

Dispersal, environmental niches and oceanic-scale turnover in deep-sea bivalves

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Patterns of beta-diversity or distance decay at oceanic scales are completely unknown for deep-sea communities. Even when appropriate data exist, methodological problems have made it difficult to discern the relative roles of environmental filtering and dispersal limitation for generating faunal turnover patterns. Here, we combine a spatially extensive dataset on deep-sea bivalves with a model incorporating ecological dynamics and shared evolutionary history to quantify the effects of environmental filtering and dispersal limitation. Both the model and empirical data are used to relate functional, taxonomic and phylogenetic similarity between communities to environmental and spatial distances separating them for 270 sites across the Atlantic Ocean. This study represents the first ocean-wide analysis examining distance decay as a function of a broad suite of explanatory variables. We find that both strong environmental filtering and dispersal limitation drive turnover in taxonomic, functional and phylogenetic composition in deep-sea bivalves, explaining 26 per cent, 34 per cent and 9 per cent of the variation, respectively. This contrasts with previous suggestions that dispersal is not limiting in broad-scale biogeographic and biodiversity patterning in marine systems. However, rates of decay in similarity with environmental distance were eightfold to 44-fold steeper than with spatial distance. Energy availability is the most influential environmental variable evaluated, accounting for 3.9 per cent, 9.4 per cent and 22.3 per cent of the variation in functional, phylogenetic and taxonomic similarity, respectively. Comparing empirical patterns with process-based theoretical predictions provided quantitative estimates of dispersal limitation and niche breadth, indicating that 95 per cent of deep-sea bivalve propagules will be able to persist in environments that deviate from their optimum by up to $2.1 \text{ g m}^{-2} \text{ yr}^{-1}$ and typically disperse 749 km from their natal site.

Keywords: distance decay; beta-diversity; niche; dispersal; approximate Bayesian computation; pattern-oriented modelling

1. INTRODUCTION

Multiple interacting processes limit, sustain and augment global biodiversity, and these processes influence biodiversity, in part, by regulating turnover in species composition among sites. Numerous studies have related the degree of turnover (beta-diversity) or its converse (similarity) between pairs of communities to either the spatial or environmental differences between them [1–4]. Strong relationships between community similarity and geographical distance are interpreted as evidence for the primacy of spatial processes such as dispersal limitation. Conversely, strong relationships between similarity and environmental distance imply a role for niche-based processes such as environmental filtering. A recent review of 158 datasets demonstrated that spatial and niche-based processes contribute relatively equally, but that most variation in community structure remained unexplained [5].

Although spatial and niche-based processes both influence community composition, their relative importance varies across systems [6–8]. For example, temperate forests appear to be more influenced by niche-based processes

than by spatial processes [9]. In contrast, spatial effects overwhelm any environmental signal in the species composition of boreal stream diatoms [10]. Despite recent attention, the debate about the relative importance of spatial and niche-based processes for patterns of diversity is as vigorous and unsettled now [11–13] as it was 85 years ago [14,15].

This debate persists, in part, owing to methodological limitations. Most studies that consider both spatial and niche-based processes infer relative importance by comparing the variance in similarity of community composition explained by differences in spatial position with that explained by differences in environmental conditions [4,8,10,16]. While a useful starting point, three obstacles limit this approach. First, because variance in similarity explained by space or by environmental factors is not a monotonic function of their respective influences [17,18], the importance of underlying processes cannot be directly inferred from explained variance. Second, even if a high level of explained variance were interpretable, traditional approaches do not provide quantitative descriptions of how dispersal limitation or environmental filtering operate. Third, most analyses of beta-diversity focus exclusively on turnover in taxonomic composition. Recent analyses do, however, build from this classic approach by including phylogenetic and functional trait information [19–23]. This additional information

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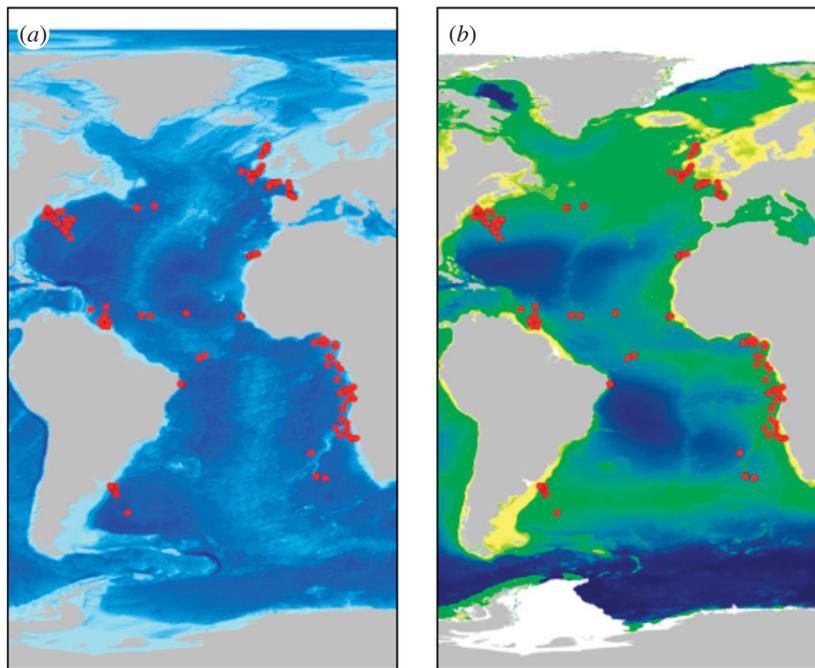


Figure 1. Spatial distribution of sampling locations indicated by red circles on a map of (a) bathymetry and (b) carbon flux.

estimates relative differences in ecological roles among species, potentially allowing greater insight into underlying processes.

Here, we work to overcome these limitations and, in turn, describe the relative degree and quantitative manner in which dispersal limitation and environmental filtering influence deep-sea bivalve communities. We focus on the deep sea because it is the largest and least-studied biome on the Earth. At large geographical scales, the deep sea exhibits considerable variation in species diversity over latitude and depth [24]. However, patterns of turnover in species composition, phylogenetic relatedness and functional traits are virtually unknown [24]. The modest work conducted on beta-diversity concentrates on the remarkably high level of faunal turnover at local scales [25–29]. Only recently has deep-sea biodiversity been linked to environment characteristics at large scales [30–33], but these studies primarily focus on explaining alpha-diversity. Given the long-distance larval-dispersal phases and large species ranges that characterize many deep-sea organisms [34], the environment, especially energy availability [24,35,36], is hypothesized to be the primary cause for determining deep-sea biodiversity patterns. However, no study has attempted to assess the relative contributions of dispersal limitation and environmental filtering to beta-diversity patterning in the deep sea.

Here, we characterize the relative contributions of dispersal limitation and environmental filtering for explaining differences in community composition of deep-sea bivalves across the Atlantic Ocean. Our approach uses a pattern-oriented simulation model [18,37,38] to couple dispersal limitation and environmental filtering to empirical descriptions of how between-community taxonomic, functional trait and phylogenetic similarity decays with spatial and environmental distance (distance decay). In addition, to compare deep-sea patterns with other systems, we use empirical distance-decay patterns to partition explained variance in similarity measures into a pure spatial

component, a pure environmental component and a spatially structured environmental component [39].

