

However, in a study utilizing precision coring with a remotely operated vehicle, McClain et al. (2011) attempted to account for some of these methodological and statistical issues. Extremely high variation was seen in dissimilarity among cores, regardless of the distance between them. Despite this variance, macrofaunal communities were slightly more dissimilar at greater distances and differed significantly from null-model expectations. The major finding was that the composition of the macrofaunal community changed approximately 1.5% for every 200 m, indicating that patchiness does have a role in structuring species composition at small spatial scales. At least part of the patchiness in composition (42%) was attributed to differences in the percentage of carbon in the sediment. We return to this point throughout this paper as forms of chemical energy appear to be important at larger scales as well (see Sections 2.2.1, 2.2.2, 2.3.1, and 4).

2.2. Regional Scales

At regional scales, considerable work has been conducted for β-diversity. This research demonstrates the central important of particulate organic carbon (POC) and the stronger patterns of β-diversity with vertical rather than horizontal distance change.

2.2.1. Megafauna. To convey the basic features of β-diversity in deep-sea megabenthic communities at regional scales in an intuitive way, we present an especially clear study, based on extensive photoreconnaissance of invertebrate megafauna in the western North Atlantic (Rowe & Menzies 1969), that recently has been reanalyzed using contemporary multivariate methods (Wei & Rowe 2009). Species ranges and abundances are shown in **Figure 1a**. Cluster analysis and nonmetric, multidimensional scaling detected nine species assemblages as defined by regions of more rapid transition (Wei & Rowe 2009), but turnover was continuous, without abrupt boundaries. The
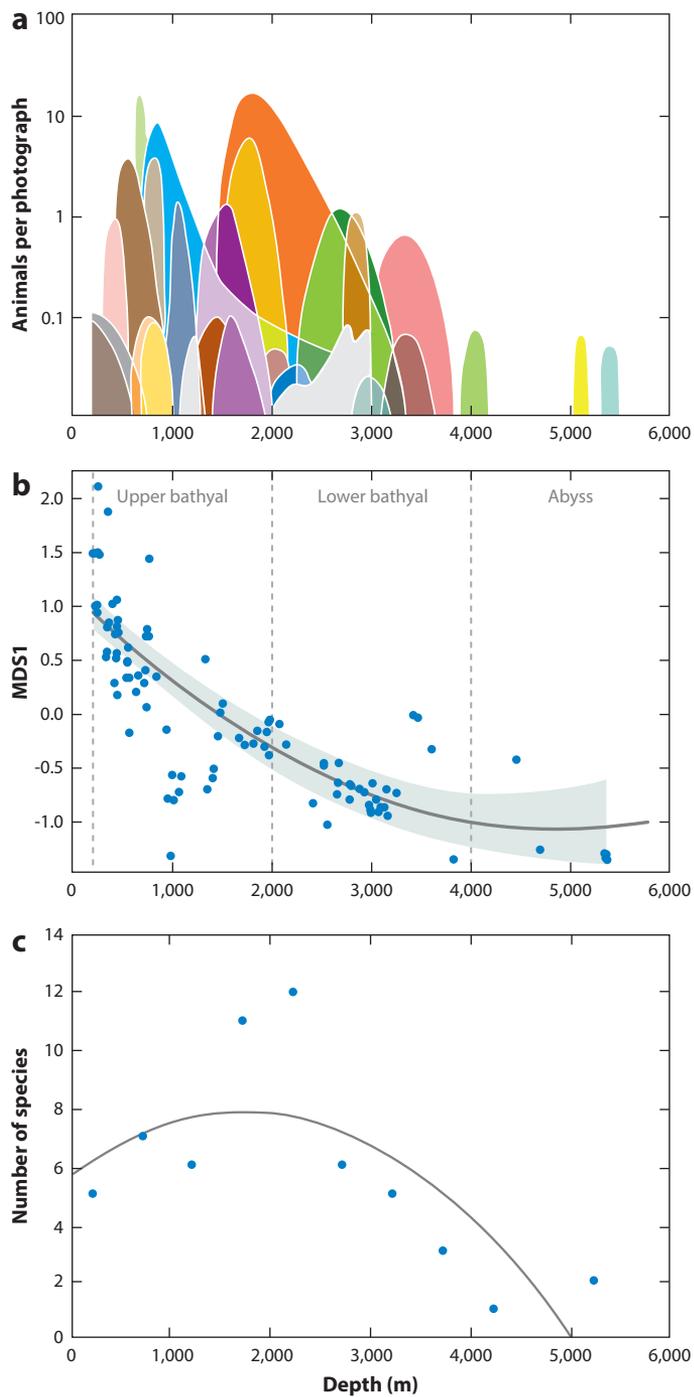
first nonmetric, multidimensional scaling axis plotted against depth revealed a gradual change in species composition that was steepest along the continental slope (200–2,000 m), then lessened on the continental rise (2,000–4,000 m) and in the abyss (>4,000 m), where only two species remained; in other words, turnover is a function of the rate of descent (**Figure 1b**). The bathymetric pattern of α-diversity is unimodal, with a peak at intermediate depths (**Figure 1c**). This is the most common pattern of α-diversity in the western North Atlantic. Extensive sampling below 5,500 m in this region revealed no megafaunal invertebrates. Although the habitat requirements of these megafaunal invertebrates are largely unknown, Rowe & Menzies (1969) speculated that bottom currents were ultimately responsible for shaping β-diversity. Bottom currents can deliver and redistribute sinking phytodetrital aggregates that fuel the benthic community, erode and deposit sediment, and disperse larvae. Depth ranges of megafaunal species may be compressed by biotic interactions, principally competition for smaller prey (Rex 1977, 1981). Consequently, the rate of turnover in megafauna is higher than in macrofauna, an important source of food for megafauna.

