

LETTER

The multidimensionality of the niche reveals functional diversity changes in benthic marine biotas across geological time

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Abstract

Despite growing attention on the influence of functional diversity changes on ecosystem functioning, a palaeoecological perspective on the long-term dynamic of functional diversity, including mass extinction crises, is still lacking. Here, using a novel multidimensional functional framework and comprehensive null-models, we compare the functional structure of Cambrian, Silurian and modern benthic marine biotas. We demonstrate that, after controlling for increases in taxonomic diversity, functional richness increased incrementally between each time interval with benthic taxa filling progressively more functional space, combined with a significant functional dissimilarity between periods. The modern benthic biota functionally overlaps with fossil biotas but some modern taxa, especially large predators, have new trait combinations that may allow more functions to be performed. From a methodological perspective, these results illustrate the benefits of using multidimensional instead of lower dimensional functional frameworks when studying changes in functional diversity over space and time.

Keywords

Benthic invertebrates, corals, functional dissimilarity, functional richness, functional traits, Palaeozoic fossils.

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INTRODUCTION

All ecosystems on Earth are currently affected by human activities (Vitousek *et al.* 1997) and one of the major components of this global change is the accelerated loss of biodiversity (Vitousek *et al.* 1997). Although biodiversity is a multifaceted concept that ranges from genetic diversity inside a population to the variety of landscapes in ecosystems, most studies have focused only on species richness (Purvis & Hector 2000). Besides its intrinsic value, biodiversity provides essential ecosystem services to human populations through genetic resources, food production and nutrient-cycle regulation (Costanza *et al.* 1997). In this context, there is a growing consensus that the functional diversity of communities (i.e. diversity of species traits, Petchey & Gaston 2006) is more informative than taxonomic richness *per se* in explaining the structure and function of ecological communities (McGill *et al.* 2006; Mokany *et al.* 2008). For instance, within marine communities, there is evidence that functional diversity of benthic communities drives important ecosystem processes (Solán *et al.* 2004).

Like taxonomic diversity, functional diversity can be measured within local communities (i.e. alpha-diversity) or among communities (i.e. beta-diversity). The former component quantifies the functional richness of the traits present in the community whereas the latter corresponds to the dissimilarity of functional composition between two or more communities. Several studies have focused on temporal dynamics of functional richness for several taxa (Flynn *et al.* 2009; Villéger *et al.* 2010) but there is to date no study assessing functional

dissimilarity trends because of a lack of a practical framework. Therefore, in the global change context, it is urgent to develop a general framework that allows assessing how changes in taxonomic diversity affect functional diversity, for both its alpha and beta components (Devictor *et al.* 2010).

Marine ecosystems, which are among the world's most productive and diverse (Costanza *et al.* 1997) and are facing unprecedented levels of human pressure today (Halpern *et al.* 2008), have been subject to both fundamental evolutionary diversifications as well as dramatic extinction crises (Erwin 2008). Such events modified – sometimes irreversibly – the biota, environments, and geochemical fluxes in marine ecosystems (Alroy 2010). For instance, the Late Cretaceous mass extinction (Schulte *et al.* 2010), which caused the demise of more than 60% of all animal taxa, altered biogeochemical processes for millions of years afterwards (D'Hondt 2005) and its biogeographic impact persists today in the marine biota (Krug *et al.* 2009). Much of our knowledge of such transitions is based on the well-preserved marine invertebrate fossil record (Foote & Sepkoski 1999), and especially that from the benthic shelf habitat (Alroy *et al.* 2008). There has been substantial progress in understanding how biological traits of marine organisms contributed to these evolutionary transitions. For example, victims of the Late Permian mass extinction were disproportionately immobile and physiologically 'unbuffered' (Bambach *et al.* 2002), whereas no such selectivity existed during the Late-Cretaceous mass extinction (Jablonski & Raup 1995), at least among benthic invertebrates (Friedman 2009). Such approaches have been generalized to focus on multiple traits simultaneously across entire

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fossil biotas (Bambach *et al.* 2007; Bush *et al.* 2007; Novack-Gottshall 2007) but quantitative assessments of temporal trajectories for both alpha and beta components of functional diversity are still missing.

Here we compare representative samples of benthic Palaeozoic (fossil) and modern biotas, testing whether changes in taxonomic diversity over time affected (1) the amount of functional space filled by these benthic assemblages (defined as functional richness, Villeger *et al.* 2008) and (2) the amount of functional space not shared by these benthic assemblages (defined as functional dissimilarity or turnover) (Fig. 1). This study quantitatively tests such functional diversity dynamics across macroevolutionary events (including mass extinction crises and major radiations) and proposes a new methodology that simultaneously considers changes in both functional richness and functional dissimilarity using a common multidimensional functional-trait framework.