2. METHODS

(a) *Datasets*

From 1962 to 1979, several expeditions sampled the deep-sea benthos across the Atlantic Ocean. Allen [40] compiled and taxonomically standardized bivalve data, collected during these research cruises stemming from the research of Allen & Sanders [41]. Samples were taken with an epibenthic sledge [42]. As discussed by Allen [40], the dataset is restricted to those samples taken by epibenthic sledge as they provide a sufficient number of specimens per sample for quantifying and assessing dominance and biogeographic distributions. The epibenthic sledge is a semiquantitative sampling device and sampling area is likely to differ among samples. However, the variation in area sampled during individual sledge tows is probably well below an order of magnitude and is unlikely to be systematically biased. This is likely to add noise to our findings, but unlikely to alter our results. We define a bivalve community as all individuals from a sample. Our dataset includes 204 068 individuals and 527 bivalve species from 11 basins and 270 sites ranging in depth from 518 to 5875 m (figure 1).

Species-level maximum body size (biovolume) was the trait used to estimate functional similarity between communities. Body size is perhaps the most fundamental trait of an organism, influencing energetic requirements, demographic rates, life history and ecological niche [43–45]. Data were collected from the literature and biovolume was calculated as length \times width² (details can be found in McClain *et al.* [46]). Intra-specific variation in biovolume is much less than interspecific variation and the choice of using median or maximum body size in molluscs is unlikely to mask ecological patterns [47].

It was not possible to construct a fully resolved molecular phylogeny for the species in our dataset. As a proxy, we constructed a taxonomic tree in which branching points coincide with different levels of taxonomic hierarchy. We used order,

family and genus as our taxonomic levels, and all species within a genus were represented as a polytomy. Each level of the taxonomic tree was assigned a branch length of one. For simplicity, the taxonomic tree is referred to throughout as the empirical phylogeny.

Environmental data for each station were taken from the National Oceanographic Data Centre (NODC) World Ocean Atlas 2009 [48]. This provides (1° grid) climatological fields of *in situ* temperature (degree Celsius), salinity (ppm), dissolved oxygen (ml l^{-1}), percentage oxygen saturation, phosphate ($\mu\text{mol l}^{-1}$), silicate ($\mu\text{mol l}^{-1}$) and nitrate ($\mu\text{mol l}^{-1}$) at 33 depth layers. Annual means of the NODC data were taken from the depth layer closest to the empirical depth. Particulate organic carbon flux (POC; $\text{g m}^{-2} \text{d}^{-1}$) to the seafloor was estimated from the Lutz *et al.* model [49], as in previous deep-sea biodiversity studies [33].

(b) Empirical analyses

Similarity was quantified between all community pairwise combinations with metrics that weight by species relative abundances. We use Bray–Curtis as our measure of taxonomic similarity, and the complement of mean pairwise distance to characterize similarity in phylogenetic and functional trait composition. Mean pairwise distance measures calculate the sum, over all individuals in a focal community, of the phylogenetic or functional differences between each individual and all individuals in a second community [50]. For each pairwise comparison, we quantified environmental distance using the normalized Euclidean distance for each environmental variable, and great circle spatial distance (accounting for the Earth's curvature) between the two sample locations.

We characterized relationships between each type of similarity and spatial and environmental distances by fitting exponential decay models. Exponential models were used as they provided better fits to the data than linear models and are standard in studies of distance decay [51]. We used maximum likelihood with normally distributed error to estimate multiple regression parameters for the exponential models. This approach allows exponential 'slope' parameters to be compared among the three types of similarity. In addition to estimating slope parameters, we partitioned variation in similarity to components explained by space, the environment and the spatially structured environment [52]. Variance partitioning on distance matrices has been criticized because it explains less variation than other approaches [39] (but see [17]), so we also conducted variance partitioning using distance-based redundancy analysis [53].

(c) Model

To understand the processes underlying empirical distance-decay patterns, we used a recently described simulation model [18] with empirical constraints specific to our dataset. The primary goal of the simulation model was to produce taxonomic, functional and phylogenetic distance-decay patterns across different regions of 'process space'. This process space has two orthogonal axes: the strength of dispersal limitation and the strength of environmental filtering. Dispersal limitation was varied by changing the variance of a Gaussian dispersal kernel, whereas environmental filtering was varied by changing the variance of a Gaussian niche function. Increasing the variance of the dispersal curve or the niche curve causes weaker dispersal limitation or weaker environmental filtering, respectively. Eleven logarithmically spaced

values on each axis were used (from 0.0001 to 10), and simulations were run across all 121 unique combinations of process strengths.

The empirical constraints placed on the model included the spatial positions of sampled bivalve communities, the carbon flux at each site, the number of individuals at each site and the topology of the bivalve taxonomic tree. Other environmental data were not used because the model is currently limited to dealing with a single environmental variable, and carbon flux explained the most variation in turnover. A full account of the model is provided by Stegen & Hurlbert [18], so only a brief description is provided here. For a given combination of dispersal limitation and environmental filtering, the following steps were taken:

1. Species' environmental optima (traits) were evolved along the taxonomic tree under a model of Brownian evolution. We also assumed that a species' geographical centre of abundance (its 'range centroid') would be similar to that of its most recent ancestor, but that it might change over evolutionary time. Thus, we allowed the geographical range centroids of species to change through evolutionary time along the taxonomic tree in a similar manner to trait evolution. Simultaneously modelling the evolution of traits and range centroids requires specifying the covariance between them. As explained more fully by Stegen & Hurlbert [18], the extent to which trait values and range positions covary through evolutionary time will necessarily depend upon the strength of environmental filtering and dispersal limitation, as well as the degree of spatial structure in environmental variables. For example, if the environment is spatially structured, and both dispersal limitation and environmental filtering are strong, then range centroids should be tightly coupled to trait values (high covariance) because closely related species would have similar geographical distributions and would have experienced selection for similar environments. Conversely, if there is little spatial structure in the environment and both processes are weak, then we would expect range centroids and traits to be largely independent of each other (low covariance).
2. Each species was then assigned a global relative abundance by drawing randomly, without replacement, from a lognormal species abundance distribution. The distribution contained 527 species, the same number across all sampled bivalve communities.
3. Next, we defined a probability of occurrence of each species in each local site as the product of the species' global relative abundance, a term based on the spatial proximity of a species' range centroid to the focal site, and a term based on how closely the environment of the focal site matched the species' environmental optimum (its evolved trait value). The probability of dispersal was maximized at distance zero and declined following a Gaussian function characterized by the assumed degree of dispersal limitation. Similarly, the term based on the degree of fit to the environment was determined via the assumed Gaussian niche function.
4. Local community assembly was then simulated by drawing individuals into each local site until the empirically observed number of individuals was reached. For each site, the species pool was sampled with replacement, where the probability of occurrence defined the probability of each species being drawn. The taxonomic, functional