Hecker (1990) surveyed photographic transects for fish and invertebrate megafauna at upper bathyal depths in the western North Atlantic to the south of Georges Bank and New England. The transects spanned 400 km horizontally, allowing her to measure both vertical and horizontal dimensions of β-diversity. Species turnover was generally gradual and continuous, modulated by slope declivity, with higher turnover in steeper areas. The faunal makeup of the transects was similar, with the exception of a shift in dominant species at upper-slope depths that was associated with a particularly steep, rocky area south of Georges Bank. The pattern was supported by trawling studies (Haedrich et al. 1975, 1980) and observations made by submersibles (Grassle et al. 1975) undertaken in the same region. The trawling studies included lower bathyal and abyssal zones where turnover and α-diversity declined. Hecker (1994) later analyzed additional transects off Cape Hatteras. Other than shifts in the dominance of several species, the fauna was similar to that found south of New England. Again, most turnover was gradual and depth related, with some horizontal variation at upper-slope depths across about 50 km. Like Rowe & Menzies (1969), Hecker attributed the general pattern of species replacement to currents and their influence on nutrient input and sediment composition.

Wei et al. (2012) analyzed β-diversity in the bottom-fish megafauna of the northern Gulf of Mexico, one of the most intensively sampled regions of the deep sea (Rowe & Kennicutt 2008). The study included depths from the shelf-slope transition to the abyssal plain (3,700 m is the greatest depth in the gulf), and a horizontal range of 1,000 km along the continental margin. The fish fauna changed gradually and continuously with depth, showing no abrupt boundaries. The highest rate of change occurred at upper- to mid-bathyal depths. Little detectable change was observed

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Figure 1

β-Diversity of megafaunal invertebrates in the deep sea of the western North Atlantic off the coast of North and South Carolina, United States (data from Rowe & Menzies 1969, Wei & Rowe 2009). (*a*) Depth ranges and densities of individual species. Colors are used to distinguish species and have no taxonomic or ecological connotation. The density of the community decreases exponentially as depth increases. (*b*) The first axis of nonmetric, multidimensional scaling, revealing a gradual change in species composition occurring with depth that is steepest at the upper bathyal depths (200–2,000 m) and lessens at lower bathyal depths (2,000–4,000 m) and in the abyss (>4,000 m). The regression equation for the line is $Y = 1.18 - X + 0.11X^2$, $R^2_{adj} = 0.69$, $F_{2,98} = 112.8$, and $P < 0.001$. The shaded area represents the confidence limits. Data and analysis courtesy of Chih-Lin Wei. (*c*) Species diversity measured as the number of coexisting species in 250-m-depth bins, showing a unimodal relationship with depth. The regression equation is $Y = 5.617 + 0.003X - 7.319 \times 10^{-7}X^2$, $R^2 = 0.613$, $F_{2,8} = 6.334$, and $P = 0.022$. Figure reproduced with permission of Elsevier and the authors.

horizontally along depth contours, with the exception of several productivity hotspots. The rate of species turnover was generally a positive function of the biomass of the macrofauna, presumably an important part of their diet. Macrofaunal biomass is, in turn, a function of surface productivity and particulate organic carbon (POC) flux to the seafloor. The rate of change in fish composition lessened at high values of macrofaunal biomass, for example, at canyon heads where sinking food is topographically concentrated. Wei et al. (2012) suggested that this lower rate of change in fish composition may result from either reduced competition for prey or the inclusion of more mobile and generalist fish.

2.2.2. Macrofauna. Because of the difficulty in collecting and sorting samples of such small animals, and the taxonomic expertise required to identify them, most analyses of β-diversity in macrofauna have focused on individual taxa, for example, isopods (Brandt et al. 2004, Wilson 2008), amphipods (Weisshapple & Svavarsson 1998), cumaceans (Jones & Sanders 1972, Watling 2009), decapods (Cartes & Sardà 1993), bivalves (Olabarria 2005), gastropods (Aldea et al. 2008), and polychaetes (Grassle et al. 1979, Patterson et al. 1998). Most show continuous turnover with depth, with some idiosyncratic features devolving from environmental heterogeneity and the specific habitat requirements of individual taxa. Two important large-scale interdisciplinary programs have examined macrofauna as a whole: the Atlantic Continental Slope and Rise study (ACSAR) in the eastern North Atlantic (Grassle & Maciolek 1992, Blake and Grassle 1994) and the Deep Gulf of Mexico Benthos study (DGoMBS) in the northern Gulf (Rowe & Kennicutt 2008, Wei et al. 2010b).

Blake & Grassle (1994) analyzed β-diversity in the southern region of the ACSAR program, off of North and South Carolina. They detected faunal change both across and along isobaths. Most species turnover was depth related; stations were ordered along the ordination axis, reflecting increasing depth. Most horizontal variation occurred among three upper- to mid-bathyal samples (600–2,000 m). Two samples taken off Cape Hatteras resided in an area of unusually high POC flux, resulting from elevated surface production from upwelling and rapid offshore and down-slope transport of nutrients from coastal bays across a narrow shelf. Both samples showed unusually high animal abundance, low α-diversity, and low distributions of evenness of species-relative abundance, resulting from high numerical dominance of several species. These characteristics commonly occur together at deep-sea sites with high nutrient loading (Rex & Etter 2010). Differences in α-diversity per se can limit calculated similarity, but these two stations were also dominated by a unique group of polychaete worms usually found at depositional sites on the continental shelf (<200 m). Another station at 600 m was located at an erosive site where the Gulf Stream scoured the bottom, and was composed of carbonate sand rather than the fine, organic mud usually found at this depth. The site showed depressed α-diversity, and had a unique dominant fauna, probably associated with a different sediment regime, less organic food, and chronic physical disturbance. Overall, the main trend in β-diversity was depth related, with most horizontal variation occurring at shallower depths where the environment is more heterogeneous at these spatial scales because of coastal influences. Although the authors drew convincing qualitative associations between faunal similarity and environmental factors for atypical sites, no predictive models were used to test for the relative importance of potential environmental causes (e.g., currents, sediment type, nutrients) in shaping β-diversity across the whole sampling design.