MATERIAL AND METHODS

Marine benthic taxa database

Three time intervals, representing the Cambrian (*c.* 501–513 million years ago, Mya), Silurian (*c.* 423–428 Mya), and present-day, were chosen to represent intervals separated by regime-changing evolutionary and ecological events. For example, the Cambrian and Silurian biotas are separated by the transition from Cambrian to Palaeozoic evolutionary faunas during the Ordovician radiation (Peters 2004) and the Late Ordovician mass extinction (and its Early Silurian recovery). The Silurian and modern biotas are separated by four mass extinctions, the transition to the Modern evolutionary fauna, and

the advent of terrestrialization (Bambach 1999) and escalatory predator–prey coevolution (Vermeij 1987).

Biota sampling

To meaningfully compare the functional diversity of modern and fossil marine biotas, we focused on samples sharing similar geographic, latitudinal, and environmental characteristics. All samples occurred in tropical to subtropical, muddy, offshore, open-shelf marine environments of *c.* 30–60 m depth from individual regions of similar geographic extent. Fossil samples were compiled from the published literature (available at paleodb.org) and represent classic Middle Cambrian and Middle Silurian deposits that are known for exceptional preservation of ecologically autochthonous assemblages. Cambrian samples are from the Wheeler and Marjum Formations of western Utah (USA). Silurian samples are from the Rochester and shale-rich portions of the Rockway Formations of western New York and the Waldron and Osgood Formations of southern Indiana (both USA); during the Silurian, both locations were connected by an elongate interior seaway. Nektonic, planktonic, and microscopic fossils and samples from dysaerobic and anaerobic palaeoenvironments were excluded in order to standardize comparisons with their modern counterparts. Modern taxa were sampled by benthic dredge surveys in the Gulf of Carpentaria (Australia) (Long *et al.* 1995) and include both epibenthic and endobenthic portions of the biota. This region was chosen because it represents one of the exceedingly few modern analogues for the tropical, epeiric (epicontinental) seaways in which the Palaeozoic samples were deposited. In order to have a similar scope of coverage between the three intervals, only commonly fossilized taxa were included here (Novack-Gottshall 2007). Finally, because many fossil occurrences can only be identified to genus level, all analyses were conducted at this taxonomic level.

The resulting database (Table 1) includes 48 collections (19 fossil and 29 modern) totalling 293 taxa (136 fossil and 157 modern).

Functional characterization of the benthic taxa

Measuring functional diversity of taxon assemblages first requires that the pool of taxa be functionally characterized using a common set of functional traits. These functional traits could be any biological feature which affects species fitness, *i.e.* which describes a relevant facet of the taxa functional niche (Violle *et al.* 2007). Here, fossil and modern taxa were characterized using nine qualitative functional traits (with a total of 27 modalities, Table S1) selected from a framework applicable to marine fossils (Novack-Gottshall 2007). The chosen functional traits focus on key resources of benthic marine organisms and their acquisition, such as diet, foraging method, modes of locomotion, reproduction and habitat use (see Table S1 in Supporting Information). All traits were categorical except body size, which was coded using ordered size classes (Table S1). It is important to note that each taxon's functional niche is determined across all 27 modalities for these nine traits instead of being coded as one of few functional entities defined a priori (*e.g.* Bambach *et al.* 2002, 2007). The combinatorial flexibility of multiple modes within each functional trait allows a rich number of even subtly distinct functional entities to be characterized. As an example, consider the enormous variety of algae-eaters, all of which share a microbivorous diet (Novack-Gottshall 2007); depending on how additional traits are classified, the new framework allows distinctions between byssate mussels (facultatively mobile, attached, supported, particle-feeding,