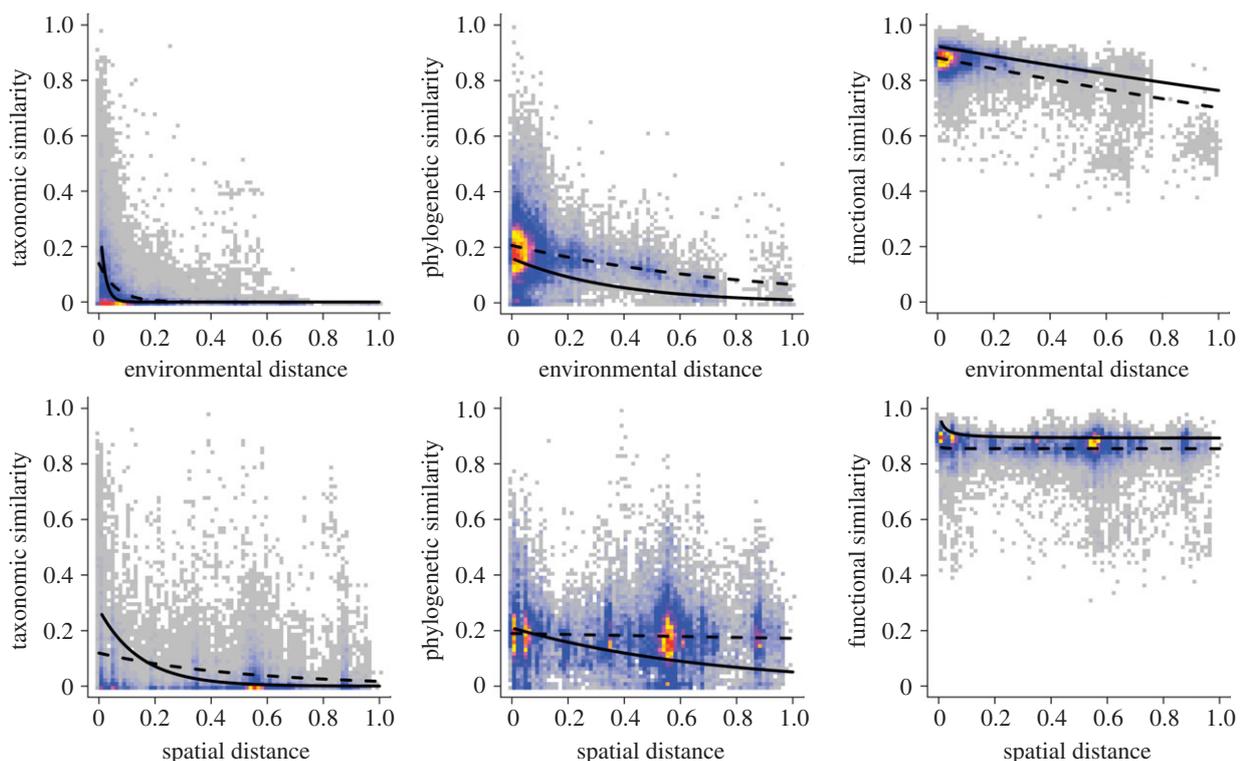


Figure 2. Empirical taxonomic, phylogenetic and functional trait distance-decay patterns. Warmer colours indicate higher densities of data, with red having the highest and grey having the lowest densities. Dashed lines indicate the best-fit regression model to the empirical data, and solid lines indicate the regression model fit to simulation data from the chosen combination of dispersal and niche breadths (figures 4 and 5). Geographical and environmental distances have been normalized.

and phylogenetic composition of each simulated community was therefore an emergent property influenced by trait evolution, geographical distribution, species global relative abundances, and the strengths of both dispersal limitation and environmental filtering.

5. Taxonomic, functional trait and phylogenetic similarity were quantified for all pairwise comparisons between communities. Exponential distance-decay functions relating similarity measures to spatial and environmental distances were fitted using maximum likelihood with normally distributed error. Maximum likelihood provides estimates for regression parameters and for the error around the regression line, which is crucial for comparing empirical and simulated data.
6. We repeated the above procedure 50 times for a given combination of dispersal limitation and environmental filtering, and calculated the mean of estimated regression parameters and error terms. Using maximum likelihood, we found the probability of the empirical data given these mean parameters (i.e. the negative log-likelihood).
7. The above steps 1–6 were repeated for each of the 121 combinations of dispersal limitation and environmental filtering, yielding negative log-likelihood values across process space. The location in process space resulting in the smallest negative log-likelihood value indicates the combination of dispersal limitation and environmental filtering that results in simulated patterns most similar to empirical patterns. Negative log-likelihood surfaces were created separately for taxonomic, functional and phylogenetic distance-decay patterns by summing the negative log-likelihood values based on the spatial distance decay and the environmental distance decay at each location in process space. We also summed across these three surfaces to

provide an integrated estimate of the *region* of process space most likely to represent the actual processes governing bivalve community composition.

3. RESULTS

(a) *Empirical analyses*

Whether considering functional, phylogenetic or taxonomic measures, geographical and environmental distances typically explained a small fraction of the observed variation in similarity (figure 2). Models incorporating both environmental and spatial distances accounted for up to 26 per cent of taxonomic, 34 per cent of functional and 9 per cent of phylogenetic differences between sites (figures 2 and 3; electronic supplementary material, table S1). Complete taxonomic turnover occurred rapidly over both environmental and geographical distances, whereas turnover in phylogenetic and functional composition was more gradual (figures 2 and 3; electronic supplementary material, table S1). In all but a few cases, the variance explained by the environment alone was greater than variance explained by space alone (figures 2 and 3; electronic supplementary material, table S1). Likewise, regression slopes related to environmental distance were generally steeper than slopes related to spatial distance (figures 2 and 3; electronic supplementary material, table S1).

Among the suite of environmental variables, carbon flux and temperature explained the most variation in functional, phylogenetic and taxonomic similarity (figure 3; electronic supplementary material, table S1). Carbon flux and temperature accounted, respectively, for 17.8 per cent and 21.3 per cent of the variation in taxonomic similarity, and for only 7.7 per cent and 6.9 per cent of variation in

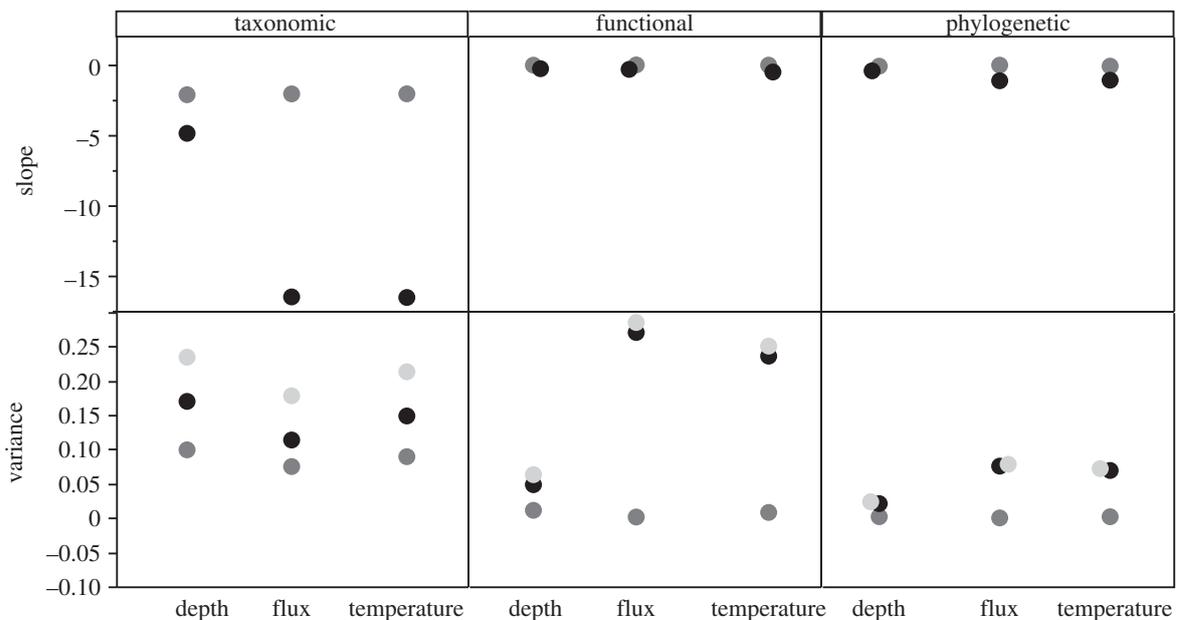


Figure 3. Partitioned variation and model slopes for taxonomic, functional and phylogenetic distance decay explained by depth, flux and temperature. We report the amount of variation explained by the spatial distance (dark grey), environmental distance (black) and a combined model (light grey) that incorporates both spatial and environmental distance.