Wei et al. (2010b) analyzed β-diversity among sites distributed between 200 and 3,700 m, covering around 1,000 km along the continental margin of the northern Gulf of Mexico (part of the DGoMBS program). The sampling design contained a major biogeographic barrier, the Mississippi River Delta, where massive terrestrial runoff is discharged. Environmental data, including salinity, satellite-derived POC flux, temperature, dissolved oxygen concentration, and

pollution indicators were collected simultaneously at the same sites allowing, for the first time, a statistical partitioning of community structure among ecological variables.

A hierarchical cluster analysis of faunal similarity among sites detected six zones, regions of relatively low turnover separated by regions of higher turnover. Upper bathyal and abyssal zones extended horizontally across the Gulf. Mid- and lower-bathyal zones were divided into east and west subdivisions. A two-dimensional nonmetric multidimensional scaling analysis revealed that faunal similarity was on a continuum with depth, without sharp boundaries, and also showed east and west differences at mid- and lower-bathyal depths, presumably due to the influence of the Mississippi River outflow.

POC flux and depth emerged as the best predictors of faunal similarity, with POC flux having a slightly higher correlation. The statistical redundancy of environmental variables with depth has been a persistent difficulty in understanding the ecology of deep-sea communities (Campbell Watts et al. 1992, Johnson et al. 2007) because so many independent variables are highly correlated with depth. For example, depth is a variable in the algorithm used by Wei et al. (2010b) to estimate POC flux at the depth of sampling sites. POC flux decreases exponentially with depth as sinking phytodetritus is mineralized by bacterial degradation. This means that correlations of environmental variables with measures of community structure could simply be spurious consequences of their mutual high correlations with depth. When the effect of depth is statistically removed from correlations of environmental variables with community structure by using partial correlation, the latter correlations often collapse into insignificance (e.g., Campbell Watts et al. 1992). This leaves the question: What other unmeasured depth-related ecological processes actually regulate community structure? Wei et al. (2010b) were the first to solve this thorny problem. The Gulf also has an east-to-west gradient of decreasing productivity along isobaths. A binary cluster analysis constrained by thresholds of the measured environmental variables was used to assess the importance of these variables on the pattern of β-diversity. POC flux best discriminated the east and west parts of mid- and lower-bathyal regions independently of depth. Although the results are correlative, as they are in virtually all large-scale biogeographic analyses, this is convincing evidence that productivity in the form of POC flux at depth shapes β-diversity in the deep-sea benthos at Gulf-wide spatial scales.

2.2.3. Meiofauna. Leduc et al. (2012) analyzed the β-diversity of nematodes on the upper continental slope off New Zealand. A very high correlation occurred between the similarity matrices based on abundances and data on presence and absence, indicating that β-diversity patterns among samples were driven primarily by compositional changes and not by differences in species abundances. Distances between sites, both horizontally and vertically, explained the greatest proportion of the variance (30% and 6%, respectively). Interestingly, the data do show an unusual pattern when compared with many other studies in which higher β-diversity was seen over horizontal rather than vertical gradients. Some of this has to do with the geographic separation of the Chatham Rise from the Challenger Plateau by the New Zealand landmass, leading to different biogeographic regimes. Environmental variables also explained approximately the same amount of variation as geographic distance. The strongest environmental predictor was sediment characteristics, which explained 30% of the variation, followed by food availability, explaining 17%.

2.3. Oceanic Scales

Fewer studies have addressed oceanic- or global-scale patterns of deep-sea β-diversity and are completely absent for megafauna. Like regional scales, the main driver appears to patterns of POC.

2.3.1. Macrofauna. Much of the theoretical treatment of deep-sea diversity has centered on macrofauna. In general, even at larger scales it is assumed that matching between the environment and species' niche requirements (i.e., environmental filtering) is the primary driver of patterns in biogeography and biodiversity (reviewed in McClain & Hardy 2010). Dispersal limitation is often seen as unimportant because the planktonic larval phases of many deep-sea invertebrates allow for long-distance dispersal and potentially large biogeographic ranges (reviewed in McClain & Hardy 2010). Yet despite this shaping much of the thinking on deep-sea diversity, it has rarely been evaluated. Given the paucity of data on deep-sea systems, especially over entire ocean basins, large oceanic-scale analyses of β-diversity are simply rare.

McClain et al. (2012b) explored patterns of β-diversity in taxonomic, phylogenetic, and functional diversity across the Atlantic Ocean, using the bivalve data set of Allen (2008). Overall, the data set included 527 bivalve species from 11 basins and 270 sites, ranging in depth from 518 to 5,875 m, an extraordinarily large compilation of data by deep-sea standards. Patterns of β-diversity were compared with an extensive environmental database similar to that of the Gulf study described above. McClain et al. (2012b) constructed a model that explicitly incorporated the relative contributions of dispersal and environmental filtering, accounting for both ecological and evolutionary processes, in a pattern-oriented simulation framework. By altering the relative strength of dispersal and environmental filtering in each simulation and comparing the model's output to the empirical patterns, the importance of these two processes could be determined (**Figure 2**). Surprisingly, both strong environmental filtering and dispersal limitation drove turnover in taxonomic, functional, and phylogenetic composition, explaining 26%, 34%, and 9% of the variation, respectively (**Figure 2**). However, rates of decay in faunal similarity were 8- to 44-fold steeper with environmental distance (i.e., environmental filtering and niche dynamics) compared with spatial distance (i.e., dispersal limitation). The only significant environmental factor predicting β-diversity was energy availability as indexed by temperature and particulate organic flux. Energy availability was the most influential variable evaluated, accounting for 3.9%, 9.4%, and 22.3% of the variation in functional, phylogenetic, and taxonomic similarity, respectively. Comparing empirical patterns with the process-based theoretical predictions provided quantitative estimates of both dispersal limitation and niche breadth, indicating that 95% of deep-sea bivalve propagules would not be able to persist in environments that deviated from their optimum by more than 2.1 g m^{-2} year^{-1} and that they could disperse 749 km from their natal site. These findings suggest that at oceanic scales, community composition is due to environmental filtering and niche-based processes, as well as to dispersal limitation. A study by Leduc et al. (2012) found similar patterns in nematode β-diversity, with 30% of the variation in species attributed to environmental variation and 26% remaining unexplained.