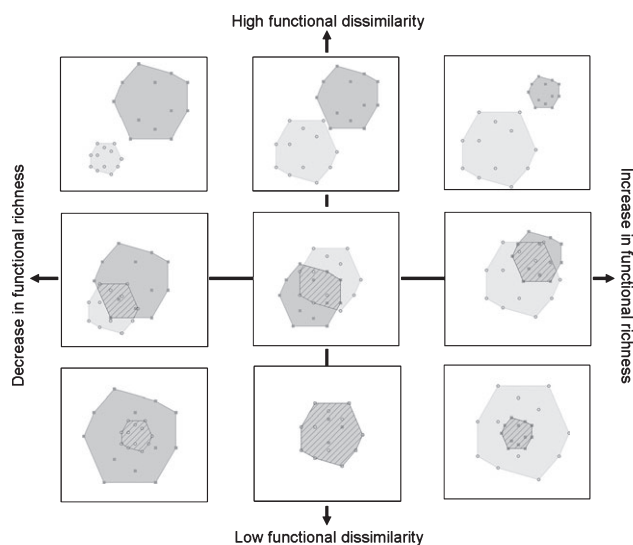


Figure 1 Theoretical changes of two independent functional diversity facets: functional richness (the amount of space filled) and functional dissimilarity (the amount of space that is not shared). Each of the nine plots represents a two-dimensional functional space. Taxa (points) are placed in this functional space according to their respective trait values. For each of the nine plots, two biotas sampled at two periods are considered: the oldest biota is in dark grey (square) and the youngest is in light grey (circles). The corresponding convex hull volumes (here a surface) are filled with respective colours and their intersection is hatched. Functional richness increases from the left to the right while functional dissimilarity increases from the bottom to the top of the figure. Note that the location of volumes in the trait-space is arbitrary.

Table 1 Taxonomic and functional richness for the three samples

	No. taxa	No. functional entities	Functional redundancy	No. vertices			Functional richness		
				2D	3D	4D	2D	3D	4D
Cambrian	29	14	2.07	6	9	14	30.2 (0.003)	5.3 (0.001)	1.6 (0.001)
Silurian	107	43	2.49	8	14	25	89.1 (0.239)	64.2 (0.443)	33.1 (0.044)
Modern	157	59	2.66	12	20	29	96.9 (0.455)	82.6 (0.511)	78.6 (0.601)

Functional redundancy is the ratio between number of taxa and number of functional entities (i.e. unique combination of functional traits) within each sample. The three last columns present, for the three dimensionalities considered, the functional richness of the three samples (expressed as the relative volume occupied by each biota compared to the volume of the global pool of taxa). Associated *P*-values obtained under the null model ($N = 999$) are provided in parentheses, values < 0.05 indicate a volume significantly lower than expected at random.

filter-feeders on typically hard lithic substrates), algal-mat-grazing limpets [intermittently mobile, free-living, bulk-feeding (because ingest intact food), mass-feeders (defined by ingesting food *en masse*) on typically hard lithic substrates], burrowing deposit-feeding nuculoid bivalves (intermittently mobile, free-living, particle-feeding mass-feeders living within soft lithic substrates), and kelp-browsing gastropods [intermittently mobile, free-living, supported, bulk-feeding, raptorial feeders (because actively seize and manipulate individual food items) living on biotic substrates]. Additional details and examples of the versatility of the classification framework are available in Novack-Gottshall (2007): especially pp. 285–286 and appendix).

Measuring functional richness and functional dissimilarity of species assemblages

Here, we present a novel framework to assess both functional richness and functional dissimilarities of species assemblages based on their species and trait compositions (i.e. only species presence/absence are taken into account but not their relative abundances).

Functional space

Once species have been characterized functionally by a set of relevant traits, it is possible to build a multidimensional functional space where each species is placed according to its functional niche (Villegger *et al.* 2008). If all the traits are quantitative and continuous, then a multidimensional functional space could be built by considering each trait as an axis (Villegger *et al.* 2008). If all the traits are not continuous, then a synthetic multidimensional functional space could be obtained in two steps: first computing functional distances between species using the Gower's distance (Gower 1966), which allows mixing different types of variables; and second, applying a PCoA (principal co-ordinates analysis) on this distance matrix. Similar to PCA, PCoA provides species coordinates in a multidimensional Euclidean space, which could be considered as synthetic functional trait values (Laliberte & Legendre 2010).

This multidimensional approach shares several similarities with those used to study morphological diversity (or disparity) (e.g. Foote 1997; McClain 2005). Although not pursued here because it is impossible to compare such diverse benthic animals using standard morphological measures, the morphological diversity approach offers a fruitful complement to the functional approach, especially in the context of understanding macroevolutionary and palaeoecological patterns of evolutionary innovation, ecological radiations, and extinction selectivity (e.g. Friedman 2009).

Functional richness

Functional richness quantifies the amount of the functional space filled by a species assemblage (Villegger *et al.* 2008) and is measured using the volume inside the convex hull enclosing all the species from this assemblage (Cornwell *et al.* 2006). The convex hull is defined by the following condition: if two points A and B are inside it, then any points on the segment AB also belong to the convex hull. Geometrically the convex hull is a polytope defined by a set of vertices (Fig. 2), i.e. the most extreme points defining the boundaries of the convex hull. Assemblages containing species exhibiting a low range of trait values have low functional richness. On the contrary, assemblages in which species have opposite extreme combinations of traits (i.e. species are located near the borders of the functional space) have a high functional richness.