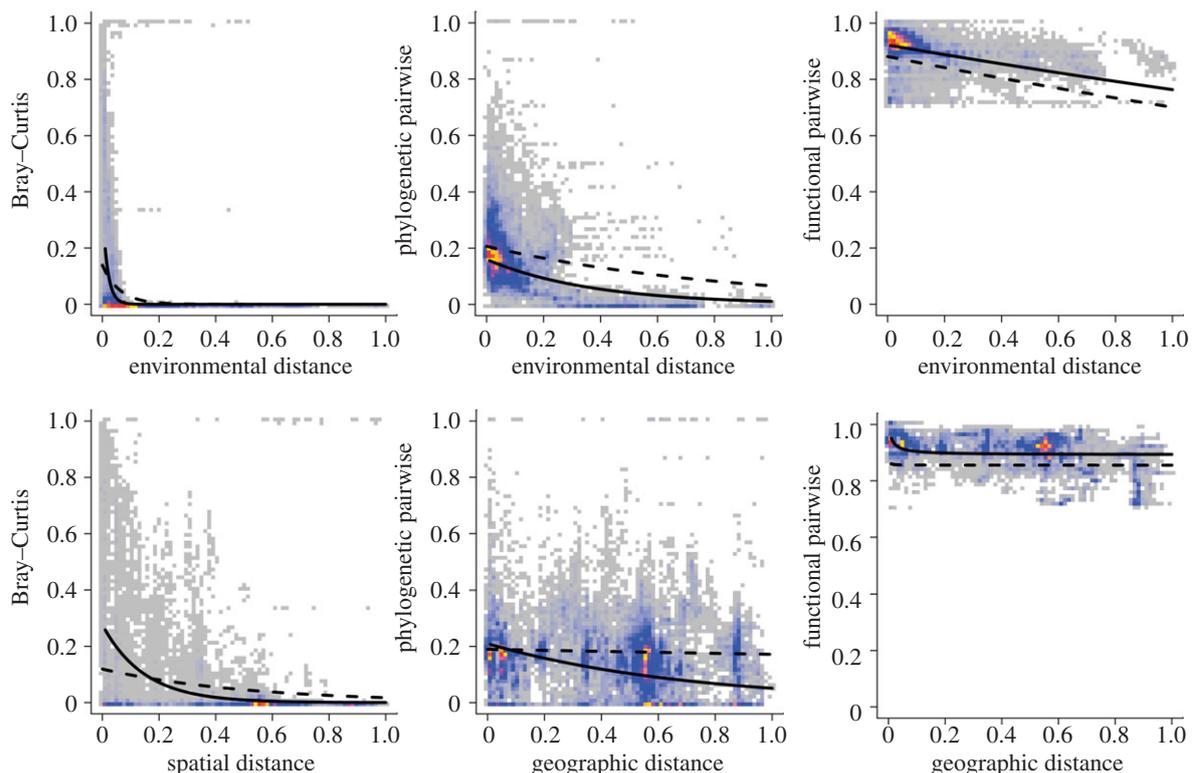


Figure 4. Simulated taxonomic, phylogenetic and functional trait distance-decay patterns. Warmer colours indicate higher densities of data, with red having the highest and grey having the lowest densities. Dashed lines indicate the best-fit regression model to the empirical data (figure 2), and solid lines indicate the regression model fit to simulation data from the chosen combination of dispersal and niche breadths (figure 5). The 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.

phylogenetic similarity (figure 3; electronic supplementary material, figure S1). In contrast, regression models using carbon flux or temperature accounted, respectively, for 29.2 per cent and 25.4 per cent of the variation in functional trait similarity. Models accounting for both temperature and carbon flux explained 33.9 per cent of

functional, 9.4 per cent of phylogenetic and 22.3 per cent of taxonomic similarity (electronic supplementary material, table S1). Because these environmental variables are correlated ($r = 0.69$), separating their unique effects is difficult. Carbon flux accounts for a slightly greater proportion of variance (1–4% more) than does temperature for both

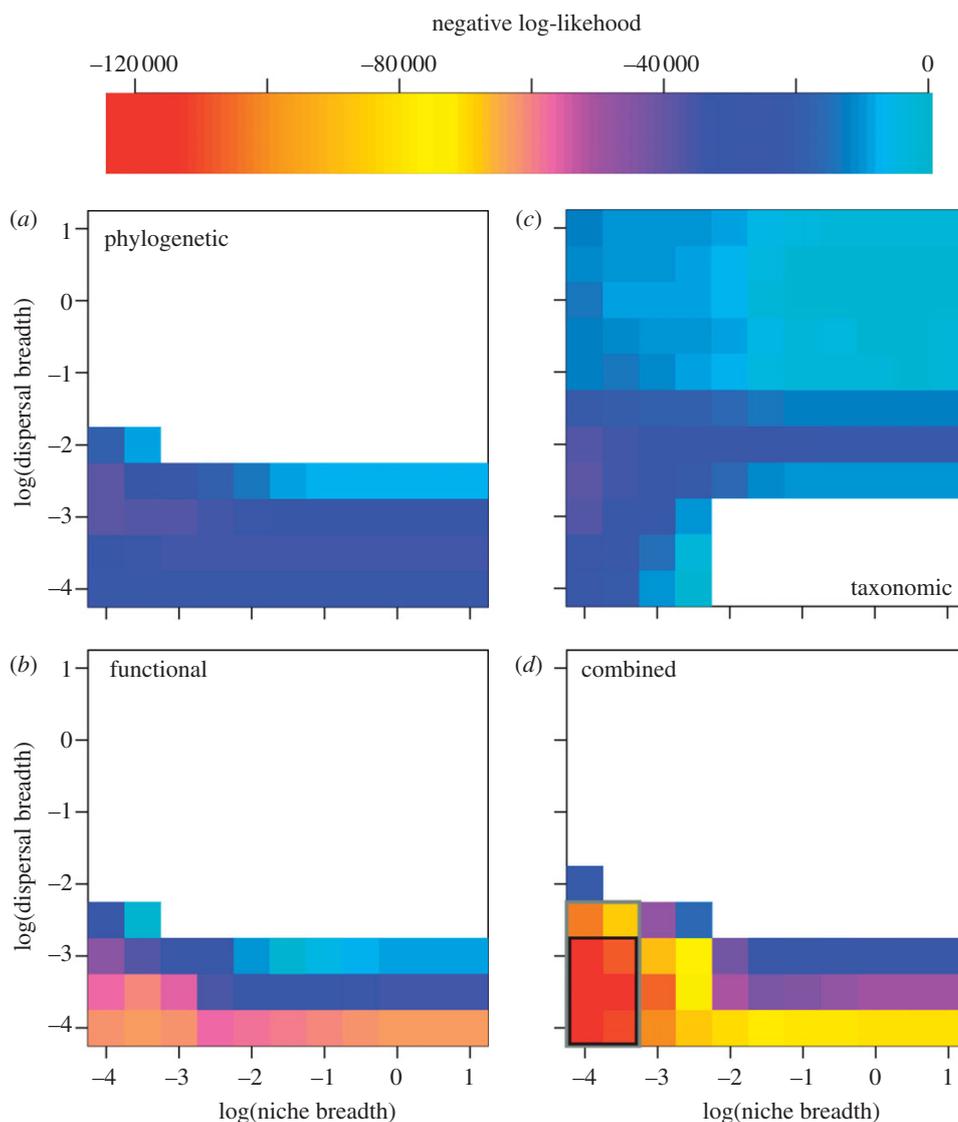


Figure 5. Negative log-likelihoods as a function of both dispersal and niche breadths. Smaller negative log-likelihood values indicate a better match between simulated and empirical data, and are shown as warmer colours (see spectrum at top). All panels are scaled the same. (a–c) Colours indicate the sum of negative log-likelihoods for regressions of similarity on geographical and environmental distances. (d) Stacks the other three panels, showing the sum of all negative log-likelihoods across phylogenetic, taxonomic and functional distance-decay patterns. The smallest 5% of negative log-likelihoods included six parameter combinations in the lower left corner (black box). The grey box encloses the minimum negative log-likelihood values from (a–c).