An interesting finding from McClain et al. (2012b) was the high variance in the model's outputs. In the highly controlled simulation systems, even with a single environmental driver, stochastic, evolutionary, and ecological processes introduced considerable noise into the distance–decay relationships (**Figure 2**). Indeed, a distance–decay line fit to the data explained less than 40% of the variation. To reiterate, much of the variation in models of β-diversity is attributed to stochasticity in the processes and not to environmental filtering or dispersal limitation. This has implications for the unexplained variance in analyses of empirical patterns of β-diversity. Many studies of β-diversity, even those using multiple independent variables, explain more than 30–50% of the variation (reviewed in McClain et al. 2012b). Often, unmeasured environmental variables are invoked to account for this low explained variance in β-diversity relationships. The findings of McClain et al. (2012b) suggest that missing variables are unlikely to improve these fits, given the importance of randomness and historical contingencies.
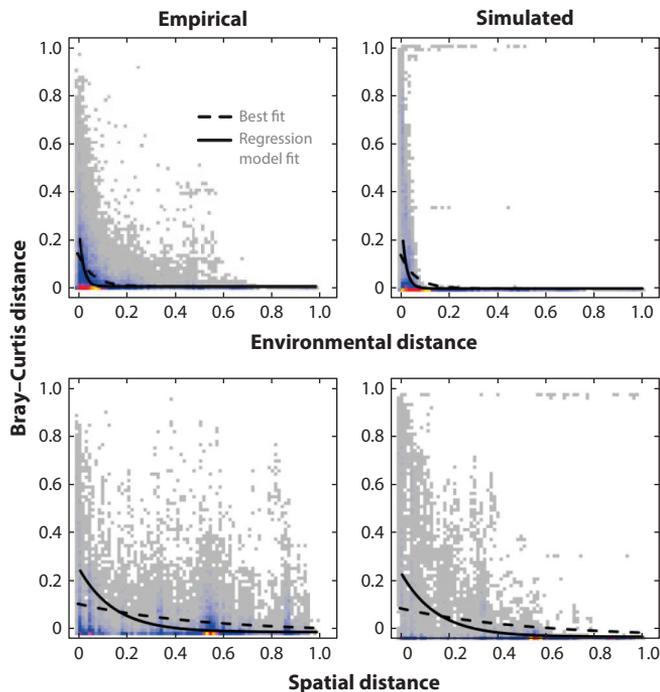
Empirical   **Simulated**

Environmental distance

Spatial distance

Figure 2

Empirical and simulated taxonomic distance–decay patterns of Atlantic deep-sea bivalves. Warmer colors indicate higher densities of data, with red having the highest density and gray having the lowest. The x-axis displays spatial or environmental distance between two sites, and the y-axis denotes taxonomic (Bray–Curtis distance), phylogenetic, or functional similarity between two sites. Dashed lines indicate the best-fit regression model to the empirical data, and solid lines indicate the regression model fit to simulation data from the chosen combination of dispersal and niche breadths. Geographic and environmental distances have been normalized. The simulated data shown represent a single replicate from the combination of dispersal and niche breadths that provided the best match between empirical and simulation data for each type of distance decay. Figure modified from McClain et al. (2012b) with permission of The Royal Society, London.

2.3.2. Meiofauna. Danovaro et al. (2008) explored patterns of nematode β-diversity across the Mediterranean Sea. Depth yielded the greatest differences between sites, with 75% dissimilarity between the shallowest and deepest stations, and 72% dissimilarity between two stations in the same region and separated by only 800 m of depth, although only the difference between the shallowest and deepest was significant. Other analyses (Danovaro et al. 2009) did, however, find significant changes in nematode composition over multiple depth transects in the Mediterranean and the nearby Portuguese margin in the Atlantic Ocean. Significant differences in assemblages were also observed across a longitudinal gradient for the entire ocean for abyssal sites but not bathyal sites. These findings suggest that gradients in β-diversity over horizontal differences are likely to vary as a function of depth. In a subsequent analysis by Gambi et al. (2013), total phytopigments and the ratio of protein to total phytopigments explained 72–95% of the variance in β-diversity among sites, again supporting energy availability as an important driver of the structure of deep-sea assemblages. However, in other studies of nematodes, productivity had a subordinate role to sedimentary characteristics (Vanreusel et al. 2010).

Gambi et al. (2013) carried out an impressive stratified sampling design of Mediterranean nematodes at small (<1 m), local (approximately 7 km), meso- (approximately 30 km) and macroscales

(>1,500 km). Food quantity drove patterns at larger scales, and the quality and bioavailability of food determined small-to-local scale patterns. β-diversity was also highest at the macroscale, an intriguing result given that studies using a distance–decay framework find the greatest rate of change at smaller scales (i.e., exponential decline). However, distance–decay relationships for deep-sea organisms may be quite variable and show considerable structure (McClain et al. 2012b). For example, the distance–decay relationships from McClain et al. (2012b) clearly possess more structure than a simple exponential decay, and have some evidence of a peak at intermediate scales.