Functional dissimilarity

Taxonomic dissimilarity among species assemblages has been widely investigated in ecology through the concept of β -diversity (Whittaker 1972; Anderson *et al.* 2011), but it has not been incorporated

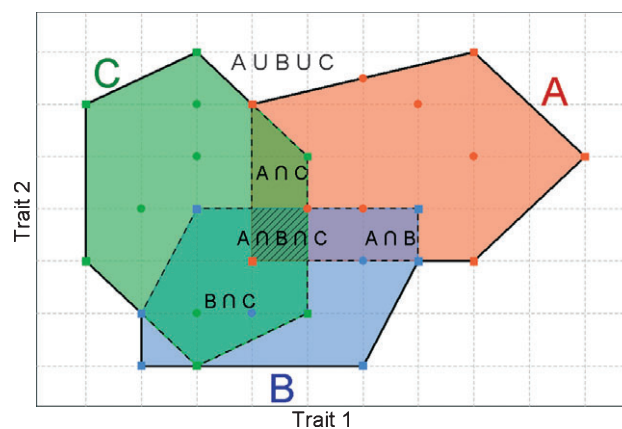


Figure 2 Graphical illustration of the computation of functional dissimilarity based on convex hull volumes overlap. Two traits are considered for convenience and scale is illustrated by the dashed grey raster. Taxa are placed in this functional space according to their respective trait values. Three biotas (A, B and C) are considered and their respective convex hull volumes (here surfaces) are filled respectively in red, blue and green. The vertices delimiting the respective convex hull are plotted with squares whereas the other taxa are plotted with points. The union of the three biotas A, B and C is delimited by the black line whereas their intersection is the small hatched square. Intersections between pairs of these three biotas correspond to the polygons in mixed-colours and their union is delimited by the black dashed line.

previously into a multidimensional framework considering the functional volume occupied by assemblages. Dissimilarity among two or more assemblages is equal to the ratio between the amount of diversity not shared between assemblages relative to their total diversity:

$$\text{Dissimilarity} = \frac{\text{Unique}}{\text{Total}} = 1 - \frac{\text{Shared}}{\text{Total}}.$$

Therefore, dissimilarity is maximal when assemblages have no taxa in common and minimal when their compositions are identical. By analogy, functional dissimilarity between assemblages can also be estimated by quantifying the dissimilarity in their functional space occupation (Fig. 2).

In the framework based on multidimensional volume (i.e. convex hull) occupied by a species assemblage, functional dissimilarity (F_{β}) becomes:

$$F_{\beta} = \frac{\text{Volume not shared}}{\text{Total volume}} = 1 - \frac{\text{Volume shared}}{\text{Total volume}} \quad (\text{Fig. 2}).$$

The intersection between two convex polytopes is a convex polytope, while their union is rarely convex. Thus, in practice, computing the intersection of N polytopes is easier than computing their union. However, the shapes of polytopes themselves are not the ultimate goal but rather it is their volumes; hereafter, the volume of any polytope P_k will be noted $V(P_k)$. We thus computed the volume of the union of N convex polytopes based on their volumes and on the volumes of their intersections thanks to the inclusion–exclusion principle (Fig. 2).

For N polytopes the inclusion–exclusion principle could be written as:

$$\begin{aligned} V\left(\bigcup_{i=1}^N P_i\right) &= \sum_{i=1}^N V(P_i) - \sum_{1 \leq i < j \leq N} V(P_i \cap P_j) \\ &+ \sum_{1 \leq i < j < k \leq N} V(P_i \cap P_j \cap P_k) - \dots \\ &+ (-1)^{N-1} V(P_1 \cap \dots \cap P_N) \end{aligned}$$

Functional dissimilarity between N assemblages is thus:

$$F_{\beta}(P_1, \dots, P_N) = 1 - \frac{V\left(\bigcup_{1 \leq i < j \leq N} P_i \cap P_j\right)}{V\left(\bigcup_{i=1}^N P_i\right)}$$

The numerator is the volume of the union of all the intersections between the $\frac{N \times (N-1)}{2}$ pairs of biotas. This volume is also obtained using the inclusion–exclusion principle.

Finally, functional dissimilarity equals:

$$F_{\beta}(P_1, \dots, P_N) = 1 - \frac{\sum_{1 \leq i < j \leq N} V(P_i \cap P_j) - 2 \times \sum_{1 \leq i < j < k \leq N} V(P_i \cap P_j \cap P_k) + \dots + (-1)^N \times (N-1) \times V(P_1 \cap \dots \cap P_N)}{\sum_{i=1}^N V(P_i) - \sum_{1 \leq i < j \leq N} V(P_i \cap P_j) + \dots + (-1)^{N-1} V(P_1 \cap \dots \cap P_N)}$$

Functional dissimilarity equals zero when the portions of the functional space filled by species assemblages are perfectly overlapping, and equals unity when assemblages do not intersect in that functional space.