phylogenetic and functional similarity (electronic supplementary material, table S2). In contrast, temperature describes a slightly greater proportion (1–4% more) of variance in taxonomic similarity (electronic supplementary material, table S2). Other environmental variables individually explained less than 10 per cent of functional, 16 per cent of taxonomic and 5 per cent of phylogenetic similarity (electronic supplementary material, table S1).

Depth emerges as a strong predictor of taxonomic similarity, explaining 23.5 per cent of the variation (electronic supplementary material, table S1). The unique proportion of variance in taxonomic similarity associated with depth (i.e. vertical distance, 17%) is nearly twice that explained by horizontal distance (9.9%; electronic supplementary material, table S2), consistent with previous studies (reviewed by Rex & Etter [24]). For both functional and phylogenetic similarity, depth is a weak predictor (2.4–6.4%; electronic supplementary material, table S1). Although depth alone describes slightly more

of the variation in taxonomic similarity than either carbon flux or temperature, these three explanatory variables are highly correlated and jointly describe 15.6–18.9% of the variation (electronic supplementary material, table S1).

(b) Comparison with simulation model

Different combinations of dispersal limitation and environmental filtering in the simulation model yielded distinctive patterns of distance decay (electronic supplementary material, figure S1). The simulation model therefore provides good resolution whereby strengths of the underlying process can be inferred by comparing empirical and simulated patterns. In addition, the model's predictions responded in an intuitive way to increasing either the strength of dispersal limitation or environmental filtering (electronic supplementary material, figures S2–S5), providing additional support for the utility of the modelling framework. Specifically, stronger environmental filtering

or dispersal limitation resulted in steeper environmental or spatial distance-decay patterns, respectively (electronic supplementary material, figures S2–S5).

Model parameters were obtained that yielded simulated patterns (figure 4) of phylogenetic, functional and taxonomic distance decay comparable with empirical patterns (figure 2). The region of process space where empirical and simulated phylogenetic distance decay best matched each other was a combination of very strong environmental filtering ($n = 10^{-4}$) and moderately strong dispersal limitation ($d = 10^{-2.5}$; figure 5a). A similar pattern was found for taxonomic distance decay, with the best match occurring in the same location of process space (figure 5c). Functional trait distance decay showed a somewhat different pattern, with good matches emerging under strong dispersal limitation independent of the strength of environmental filtering. The best match, however, occurred where dispersal limitation and environmental filtering were both quite strong ($n = 10^{-3.5}$ and $d = 10^{-4}$; figure 5b).

After combining negative log-likelihoods from taxonomic, phylogenetic and functional trait analyses, the lowest 5 per cent of negative log-likelihoods included six parameter combinations in the lower left corner of process space (black box, figure 5d). These six parameter combinations varied from dispersal breadths of 10^{-4} to 10^{-3} , and from niche breadths of 10^{-4} to $10^{-3.5}$.

4. DISCUSSION

Our findings provide evidence that distance-decay patterns of the deep-sea benthos at oceanic scales are driven by both environmental filtering and dispersal limitation. In the best statistical models, variation in environmental parameters uniquely explained more of the variation in taxonomic, functional and phylogenetic similarity than spatial distance. In addition, rates of decay in similarity with environmental distance were eightfold to 44-fold steeper than with spatial distance. Together these patterns suggest that the niche-based process of environmental filtering more strongly influences deep-sea bivalve communities than the spatial process of dispersal limitation. Comparing empirical distance-decay patterns with simulation model predictions provided additional insight into how much stronger environmental filtering is than dispersal limitation, which cannot be directly inferred from variation partitioning or regression analyses [18]. Specifically, the empirical–theoretical comparison confirmed that environmental filtering is stronger than dispersal limitation, but not dramatically. Our analyses therefore suggest that both niche-based processes and spatial processes strongly influence deep-sea bivalve community composition at the oceanic scale.

Many deep-sea taxa possess substantial dispersal abilities augmented by extended larval development in cold deep waters [34,54], yet our model showed that dispersal limitation strongly influences oceanic-scale patterns of turnover in community structure. Simulations in which the dispersal breadth parameter ranged from 10^{-4} to 10^{-3} best matched empirical distance-decay patterns. Because this parameter is the variance of a Gaussian dispersal kernel, and because geographical distance in the simulations is scaled to the maximum observed inter-site distance, we can interpret d -values in a probabilistic context based on empirical distances. In this case, the

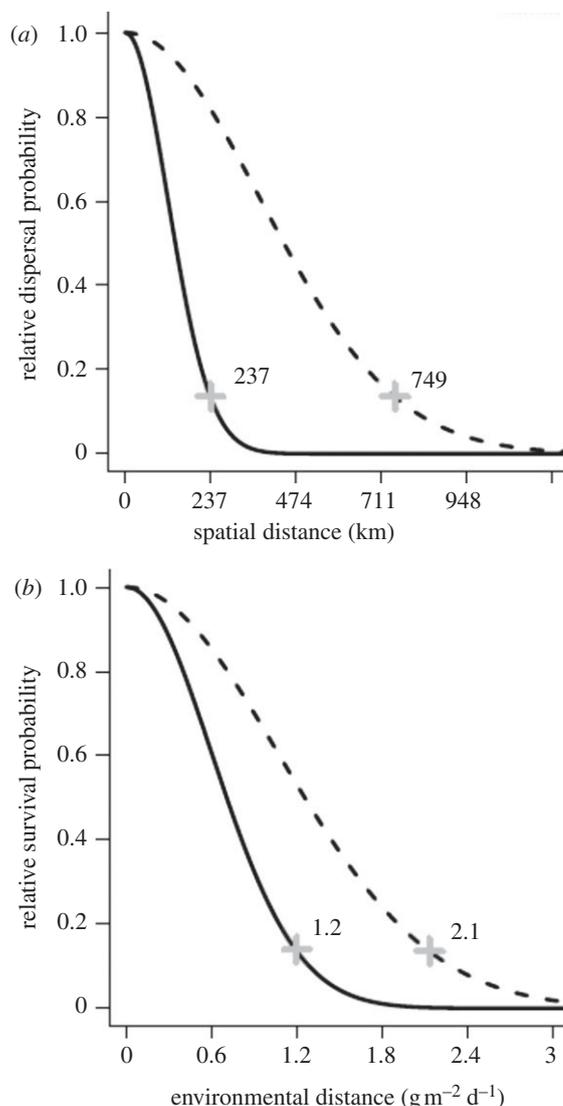


Figure 6. Quantitative descriptions of how dispersal limitation and environmental filtering operate in deep-sea bivalves. More specifically, shown are Gaussian (a) dispersal (dashed line, $d = 10^{-3}$; solid line, $d = 10^{-4}$) and (b) survival (dashed line, $n = 10^{-3.5}$; solid line, $n = 10^{-4}$) curves estimated by comparing empirical and simulated distance-decay patterns. Spatial distance is with reference to the spatial position of a reproducing individual and environmental distance is with reference to the environmental optimum of an individual. Solid curves are characterized by the smallest estimated variance for each type of curve, and therefore the strongest estimated strength of each process. Dashed curves are characterized by the largest estimated variances, and thus the weakest estimated strength of each process. The estimated range in variances is delineated by the lowest 5% of negative log-likelihoods from figure 5d. Plus symbols indicate the 95th percentile of each function, and the corresponding x -axis values are indicated.