3. INTERRUPTIONS OF β-DIVERSITY

Although β-diversity along depth gradients on uncomplicated continental margins is generally continuous and gradual, modulated by the rate of descent, patterns can be strongly affected or even interrupted by major topographic and oceanographic features. Horizontal shifts in β-diversity can also occur at submarine canyons that concentrate benthic biomass (De Leo et al. 2010, Vetter et al. 2010), sites of unusual productivity or shifts in the sedimentary regime (Blake & Grassle 1994), and deltas formed by riverine input (Wei et al. 2012). Seaward vertical shifts in species makeup occur within deep-sea trenches that separate continental margins from abyssal plains (Danovaro et al. 2003). The most well-known causes of abrupt vertical changes in β-diversity are oxygen minimum zones and large topographic structures that influence water masses.

3.1. Oxygen Minimum Zones

Oxygen minimum zones (OMZs) are layers of hypoxic water (dissolved $O_2 < 0.5$ mL L^{-1}) that impinge on the upper continental slope and extend seaward. They are caused by a combination of heavy nutrient loading that depletes oxygen and stagnant water masses that prevent mixing. They are extensive, permanent features in many areas of the Indo-Pacific, eastern Pacific, and eastern South Atlantic (Levin 2003, Helly & Levin 2004), and are expanding due to anthropogenic influences (Diaz & Rosenberg 2008, Stramma et al. 2010). Where OMZs intersect the slope, they create an extreme benthic environment of reduced oxygen and unconsolidated organic-rich sediments. Their core is dominated by a distinctive group of meiofauna and bacteria, and is inimical to all but a few hypoxia-tolerant macro- and megafaunal species. At their upper and lower boundaries, more oxic conditions permit an abundant, and progressively more normal, benthic community. **Figure 3a** illustrates the drastic effects of an OMZ on β-diversity along the Pakistan margin (Gooday et al. 2010). There is a sharp decline in oxygen at the upper boundary (approximately 200 m), and a rapid increase near and below the lower boundary (approximately 1,000 m). There is virtually no species turnover of macro- and megafauna in the core of the OMZ, where both size categories were nearly absent. Turnover resumes near the lower boundary, and reaches typically high levels for the upper slope below the OMZ. The megafauna appears to be more susceptible to hypoxic conditions in the sense that it begins to recover at higher oxygen levels.

3.2. Major Topographic Features

The most well-studied case of how a major topographic feature and altered current patterns influence β-diversity is the Greenland–Iceland–Faroe Ridge that separates the North Atlantic from the Norwegian Sea at a sill depth of only 200–600 m (Bett 2001, Narayanaswamy et al. 2010). Warm Atlantic water flows northward over the ridge where it covers very cold, deep water in the Norwegian Sea. Species diversity and composition are similar on both sides of the ridge at less
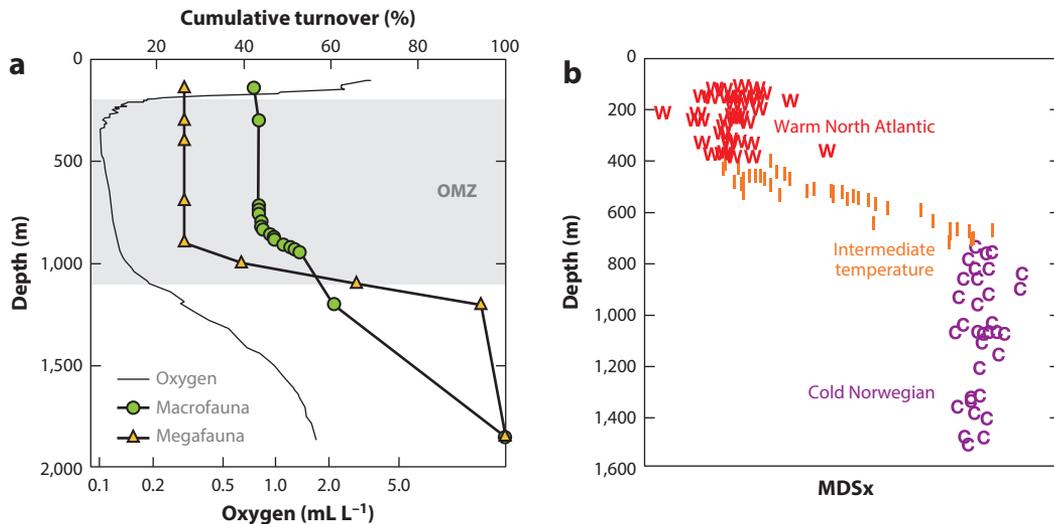
Figure 3

Patterns of β-diversity, which are generally gradual on uncomplicated continental margins, can be strongly modulated or even interrupted by major oceanographic shifts. (*a*) Effects of an oxygen minimum zone (OMZ) on the Pakistan margin. The OMZ (*gray*) is a sharply defined layer of hypoxic conditions. Within the OMZ β-diversity of both the macro- and megafauna do not change, and below the OMZ normal patterns are resumed. Panel *a* modified from Gooday et al. (2010) with permission of Wiley Blackwell and the authors. (*b*) Strong shift in β-diversity (MDSx) north of the Greenland–Iceland–Faroe Ridge that separates the North Atlantic and Norwegian Seas. W represents warm North Atlantic water that overlies cold (C) Norwegian Sea water. There is an abrupt shift in species composition through water of intermediate (I) temperature. Panel *b* reproduced from Bett (2001) with permission of Elsevier and the authors.

than 500 m, but at greater than 500 m, diversity is higher on the Atlantic side, and β-diversities diverge north and south. **Figure 3b** shows β-diversity north of the ridge. The shared warm-water fauna sharply transitions into cold-water fauna between approximately 400 and 700 m. Bett (2001) attributed the shift to temperature effects. It could also be related to differences in productivity. Phytodetrital aggregates have been observed on the bottom south of the ridge, but not on the north. Here, we see again that both thermal energy, reflected by temperature, and chemical energy, in the form of food supply, can potentially affect the structure of the deep-sea communities (Tittensor et al. 2011; McClain et al. 2012a,b). Clearly, differences in water mass can be associated with rapid changes in community structure at fairly small regional scales.