Assessing and testing changes in functional diversity of benthic biotas

Functional distances between all the taxa (i.e. fossil and modern) were computed according to their trait values using the Gower's distance (Gower 1966). Then a PCoA was carried out on this distance matrix to obtain taxa coordinates in a multidimensional functional space (Villéger *et al.* 2008; Laliberté & Legendre 2010). Analyses were run in three sets of dimensionalities, with two to four axes used to define each functional space. These three functional spaces respectively summarized 69, 76 and 81% of the inertia present in the initial Gower distance matrix (Table S2).

The functional volume filled by each sample was computed for these three dimensionalities of functional space. These raw convex hull volumes were then standardized by the volume filled by the global pool of taxa (i.e. from the three periods) to obtain values constrained between 0 and 100%. Functional dissimilarity was computed between the three samples and among their three pairs for each dimensionality of functional space.

Observed functional diversity indices are informative by themselves, but in order to test ecological hypothesis, these values have to be compared to values expected under appropriate null hypotheses (e.g. Villéger *et al.* 2010). Here, we tested two hypotheses: (1) whether the functional richness in each sample is significantly lower than expected given taxonomic richness, and (2) whether functional dissimilarity between samples is significantly greater than expected given differences in taxonomic richness.

These hypotheses were tested using randomized permutation tests (Manly 1997). For each of 999 iterations, the age (i.e. the geological period) of each taxon occurrence was randomized such that taxonomic richness was kept constant for each period and no taxon was assigned to different periods simultaneously. Functional richness and functional dissimilarity were then computed using the three simulated samples. This randomization was repeated for each level of functional space dimensionality (i.e. two, three, or four dimensions). For each dimensionality and functional diversity index, P -values were computed by comparing observed values to the distribution of simulated values (Manly 1997). Computation of convex hull volumes was carried out using MATLAB software (using the Geometric Bounding Toolbox 7.3); other statistical analyses were performed with R (R Development Core Team 2009).

Although the samples included here represent extensive sampling of their respective regions, it remains possible that differences in species richness could also represent artefacts of differential preservation, which could bias patterns of functional diversity. Similarly, the modern sample has a different degree of functional redundancy (the

number of taxa sharing the same traits) than the fossil samples, which could induce bias. Two rarefaction analyses were carried out to test such potential biases (Novack-Gottshall 2007; Friedman 2009). The first test randomly sub-sampled ($N = 999$) the modern sample down to the number of taxa present in Cambrian and Silurian samples. This analysis tests whether a modern sample with a taxonomic richness equal to that of fossil assemblages has a functional richness significantly different than expected at the same level of taxonomic richness. The second rarefaction test (further evaluated with permutations tests) was conducted by focusing, instead, on the number of functional entities (i.e. unique trait combinations) in each sample rather than on their taxonomic richness. This second test can distinguish instances where taxonomic diversity increases without corresponding increases in functional diversity because multiple taxa can be functionally identical (i.e. functionally redundant).

RESULTS

The overall database includes a total of 293 taxa: 29 Cambrian, 107 Silurian and 157 modern (Table 1). Although the nine traits considered allow 46 080 possible trait combinations, the 293 taxa in the database represented only 91 different functional entities, respectively: 14 for Cambrian, 43 for Silurian and 59 for Modern samples (Table 1). Redundancy within functional entities ranged from 1 to 20 taxa (median = 2) per functional entity. Forty-four percent of functional entities with at least three taxa were represented by both fossil and modern taxa. The functional space of each sample can be represented graphically by a scatterplot defined by its functional entities, with functionally redundant taxa superimposed (Fig. 3). The distribution of trait modalities in the functional space (Fig. S1) demonstrates that the position of each taxon in the functional space is not driven by only a few traits but from the combination of modalities for all nine functional traits.

Functional richness increased through geological time (Table 1, Fig. 3, Fig. S2). For instance, Cambrian and Silurian samples filled respectively 1.6 and 33% of the four-dimensional functional space available, whereas the modern sample filled 78% of this volume. Moreover, both fossil samples had significantly lower functional richness than expected by chance given their respective taxonomic richness (Table 1), although Silurian functional richness is only lower than expected for the four-dimensional functional space. Conversely, although the modern sample occupies a larger proportion of the functional space potentially available (Fig. 3), this functional richness is not significantly greater than expected given its large taxonomic richness whatever the number of dimensions (Table 1).

Additional results (Table S3), focusing on the number of functional entities in each sample independently from taxonomic richness, show that our conclusions are robust regarding the level of functional redundancy which is variable between periods.