95th percentile of the dispersal kernel corresponds to somewhere between 237 and 749 km, based on estimates of $d = 10^{-4}$ and $d = 10^{-3}$, respectively (figure 6a). This indicates that on average across species, 95 per cent of deep-sea bivalve propagules disperse somewhere between 237 and 749 km from their natal site. Although actual larval dispersal distances are unknown for deep-sea soft-bottom bivalves, these estimates are reasonable given a simple model of potential larval dispersal. *Bathymodiolus*

childressi, a cold seep mussel, has a planktonic larval duration of up to 270 days [55], yielding a dispersal distance up to approximately 1000 km based on moderate currents [34]. Given a potential shorter larval duration of 15–40 days for the bivalves in this study, dispersal distances would be 200–500 km under mild bottom currents [34], similar to our theoretical predictions.

Our results suggest that dispersal limitation and environmental filtering simultaneously influence community composition, and that energy availability is the most influential environmental variable evaluated here. In addition, our comparison of empirical and simulated distance–decay patterns estimated the variance of the Gaussian niche curve ranges from 10^{-4} to $10^{-3.5}$. As with the measure of dispersal breadth, this value can be interpreted in terms of relevant environmental differences on an absolute scale. Based on the 95th percentile of the niche function related to carbon flux, 95 per cent of deep-sea bivalve propagules will be able to persist in environments that deviate from their optimum by 1.2 to $2.1 \text{ g m}^{-2} \text{ yr}^{-1}$. The deep oceans are exceptionally energy-limited, so it makes biological sense that deep-sea organisms would be sensitive to such small changes in carbon flux [24,36,56,57]. In addition, functional attributes such as body size have long been hypothesized to reflect patterns in carbon flux to the deep seafloor [58,59], but such relationships have never been quantitatively tested. Consistent with this hypothesis, we show that body size differences among locations are primarily owing to differences in carbon flux.

In our analyses, most of the variation in similarity remained unexplained. Low explained variance appears to be a general pattern across systems [5,8,11,60,61]. In part, low explained variance could be due to unmeasured environmental variables. For example, sediment characteristics not included in this study correlate with deep-sea species richness [30]. Unfortunately, other datasets characterizing environmental variables across the Atlantic Ocean do not exist beyond the seven variables examined here. In addition, one need not invoke unmeasured environmental variables to account for low explained variance as our simulation model shows that even with a single environmental driver, stochastic evolutionary and ecological processes introduce considerable noise into distance–decay relationships.

We found good correspondence between empirical patterns and theoretical predictions, but the match was not exact. The most apparent difference was the greater scatter in empirical values for functional trait (cf. figures 2 and 4, right panels) and taxonomic similarity versus environmental distance (cf. figures 2 and 4, top left panels). This departure from simulation predictions may be owing to stochastic disturbances in the empirical system. In addition, increased scatter in empirical functional similarity may suggest that additional traits besides body size have important influences on community assembly. A more subtle departure from simulation predictions was found in the pattern of spatial phylogenetic distance decay at very large spatial distances, in which predicted similarity was less than that observed empirically. A likely cause for this is rare, very long dispersal events that occurred in deep evolutionary time. Replacing the Gaussian curve with a heavy-tailed function such as the Weibull distribution, thereby allowing for

these rare dispersal events, could prove useful in determining the cause of the difference in empirical and simulated phylogenetic distance–decay patterns.

Discrepancies between the empirical and model-generated patterns may also reflect simplifying assumptions of the simulation model. First, we assumed that dispersal limitation and environmental filtering are the two most influential processes governing community structure. We also implicitly invoke competition by making the probability of occurrence at a given site dependent on the presence of other species that are better suited to the site's environment. However, it would be useful to explicitly include species interactions in future modelling efforts. Second, we assumed the probability of dispersing to a given site declines the further that site is from a species geographical centre of abundance—a significant unknown for deep-sea organisms. Third, we modelled the average way in which dispersal limitation and environmental filtering influence all species. Thus, we do not incorporate interspecific variation in dispersal ability or degree of environmental specialization. These are simplifying assumptions that help make the framework more tractable and its predictions more interpretable. Nonetheless, we encourage further development of the simulation approach taken here, and note that Stegen & Hurlbert [18] provide a full account of the model's assumptions and point to reasonable ways in which these assumptions could be altered.

While minor differences between our theoretical predictions and the empirical patterns exist, the striking degree of empirical–theoretical correspondence supports our quantitative estimates of average dispersal abilities and environmental tolerances. Our estimates of the absolute geographical distances and environmental differences that affect probabilities of successful dispersal and colonization should, however, be interpreted as first approximations. Nonetheless, our study suggests that deep-sea bivalves will be considerably impacted by climate change. Recent work indicates that a 1 per cent reduction of median phytoplankton production occurred annually over the last century [62] and that there has been a considerable redistribution of production at the ocean's surface [63]. Over the same period, the heat capacity of the deep oceans increased from 16 to 89 per cent [64]. Previous work predicts that deep-sea fauna will respond rapidly to changes in energy availability [65,66], and our results further suggest that reduction and redistribution of global phytoplankton production and temperature regimes could severely impact global patterns of deep-sea biodiversity and community composition.

Very little is known about large-scale patterns of turnover in taxonomic, functional and phylogenetic composition in the Earth's largest environment, the deep sea. Here, we demonstrate a link between deep-sea community structure and both energetics and dispersal limitation. This study also illustrates the utility of a modelling approach incorporating both ecological and evolutionary dynamics as they relate to space and the environment. In doing so, we have provided strong clues about the relative effects of spatial and niche-based processes on oceanic-scale patterns of community structure while obtaining community-level estimates of niche breadth and dispersal ability.