4. SPECIES REPLACEMENT AND NESTEDNESS ALONG BATHYMETRIC GRADIENTS

Rex et al. (2005) pointed out that much of the abyssal molluscan fauna in the North Atlantic is composed of highly attenuated range extensions of bathyal species that have larval-dispersal ability. Nearly all abyssal mollusks are minute, gonochoristic, and have extremely low mobility as adults. These factors combined with low population densities because of extremely reduced energy input make it unlikely that they could be reproductively viable. This has raised the possibility that rare abyssal populations are sinks that experienced chronic local extinction from vulnerabilities to Allee effects, and are maintained by continued migration from more abundant bathyal source populations. Moreno et al. (2008) first proposed that a nested analysis could be used as a

comparative test of the source–sink hypothesis. A nested pattern occurs when smaller communities form ordered, nested subsets of the species composition of larger communities (Atmar & Patterson 1993, Rodríguez-Gironés & Santamaría 2006, Ulrich et al. 2009). If source–sink dynamics apply, then abyssal communities should be nested subsets of bathyal communities.

β-diversity in the deep sea previously has been viewed entirely as spatial species replacement occurring along or across depth gradients. But Baselga (2010, 2012) recently showed that it can be partitioned into turnover and species loss, leading to nestedness. The two processes are distinct and require different interpretations. Brault et al. (2013a,b) explored the relative influence of turnover and nestedness in bathyal and abyssal deep-sea mollusks. Predatory neogastropods in the eastern North Atlantic showed both turnover and nestedness, but turnover is more important at less than 3,000 m, and nestedness at greater than 3,000 m. As source–sink theory predicts, nestedness increases with depth, and the rank order of nestedness among sites is a negative function of macrofaunal density, and a positive function of the proportion of species with larval-dispersal ability (Brault et al. 2013a). Bivalves present contrasting patterns of nestedness in the deep eastern and western North Atlantic (**Figure 4**). The species diversity of bivalves decreases from bathyal to abyssal depths in the west (**Figure 4a**), but increases in the east (**Figure 4c**). This difference results from higher surface productivity in the east, and consequently higher POC flux, extending seaward and supporting higher diversity overall, including higher abyssal diversity and endemism than is found in the west. Nestedness increases toward the abyss in the west (**Figure 4b**) but decreases in the east (**Figure 4d**), where turnover dominates along the entire depth gradient (Brault et al. 2013b). Eastern Atlantic echinoderms also exhibit turnover across the whole depth gradient (Wagstaff et al. 2014).

These results show that both turnover and nestedness can be important components of β-diversity in the deep sea and that they require different explanations. In mollusks, highly oligotrophic abyssal conditions are likely to cause abyssal nestedness, suggesting that abyssal communities are maintained partly by source–sink dynamics. Where abyssal food supply is sufficient to support a rich and abundant abyssal community, turnover continues down-slope, resulting in abyssal endemism. Not all taxa experience the decreased abyssal diversity that may be associated with source–sink dynamics. Holothurians maintain high abyssal diversity, possibly because they can rapidly and efficiently exploit sinking phytodetritus (Billett et al. 2001), as do isopods because they have made unique life-history adaptations to live at low density (Wilson 1991, 1998). The relative significance of turnover and nestedness is likely to depend both on patterns of productivity and the adaptive properties of different taxa.

5. β-DIVERSITY OVER VERTICAL AND HORIZONTAL DIMENSIONS, AND THE INTERACTION BETWEEN THEM

It is clear from multiple studies of deep-sea β-diversity that turnover is greater over depth gradients than along isoclines. This is not surprising because rates of environmental change are much greater with depth than with horizontal distance. More interestingly, β-diversity over horizontal distances may vary with depth itself. Indeed, the high α-diversity at intermediate depths may be related to increased small-scale β-diversity at those depths (Etter and Grassle 1992, McClain 2005, McClain & Barry 2010). For example, Danovaro et al. (2009) found significant patterns of longitudinal turnover across abyssal sites but not bathyal sites. Buzas et al. (2013) found that for forams from 333 stations distributed globally β-diversity was greatest for stations at less than 1,500 m depth. In **Figure 5** we plot data from Allen (2008) and McClain et al. (2012b) on bivalves of the Atlantic Ocean. We separated out samples into those occurring in three intervals (2,000–2,999 m, 3,000–3,999 m, and >4,000 m). Bray–Curtis similarities were calculated among samples within each
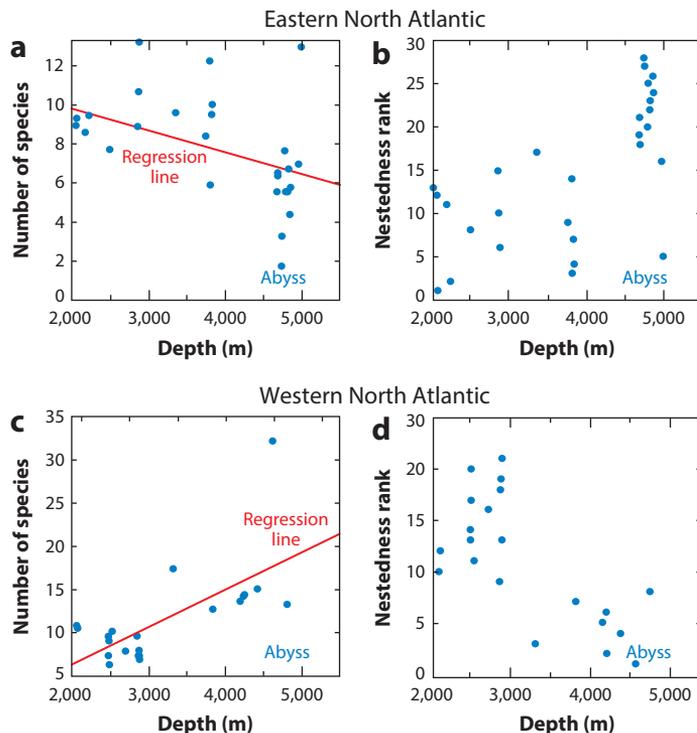
Figure 4