These patterns are also maintained when using rarefaction to control for differences in sample size. Modern functional richness estimated after rarefaction (i.e. sub-samples of 29 and 107 taxa, respectively) was, as expected, lower than the functional richness of the 157 modern taxa (Fig. S3). However, when considering the four-dimensional functional space, more than 95% of these rarefied modern samples still had greater functional richness than both the Cambrian and Silurian samples (Fig. S3). Furthermore, the functional richness of most (i.e. >95%) of the rarefied modern samples is not significantly different than expected given their number of taxa (Table S4). Similar results were obtained when considering rarefaction of functional entities instead of taxonomic richness (Fig. S3, Table S4). Taken together, these complementary analyses demonstrate that the higher functional richness of modern benthic samples is not an artefact due to the higher number of taxa or functional entities present in these modern samples.

In terms of functional dissimilarity, the Cambrian sample is functionally distinct from the Silurian and modern samples, with dissimilarity values ranging from *c.* 70 to >96%, depending on the number of functional dimensions considered (Table 2). These dissimilarities are also significantly greater than expected given their differences in taxonomic richness. Although functional dissimilarity between the Silurian and Modern samples is also relatively high (69%) in four-dimensions, this value, and those at fewer dimensionalities, was not statistically significant under the null hypothesis. Total dissimilarity between all three periods is high and significantly greater than expected, but only when considering four dimensions (Table 2).

DISCUSSION

Taxonomic richness increases incrementally between the Cambrian, Silurian and modern samples (Table 1), which is consistent with both increasing global and within-community (i.e., alpha) diversity between these Phanerozoic intervals (Powell & Kowalewski 2002; Bush & Bambach 2004; Alroy *et al.* 2008). This increasing taxonomic richness is mirrored both in the increasing number of functional entities (Table 1), a pattern also consistent with that documented by Bambach *et al.* (2007), and also in the increasing functional redundancy from the Cambrian (2.07 taxa/functional entity) to the modern interval (2.66 taxa/functional entity) (Table 1). The greater taxonomic richness of the modern biota is thus not only associated with a stronger functional

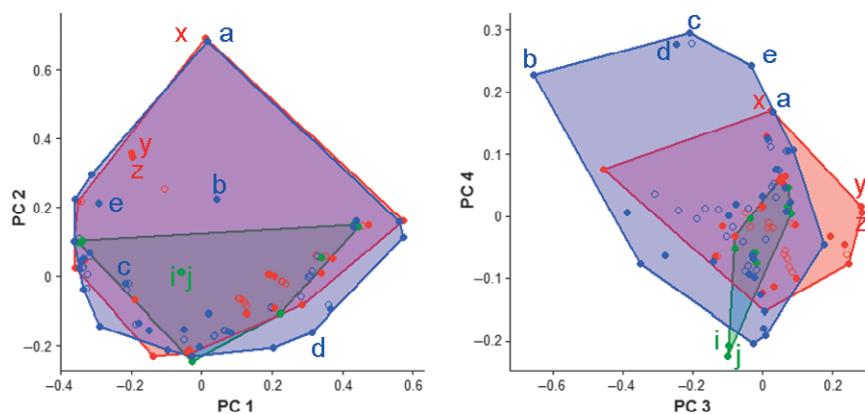


Figure 3 Functional diversity in the four-dimensional functional space. The Cambrian sample is plotted in green, the Silurian in red, and the Modern in blue. All functional entities are plotted with circles; only entities being vertices in the four-dimensional space are filled with corresponding colours. Projections of the convex hull volumes in four dimensions are illustrated by the coloured surfaces. Letters correspond to key functional entities discussed in the text.

Table 2 Functional dissimilarity among samples

Functional dissimilarity (F_{β})	2D	3D	4D
Cambrian-Silurian	67 (0.990)	92 (0.993)	96 (0.999)
Silurian-Modern	12 (0.711)	47 (0.764)	69 (0.865)
Cambrian-Modern	69 (0.995)	94 (0.998)	98 (0.999)
Cambrian-Silurian-Modern	11 (0.826)	47 (0.865)	68 (0.994)

Functional dissimilarity values (percentage of non-overlap between convex hulls) between pairs of samples and among all three samples. Associated P -values obtained under the null model ($N = 999$) are provided in parentheses, values > 0.95 indicate that dissimilarity is significantly greater than expected at random.

redundancy between taxa but also results in a functional diversification (i.e. increase of functional richness) through time. For example, among the 14 functional entities present in the Cambrian sample, only five do not re-occur in Silurian or modern assemblages, and these uniquely Cambrian functional entities are relatively similar to those exhibited by such later taxa. Consequently, the Cambrian sample did not contribute much to the filling of overall functional space. Two entities (i and j in Fig. 3), however, did exhibit unique trait combinations compared to those in later samples. These entities include six genera of agnostids, distinctive blind and small trilobites that likely swam along the sea floor, feeding raptorially as microbivores (Robinson 2007). Similarly, some functional entities from the Silurian sample, including corals and some sedentary colonial filter-feeders (e.g. bryozoan genera and the graptolite *Reticulograptus*), exhibit unique combinations of traits (y and z, Fig. 3). In both of these fossil exceptions, however, these unique functional entities are not wholly distinct from the regions of functional space occupied by members of the modern sample, whereas members of the modern sample also tend to inhabit other and more extreme regions of the functional space not previously occupied by these fossil samples.