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REFERENCES

- 1 Van der Gucht, K. *et al.* 2007 The power of species sorting: local factors drive bacterial community composition over a wide range of spatial scales. *Proc. Natl Acad. Sci. USA* **104**, 20 204–20 409. (doi:10.1073/pnas.0707200104)
- 2 Vanschoenwinkel, B., De Vries, C., Seaman, M. & Brendonck, L. 2007 The role of metacommunity processes in shaping invertebrate rock pool communities along a dispersal gradient. *Oikos* **116**, 1255–1266. (doi:10.1111/j.0030-1299.2007.15860.x)
- 3 Jones, M. M., Tuomisto, H., Borcard, D., Legendre, P., Clarke, D. B. & Olivas, P. C. 2008 Explaining variation in tropical plant community composition: influence of environmental and spatial data quality. *Oecologia* **155**, 593–604. (doi:10.1007/s00442-007-0923-8)
- 4 Sattler, T., Borcard, D., Arlettaz, R., Bontadina, F., Legendre, P., Obrist, M. & Moretti, M. 2010 Spider, bee and bird communities in cities are shaped by environmental control and high stochasticity. *Ecology* **91**, 3343–3353. (doi:10.1890/09-1810.1)
- 5 Cottenie, K. 2005 Integrating environmental and spatial processes in ecological community dynamics. *Ecol. Lett.* **8**, 1175–1182. (doi:10.1111/j.1461-0248.2005.00820.x)
- 6 Thompson, R. & Townsend, C. 2006 A truce with neutral theory: local deterministic factors, species traits and dispersal limitation together determine patterns of diversity in stream invertebrates. *J. Anim. Ecol.* **75**, 476–484. (doi:10.1111/j.1365-2656.2006.01068.x)
- 7 Soininen, J., Lennon, J. J. & Hillebrand, H. 2007 A multivariate analysis of beta diversity across organisms and environments. *Ecology* **88**, 2830–2838. (doi:10.1890/06-1730.1)
- 8 Bennett, J. R., Cumming, B. F., Ginn, B. K. & Smol, J. P. 2010 Broad-scale environmental response and niche conservatism in lacustrine diatom communities. *Glob. Ecol. Biogeogr.* **19**, 724–732. (doi:10.1111/j.1466-8238.2010.00548.x)
- 9 Gilbert, B. & Lechowicz, M. 2004 Neutrality, niches, and dispersal in a temperate forest understory. *Proc. Natl Acad. Sci. USA* **101**, 7651. (doi:10.1073/pnas.0400814101)
- 10 Heino, J., Bini, L., Karjalainen, S., Mykrä, H., Soininen, J., Vieira, L. & Diniz-Filho, J. 2010 Geographical patterns of micro-organismal community structure: are diatoms ubiquitously distributed across boreal streams? *Oikos* **119**, 129–137. (doi:10.1111/j.1600-0706.2009.17778.x)
- 11 Condit, R. *et al.* 2002 Beta-diversity in tropical forests trees. *Science* **295**, 666–669. (doi:10.1126/science.1066854)
- 12 Tuomisto, H., Ruokolainen, K. & Yli-Halla, M. 2003 Dispersal, environment, and floristic variation of western Amazonian forests. *Science* **299**, 241. (doi:10.1126/science.1078037)
- 13 Kembel, S. W. & Hubbell, S. P. 2006 The phylogenetic structure of a neotropical forest tree community. *Ecology* **87**, 86–99. (doi:10.1890/0012-9658(2006)87[86:TP SOAN]2.0.CO;2)
- 14 Gleason, H. A. 1926 The individualistic concept of plant association. *Bull. Torrey Bot. Club* **53**, 7–26. (doi:10.2307/2479933)
- 15 Clements, F. E. 1936 Nature and structure of the climax. *J. Ecol.* **24**, 252–284. (doi:10.2307/2256278)
- 16 Lindo, Z. & Winchester, N. N. 2007 Resident corticolous oribatid mites (Acari: Oribatida): decay in community similarity with vertical distance from the ground. *Ecoscience* **14**, 223–229. (doi:10.2980/1195-6860(2007)14[223:RCOMAO]2.0.CO;2)
- 17 Smith, T. W. & Lundholm, J. T. 2010 Variation partitioning as a tool to distinguish between niche and neutral processes. *Ecography* **33**, 648–655. (doi:10.1111/j.1600-0587.2009.06105.x)
- 18 Stegen, J. C. & Hurlbert, A. H. 2011 Inferring eco-evolutionary processes from taxonomic, phylogenetic and functional trait β -diversity. *PLoS ONE* **6**, e20906. (doi:10.1371/journal.pone.0020906)
- 19 Graham, C. H. & Fine, P. V. A. 2008 Phylogenetic beta diversity: linking ecological and evolutionary processes across space and time. *Ecol. Lett.* **11**, 1265–1277. (doi:10.1111/j.1461-0248.2008.01256.x)
- 20 Graham, C. H., Parra, J. L., Rahbek, C. & McGuire, J. A. 2009 Phylogenetic structure in tropical hummingbird communities. *Proc. Natl Acad. Sci. USA* **106**, 19 673–19 678. (doi:10.1073/pnas.0901649106)
- 21 Devictor, V., Mouillot, D., Meynard, C., Jiguet, F., Thuiller, W. & Mouquet, N. 2010 Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: the need for integrative conservation strategies in a changing world. *Ecol. Lett.* **13**, 1030–1040.
- 22 Scheckenbach, F., Hausmann, K., Wylezich, C., Weitere, M. & Arndt, H. 2010 Large-scale patterns in biodiversity of microbial eukaryotes from the abyssal sea floor. *Proc. Natl Acad. Sci. USA* **107**, 115–120. (doi:10.1073/pnas.0908816106)
- 23 Swenson, N. G. 2011 Deterministic tropical tree community turnover: evidence from patterns of functional beta diversity along an elevation gradient. *Proc. R. Soc. B* **278**, 877–884. (doi:10.1098/rspb.2010.1369)
- 24 Rex, M. A. & Etter, R. J. 2010 *Deep sea biodiversity: pattern and scale*. Cambridge, MA: Harvard University Press.
- 25 Jumars, P. A. 1975 Environmental grain and polychaete species' diversity in a bathyal community. *Mar. Biol.* **30**, 253–266. (doi:10.1007/BF00390748)
- 26 Jumars, P. A. 1978 Spatial autocorrelation with RUM: vertical and horizontal structure of a bathyal benthic community. *Deep Sea Res.* **25**, 589–604. (doi:10.1016/0146-6291(78)90615-X)
- 27 Thistle, D. 1978 Harpacticoid dispersion patterns: implications for deep-sea diversity maintenance. *J. Mar. Res.* **36**, 377–397.
- 28 Lamont, P. A., Gage, J. D. & Tyler, P. A. 1995 Deep-sea macrobenthic communities at contrasting sites off Portugal, preliminary results: II spatial dispersion. *Int. Rev. Hydrobiol. Hydrogr.* **80**, 251–265. (doi:10.1002/iroh.19950800212)
- 29 McClain, C. R., Nekola, J. C., Kuhn, L. & Barry, J. P. 2011 Local-scale turnover on the deep Pacific floor. *Mar. Ecol. Prog. Ser.* **442**, 193–200. (doi:10.3354/meps08924)
- 30 Etter, R. J. & Grassle, J. F. 1992 Patterns of species diversity in the deep sea as a function of sediment particle size diversity. *Nature* **360**, 576–578. (doi:10.1038/360576a0)
- 31 Glover, A. G., Goetze, E., Dahlgren, T. G. & Smith, C. R. 2005 Morphology, reproductive biology and genetic structure of the whale-fall and hydrothermal vent specialist, *Bathylkurila guaymasensis* Pettibone, 1989 (Annelida: Polynoidae). *Mar. Ecol. Prog. Ser.* **26**, 223–234. (doi:10.1111/j.1439-0485.2005.00060.x)
- 32 Wei, C.-L. *et al.* 2010 Bathymetric zonation of deep-sea macrofauna in relation to export of surface phytoplankton production. *Mar. Ecol. Prog. Ser.* **399**, 1–14. (doi:10.3354/meps08388)