Species turnover and nestedness as components of β-diversity, showing the number of species and nested rank order of bivalve assemblages occurring with depth in the (*a,b*) eastern and (*c,d*) western North Atlantic. In the western North Atlantic, low surface productivity over the abyssal region results in low particulate organic carbon (POC) flux to the abyss, causing depressed species diversity. Abyssal assemblages are nested subsets of bathyal communities as shown by the significant increase in nestedness with depth ($\tau = 0.402$, $P = 0.002$). In the east, the opposite relationships obtain. Higher surface productivity extends seaward over the abyss, and abyssal diversity remains high and shows high endemism. Nested rank order decreases significantly with depth ($\tau = -0.368$, $P = 0.02$). The regression lines in panels *a* and *c* are meant to show only the general trends, and both are significant (for panel *a*, $P = 0.02$; for panel *c*, $P = 0.001$). The nestedness component of β-diversity depends ultimately on POC flux to great depths. Data from Brault et al. (2013a,b) with permission of Elsevier and the authors.

interval, and the distance–decay relationships were calculated. At the shallowest interval (2,000–2,999 m), the slope is nearly twice as steep as deeper basins, with similarity decreasing as a function of geographic distance between samples (**Figure 5**). The deeper relationships are statistically indistinguishable from one another, less negative, and considerably weaker. This suggests that at oceanic scales lower-slope and abyssal habitats show less turnover with horizontal distance than upper-slope habitats, possibly reflecting within-basin patterns in which coastal influences result in more horizontal variation at upper bathyal depths (e.g., Blake & Grassle 1994).

6. β-DIVERSITY IN DIFFERENT BODY-SIZE CATEGORIES

An obvious and important macroecological question is whether the body-size categories (meio-, macro- and megafauna) of deep-sea organisms affect β-diversity. Body size reflects a wide variety of processes operating at multiple scales, such as dispersal ability, speciation, and niche width (Brown

Distance-decay relationships for three isoclines for deep-sea bivalves in the Atlantic Ocean: (*a*) 2,000–2,999 m, (*b*) 3,000–3,999 m, and (*c*) 4,000–4,999 m. Solid red lines indicate linear fit for the specific depth group. Dotted lines indicate linear fits for the other depth groups for comparison. Relationships are all significant at $P < 0.0001$. Data are from Allen (2008) and McClain et al. (2012b).
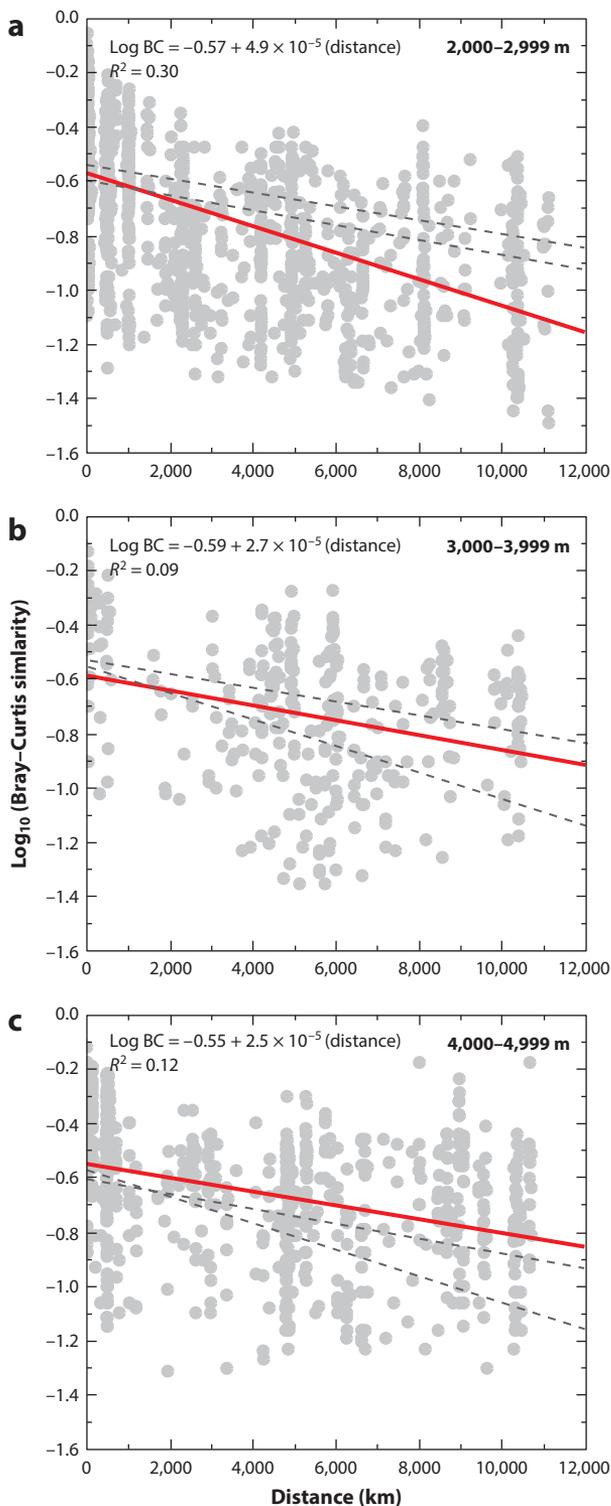
1995), many of the same factors that govern community structure. Community-wide bathymetric trends of β-diversity are partly a function of the representation of size categories. Because of the steep decrease in food supply that occurs with depth, and the higher energy demands of larger organisms, the standing stock of megafauna is lower and decreases faster than do macro- and meiofauna (Rex et al. 2006, Wei et al. 2010a). This drives overall β-diversity, as smaller organisms replace larger organisms as depth increases. Energy also shapes β-diversity through species loss in oligotrophic basins (**Figure 4**).