In general, the low functional richness of fossil samples and their dissimilarity with the modern sample is linked to their less extensive occupation of the functional space, particularly for extreme values on three of the four functional axes considered. Indeed, despite the remarkable similarity of functional space filled by benthic samples along axis PC1 (which accounts for the majority of variation in the data), the amount of functional space filled by benthic samples increased through time for the other three axes (Fig. 3, Fig. S2). For example, high positive values along axis PC2 represent corals, a functionally peculiar entity encompassing both sessile suspension-feeders and raptorial microcarnivores. The most extreme functional entity (denoted as entity x on Fig. 3) is composed of a single Silurian coral (*Favosites*), while less extreme entities (entity a and to a lesser extent entities y and z) include six other coral taxa (including four Silurian and two modern corals, both of which are functionally redundant with Silurian *Striatopora* as entity a). In large part, these patterns reflect the paucity of sessile, microcarnivorous corals (or taxa with functionally similar traits) from Cambrian sea floors (Pratt *et al.* 2001) and their diversification during the ensuing Ordovician radiation (Webby *et al.* 2004). Similarly, functional entities with high negative values on axis PC3 and high positive values on PC4 are exclusively members of the modern sample and contribute to the strong dissimilarity with the Cambrian sample, and less so, with the Silurian sample. The most distinctive entity (b in Fig. 3) is the modern gastropod *Balcis*, which lives as an ectoparasite on echinoderms. Other functionally distinctive entities in the modern sample include the gastropod *Volva* (entity c), which lives and feeds primarily on soft

corals; comatulid crinoids (entity d), which are mobile, microbivorous filter-feeders that generally nestled among other animals; and octopuses (entity e), which are relatively large, mobile predators. This part of the functional space is especially enriched in organisms that live on other animals (i.e., functional trait modalities involving being supported on biotic substrates), a characteristic not typical of Palaeozoic fossil biotas (Novack-Gottshall 2007). As noted by Bush *et al.* (2007) it remains possible that some of these unique modern taxa represent functional entities that would be less likely to be preserved or recognized within typical fossil assemblages, and therefore this pattern should perhaps be taken with more caution than other results reported here. While it remains difficult to evaluate the potential strength of such functional-group or mineralogical preservational biases analytically in this data, it is reassuring that previous studies (Bambach *et al.* 2007; Bush *et al.* 2007) found that their effect was relatively minor when describing functional traits of typical benthic assemblages, as it is done here.

Overall, the functional diversity dynamics between the Cambrian, Silurian, and modern intervals are best represented by the centre-right panel of Fig. 1 with later biotas overlapping, and even remaining centred on, the functional space occupied by past biotas. In other words, functional richness and dissimilarity both increased progressively throughout geological time. The increases from the Cambrian to the Silurian were much greater than that after the Silurian, despite the latter interval being more than four times longer and encompassing significantly more ecological and evolutionary impacts. This trend is also highlighted by functional dissimilarity because Cambrian and Silurian samples show higher dissimilarity values than Silurian and modern samples. Although based on only these three intervals, the patterns here appear to be consistent with a diffusional occupation of functional space through time in which most of the newer functional entities are functionally similar with previous ones. However, those relatively few novel functional entities, with original combinations of traits, contribute significantly to both an increase of functional richness and functional dissimilarity. This interpretation augments prior claims that placed primary emphasis on the expansion of novel functional entities (Knoll & Bambach 2000; Bush *et al.* 2007), although Bush *et al.* (2011) note a similar deceleration of functional changes across geological time with a greater functional dissimilarity between the Ediacaran and the Cambrian biotas than between the Cambrian and modern biotas. Thus, we demonstrate marked changes in functional diversity of marine benthic biota across geological time when considering multiple niche dimensions. Although inclusion of additional intervals, especially representing the intervening Mesozoic Era, would be beneficial to better understand the patterns of functional diversification, such analyses must await future efforts. Nevertheless, inclusion of these three intervals does allow comparison with previous, less analytical efforts (e.g. Bambach *et al.* 2007; Bush *et al.* 2007; Novack-Gottshall 2007), and the results suggest that the net functional changes between the first two geological intervals were more substantial than in the ensuing 400-million-years. Although these regional samples represent typical samples of the larger global fauna during these intervals (Bambach *et al.* 2007; Bush *et al.* 2007; Novack-Gottshall 2007), it is important to recognize that the patterns and ensuing discussion are necessarily limited to these samples.