- 33 Tittensor, D. P., Rex, M. A., Stuart, C. T., McClain, C. R. & Smith, C. R. 2011 Species–energy relationships in deep-sea mollusks. *Biol. Lett.* **7**, 718–722. (doi:10.1098/rsbl.2010.1174)
- 34 McClain, C. R. & Hardy Mincks, S. 2010 The dynamics of biogeographic ranges in the deep sea. *Proc. R. Soc. B* **277**, 3533–3546. (doi:10.1098/rspb.2010.1057)
- 35 Gooday, A. J. 2002 Biological responses to seasonally varying fluxes of organic matter to the ocean floor: a review. *J. Oceanogr.* **58**, 305–332. (doi:10.1023/A:1015865826379)
- 36 Smith, C. R., De Leo, F. C., Bernardino, A. F., Sweetman, A. K. & Arbizu, P. M. 2008 Abyssal food limitation, ecosystem structure and climate change. *Trends Ecol. Evol.* **23**, 518–528. (doi:10.1016/j.tree.2008.05.002)
- 37 Grim, V. *et al.* 2005 Pattern-oriented modeling of agent-based complex systems: lessons from ecology. *Science* **310**, 987–991. (doi:10.1126/science.1116681)
- 38 Rangel, T. F., Diniz-Filho, J. A. & Colwell, R. K. 2007 Species richness and evolutionary niche dynamics: a spatial pattern-oriented simulation experiment. *Am. Nat.* **170**, 602–616. (doi:10.1086/521315)
- 39 Legendre, P., Borcard, D. & Peres-Neto, P. R. 2005 Analyzing beta diversity: partitioning the spatial variation of community composition data. *Ecol. Monogr.* **75**, 435–450. (doi:10.1890/05-0549)
- 40 Allen, J. A. 2008 Bivalvia of the deep Atlantic. *Malacologia* **50**, 57–173. (doi:10.4002/0076-2997-50.1.57)
- 41 Allen, J. A. & Sanders, H. L. 1996 The zoogeography, diversity and origin of the deep-sea protobranch bivalves of the Atlantic: the epilogue. *Prog. Oceanogr.* **38**, 95–153. (doi:10.1016/S0079-6611(96)00011-0)
- 42 Hessler, R. R. & Sanders, H. L. 1967 Faunal diversity in the deep sea. *Deep Sea Res.* **14**, 65–78.
- 43 Peters, R. H. 1983 *The ecological implications of body size*. Cambridge, UK: Cambridge University Press.
- 44 Calder, W. A. 1984 *Size, function, and life history*. Mineola, NY: Dover Publications, Inc.
- 45 Brown, J. H. 1995 *Macroecology*. Chicago, IL: University of Chicago Press.
- 46 McClain, C. R., Gullet, T., Jackson-Ricketts, J. & Unmack, P. J. In press. Increased energy promotes size-based niche availability in marine mollusks. *Evolution*.
- 47 McClain, C. R. 2004 Connecting species richness, abundance, and body size in deep-sea gastropods. *Glob. Ecol. Biogeogr.* **13**, 327–334. (doi:10.1111/j.1466-822X.2004.00106.x)
- 48 Locarnini, R. A., Mishonov, A. V., Antonov, J. I., Boyer, T. P., Garcia, H. E., Baranova, O. K., Zweng, M. M. & Johnson, D. R. 2010 World Ocean Atlas 2009, Vol. 1: temperature. In *NOAA Atlas NESDIS 68* (ed. S. Levitus), Washington, DC: US Government Printing Office.
- 49 Lutz, M. J., Caldiera, K., Dunbar, R. B. & Behrenfeld, M. J. 2007 Seasonal rhythms of net primary production and particulate organic carbon flux describes biological pump efficiency in the global ocean. *J. Geophys. Res.* **112**, C10011. (doi:10.1029/2006JC003706)
- 50 Swenson, N. G. 2011 Phylogenetic beta diversity metrics, trait evolution and inferring the functional beta diversity of communities. *PLoS ONE* **6**, e21264. (doi:10.1371/journal.pone.0021264)
- 51 Nekola, J. C. & White, P. S. 1999 The distance decay of similarity in biogeography and ecology. *J. Biogeogr.* **26**, 867–878. (doi:10.1046/j.1365-2699.1999.00305.x)
- 52 Legendre, P. 2008 Studying beta diversity: ecological variation partitioning by multiple regression and canonical analysis. *J. Plant Ecol.* **1**, 3–8. (doi:10.1093/jpe/rtn001)
- 53 Legendre, P. & Anderson, M. J. 1999 Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. *Ecol. Monogr.* **69**, 1–24. (doi:10.1890/0012-9615(1999)069[0001:DBRA TM]2.0.CO;2)
- 54 O'Connor, M. I., Bruno, J. F., Gaines, S. D., Halpern, B. S., Lester, S. E., Kinlan, B. P. & Weiss, J. M. 2007 Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. *Proc. Natl Acad. Sci.* **104**, 1266–1271. (doi:10.1073/pnas.0603422104)
- 55 Arellano, S. M. & Young, C. M. 2009 Spawning, development, and the duration of larval life in a deep-sea cold-seep mussel. *Biol. Bull.* **216**, 149–162.
- 56 Lampitt, R. S. & Anita, A. N. 1997 Particle flux in the deep seas: regional characteristics and temporal variability. *Deep Sea Res. I* **44**, 1377–1403. (doi:10.1016/S0967-0637(97)00020-4)
- 57 McClain, C. R. 2010 An empire lacking food. *Am. Sci.* **98**, 470–477.
- 58 McClain, C. R., Rex, M. A. & Jabbour, R. 2005 Deconstructing bathymetric patterns of body size in deep-sea gastropods. *Mar. Ecol. Prog. Ser.* **297**, 181–877. (doi:10.3354/meps297181)
- 59 McClain, C. R., Boyer, A. & Rosenberg, G. 2006 The island rule and the evolution of body size in the deep sea. *J. Biogeogr.* **33**, 1578–1584. (doi:10.1111/j.1365-2699.2006.01545.x)
- 60 La Sorte, F. A., McKinney, M. L., Pysek, P., Klotz, S., Rapson, G. L., Celesti-Grapo, L. & Thompson, K. 2008 Distance decay of similarity among European urban floras: the impact of anthropogenic activities on beta diversity. *Glob. Ecol. Biogeogr.* **17**, 363–371. (doi:10.1111/j.1466-8238.2007.00369.x)
- 61 Lindo, Z. & Winchester, N. N. 2009 Spatial and environmental factors contributing to patterns in arboreal and terrestrial oribatid mite diversity across spatial scales. *Oecologia* **160**, 817–825. (doi:10.1007/s00442-009-1348-3)
- 62 Boyce, D. G., Lewis, M. R. & Worm, B. 2010 Global phytoplankton decline over the past century. *Nature* **466**, 591–596. (doi:10.1038/nature09268)
- 63 Behrenfeld, M. J. *et al.* 2006 Climate-driven trends in contemporary ocean productivity. *Nature* **444**, 752–755. (doi:10.1038/nature05317)
- 64 Levitus, S., Antonov, J. I., Boyer, T. P. & Stephens, C. 2000 Warming of the world ocean. *Science* **287**, 2225–2229. (doi:10.1126/science.287.5461.2225)
- 65 Danovaro, R., Dell'Anno, A. & Pusceddu, A. 2004 Biodiversity response to climate change in a warm deep sea. *Ecol. Lett.* **7**, 821–828. (doi:10.1111/j.1461-0248.2004.00634.x)
- 66 Ruhl, H. A. 2008 Community change in the variable resource of the abyssal northeast Pacific. *Ecology* **89**, 991–1000. (doi:10.1890/06-2025.1)