However, the databases used to detect these trends are global in scope, and allow little geographic control. What is needed to critically address the relationship between body size and β-diversity is to measure the strength and shape of β-diversity among meio-, macro-, and megafaunal size categories synoptically, and compare them among basins with different productivity regimes. This has not been done. Rex (1977, 1981) showed that distance decay varies among some subgroups of macro- and megafauna in the North American Basin, with larger organisms and predators having higher rates of species replacement with depth. The generality of these trends remains unclear.

7. THE ROLE OF EVOLUTIONARY–HISTORICAL PROCESSES

There are strong large-scale gradients of β-diversity in the deep sea that have clearly resulted from the origination, adaptive radiation, and global expansion of higher taxa. One of the most well-documented cases is revealed in the taxonomic makeup of isopods (Wilson 1998). They show a strong decreasing gradient of α-diversity from south to north across the entire Atlantic Ocean. This gradient is composed of two distinct taxa, the asellots, which represent an ancient in situ radiation resulting in a highly diverse and endemic fauna in both the North and South Atlantic. Superimposed on this fauna is a newer invasion of flabelliferan isopods centered in the South Atlantic, which is gradually spreading northward, resulting in the overall south-to-north diversity gradient and accounting for the attendant change in faunal composition.

Another exceptionally clear case involves foraminiferans, which have left a detailed fossil record in deep seabed cores. With global cooling occurring since the Eocene, productivity at high latitudes in the southern hemisphere became more seasonal, favoring more opportunistic phytodetritus-exploiting species toward the pole (Thomas & Gooday 1996, Sun et al. 2006). This increase creates a poleward gradient in species composition. Although larger deep-sea organisms essentially lack a fossil record due to high dissolution rates of $CaCO_3$, molecular genetic studies are beginning to reveal more about the phylogeography of taxa that will be useful in understanding the generation of large-scale patterns of β-diversity.

8. CONCLUSIONS

It is important to emphasize that most of the deep ocean remains unexplored, and that much more sampling needs to be done to accurately characterize and explain β-diversity. At regional scales on uncomplicated continental margins, macrofauna and megafauna show continuous and gradual changes in β-diversity with depth, the rate of change being proportional to the rate of descent and, presumably, the rate of environmental change. Horizontal β-diversity along isobaths is generally less pronounced than vertical change, except at upper bathyal depths where coastal influences are strongest. Although the causes of β-diversity must be highly multivariate, involving adaptation to conditions at different depths and dispersal abilities, energy supply to the benthos appears to be a consistent determinant of turnover. Meiofauna show both vertical and horizontal variation that appears to be associated with both sediment composition and food availability, possibly because such minute organisms experience the environment as more coarse-grained.

Although most bathymetric patterns of β-diversity are gradual and continuous, patterns can either be interrupted or even changed abruptly by major oceanographic features, such as OMZs, prominent topographic features, currents, and transitions in water masses. Much less is known about β-diversity at oceanic scales. A pan-Atlantic analysis of bivalve composition found that energy availability (POC flux and temperature) was the most effective predictor of taxonomic β-diversity, as well as phylogenetic and functional similarity. At these very large scales, both environmental filtering and dispersal limitation shape β-diversity. Energy availability also explains most of the β-diversity in meiofauna throughout the Mediterranean.

β-diversity is composed of two distinct components along environmental gradients: spatial turnover in species composition and nestedness resulting from species loss. Both processes operate in the deep sea and have different causes. Nestedness results from faunal attenuation with severe energy depletion in oligotrophic basins, and may reflect source–sink dynamics. Evolutionary–historical processes also drive β-diversity in the deep sea, and are represented by large-scale shifts in species composition associated with past climate change and spatiotemporal patterns of the invasion and spread of higher taxa.

FUTURE ISSUES

1. Future studies should strive to include more explicit tests of historical influences on patterns of β-diversity. Studies could potentially include clade age as one such factor in multivariate analyses. A more explicit phylogenetic framework, already used widely in terrestrial studies of β-diversity, also seeks to expose a multitude of evolutionary and historical insights.

2. Community standards need to be set for studies of deep-sea β-diversity. We propose that distance–decay analyses (Nekola & White 1999) become a standard for studies. These provide a variety of metrics that can be easily compared across studies (e.g., Soininen et al. 2007a,b). Slopes and effect sizes could be garnered from studies to allow for meta-analyses that could test how β-diversity varies across regions, spatial scales, gear biases, dispersal ability, clades, clade age, body size, and other variables.

3. Much more precise sampling and experimental work needs to be performed to identify relevant spatiotemporal scales and causes of small-scale turnover, and to target patterns across spatial scales.

4. More multivariate studies linking dispersal, environment, and history are greatly needed to detect the relative importance of these processes.

5. One of the most outstanding challenges remains how to measure and evaluate the role of biotic interactions in generating patterns of deep-sea biodiversity.

6. Published studies should be required to archive their data on diversity. This would allow for macroecological work that could potentially untangle the underlying causes of β-diversity and provide new directions for research. Likewise, the loss of historical and invaluable data sets would represent a major loss of information and effort.

7. Deep-sea ecologists need to recognize that there are two components of β-diversity: turnover (spatial replacement) and nestedness, representing species loss. The two processes can be measured and have distinctly different causes.

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