Use of modern samples from other regions is unlikely to substantially alter these patterns. For example, temperate Western Atlantic samples analyzed in Novack-Gottshall (2007) are not substantially different, in terms of their distribution of functional entities in ordination space, than those of the Gulf of Carpentaria used

here. The most significant functional difference between these two modern regions points out a minor enrichment in raptorial and habitually mobile predators within the Australian samples. This functional difference between different modern regions would potentially overstate the relatively minor dissimilarity between the Silurian and modern samples demonstrated here because of the well documented increase in active predation during the ensuing Mesozoic (Vermeij 1987). Bush *et al.* (2007) also made similar claims about the lack of significant differences between tropical and temperate Cenozoic fossil samples and the enrichment in tropical predatory snails. In addition, we demonstrate that the functional originality (extreme combinations of traits) of the taxa present only in the modern sample has a stronger influence on its higher functional richness than its higher number of taxa or functional entities.

Changes in the functional diversity of benthic fauna could have consequences on the functioning and stability of ecosystems (Solan *et al.* 2004). For instance, an increase of predator diversity could modify the connectivity in the trophic network and the intensity of trophic cascades on primary production (Huntley & Kowalewski 2007; Schmitz *et al.* 2010), while the increasing preponderance of mobile organisms could increase the bioturbation of sediments and thus nutrient cycling (Solan *et al.* 2004). Although such consequences are not explicitly demonstrated here, such approaches have the potential to better understand the long-term dynamics of ecosystem functioning because the traits of species ultimately govern the ecosystem-level consequences of benthic diversity shifts (Solan *et al.* 2004).

In addition, from a methodological perspective, our results clearly illustrate the impact that functional space dimensionality bears on biological conclusions. Indeed, the observed values of both measures of functional diversity (richness and dissimilarity), and consecutively their statistical significance, are strongly dependent of the number of functional axes considered. This is a good illustration of the bias that can occur when over-reducing functional space dimensionality, which inevitably results in loss of information. For example, centrally located modern entities b, c, and e on axes PC1 and PC2 in Fig. 3 are only recognized as functionally distinctive when examining four functional dimensions. We have only discussed the results obtained with the four-dimensional functional space. Theoretically, we could have kept the 90 axes provided by the PCoA (constrained by the 91 unique combinations of traits present). Our choice was determined by a trade-off between the interpretability of the data (i.e. 81% is still a meaningful proportion of information, Table S2), the computational limits for the dissimilarity and permutation tests, and the simplicity of visualizing up to four dimensions.

The results demonstrate that the two metrics of functional diversity presented here are useful tools for quantifying the amount of functional space filled by a species assemblage and shared with others, while providing a means to test observed values against comprehensive null models (Villegger *et al.* 2008). Therefore, the methodology presented here may be of interest for other ecological purposes. So long as the taxa of interest are characterized by the same functional traits, it is possible to quantitatively assess differences in the functional diversity of assemblages. In particular, it would be interesting to extend our palaeoecological approach across additional geological intervals (especially during the Mesozoic and Cenozoic eras, Aberhan *et al.* 2006), and immediately before and after individual major extinctions (Friedman 2009). More specifically, it would be challenging to assess how the changes in taxa richness are reflected in functional diversity within and among assemblages.

Temporal changes of functional richness and functional dissimilarity are also of particular interest at a smaller time scale, for instance within the current global change context. Several studies have studied impacts of anthropogenic stressors on the functional richness of communities (Flynn *et al.* 2009; Villegger *et al.* 2010). In contrast, assessments of change in functional dissimilarity are still lacking despite the claim that functional homogenization (i.e. loss of functional dissimilarity because of non-native species introduction and endemic species extirpation) may strongly affect ecosystem processes and their stability (Olden 2006). Patterns of functional diversity changes across space are also a key issue in biogeography, be they at small (e.g. between habitats in a given ecosystem) or large (e.g. between similar ecosystems from different continent) spatial scales. For instance, understanding how functional richness and functional dissimilarity vary along gradient of taxonomic richness would be of significant help to design protected areas networks (Devictor *et al.* 2010). More generally, this framework has a great potential for disentangling community assembly rules (e.g. environmental or biotic filtering) (Cornwell *et al.* 2006) and for detecting evolutionary convergence and adaptive radiation (Ricklefs 2010).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Functional space of benthic taxa.

Figure S2 Functional diversity of marine samples.

Figure S3 Rarefaction analyses.

Table S1 Functional traits for benthic marine taxa.

Table S2 Explanation percentages of the principal co-ordinates analysis (PCoA) axes.

Table S3 Tests on functional richness.

Table S4 Tests on functional richness after rarefaction.

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