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Impacts of spatial and environmental differentiation on early Palaeozoic marine biodiversity

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Abstract

The unprecedented diversifications in the fossil record of the early Palaeozoic (541-419 Ma) increased both α (within-sample) and γ (global) diversity, generating considerable ecological complexity. Faunal difference (β diversity), including spatial heterogeneity, is thought to have played a major role in early Palaeozoic marine diversification, though α diversity is the major determinant of γ diversity through the Phanerozoic. Drivers for this Phanerozoic shift from β to α diversity are not yet resolved. Here, we evaluate the impacts of environmental and faunal heterogeneity on diversity patterns using a global spatial grid. We present early Palaeozoic genus-level α, β and γ diversity curves of molluscs, brachiopods, trilobites and echinoderms and compare them with measures of spatial lithological heterogeneity, which is our proxy for environmental heterogeneity. We find that α and β diversity are associated with increased lithological heterogeneity, and that β diversity declines over time while α increases. We suggest that the enhanced dispersal of marine taxa from the Middle Ordovician onwards facilitated increases in α diversity by encouraging the occupation of narrow niches and increasing the prevalence of transient species, simultaneously reducing spatial β diversity. This may have contributed to a shift from β to α diversity as the major determinant of γ diversity increase over this critical evolutionary interval.

Introduction

The early Palaeozoic fossil record shows tremendous diversification, often conceptualized as two episodes: the Cambrian Explosion (CE) and the Great Ordovician Biodiversification Event (GOBE), with contrasting impacts on global diversity and palaeoecology[1–10]. The CE includes the appearance of most metazoan phyla, and widespread metazoan burrowing, macropredation, motility and reef building[11]. During the GOBE, marine family- and genus-level diversity rose, increasing ecological tiering, plankton diversity and bioturbation, and changing the composition of reef communities[2,8]. However, the mechanisms driving early Paleozoic diversity accumulation remain elusive[12].To address this issue, α, β and γ diversity are widely used to quantify the contributions of within-sample diversity (α) and faunal heterogeneity (β) to total diversity (γ) (e.g. [1,13–15], see review in[16]).

γ and α diversity rose during the early Palaeozoic[13,17,18], but the role of β diversity is less obvious. Diversity may be measured in spatial or environmental units, including continents, depositional basins, rock outcrops, palaeoenvironments or formations, which here means rock units with formally described characteristics which distinguish them from surrounding rocks. One recent study of within-formation diversity found that during the initial stages of diversifications, including in the early Palaeozoic, γ diversity is driven by β diversity until it saturates[14]. Then, α diversity becomes the main γ diversity driver, as predicted by theoretical models[19].

While within-formation β diversity focuses on environmental faunal differentiation, geographic β diversity (geodisparity[13,20]) may have played an important role in early Palaeozoic diversification. During the CE, geodisparity increased in concord with continental fragmentation[13], and during the GOBE it may have been affected by dispersal, which facilitated speciation[21,22] and geographic range expansion[23]. β diversity patterns within and between palaeocontinents suggest that at regional scales, Ordovician geographic β diversity declined as taxa dispersed and integrated into communities, increasing α diversity[24].

Here, we assess the impact of spatial and environmental faunal differentiation at global scale. We adopt a spatial approach to β diversity, which should capture the effects of large-scale processes such as continental fragmentation, dispersal and integration of taxa between areas, the development of climatic gradients, and biogeographic change, which are implicated in early Palaeozoic diversification[13,21,25,26]. We also evaluate the role of faunal differentiation between lithologies in generating geographic β diversity. This spatial approach complements studies of diversity dynamics based on palaeoenvironments (e.g. [1]) or on collections from lithological formations (e.g. [14]).

We constructed global Cambrian-Silurian genus-level geographic α and β diversity curves of echinoderms, trilobites, brachiopods and molluscs, using equal-area hexagonal grids of side 111 km. This time window includes the CE and GOBE, as well as the Hirnantian extinction. We use additive β diversity partitioning to evaluate the contributions of taxon replacement and loss to β diversity, as a means of evaluating the impact of dispersal. We also test the hypothesis that rising α diversity during the Cambrian-Silurian is related to the development of more heterogeneous habitats, and that faunal and lithological β diversity are linked. Consideration of both environmental and spatial faunal differentiation is essential for resolving the mechanisms driving early Palaeozoic diversification.

Results

After rising in the early Cambrian, β diversity estimates show generally high values across most time bins, only dipping below 0.5 in the Hirnantian (Figure 1b). An initial sharp increase from the Terreneuvian to Cambrian Series 2 is in agreement with previously published work on geographic β diversity change in the Cambrian, which shows an initial increase followed by decline, though our time bins do not permit detection of a later Cambrian recovery[13]. In the Ordovician, β diversity initially increases between the Tremadocian and the Floian, then gradually declines towards the Katian, though it remains high (above 0.8). This is followed by a sharp decline to 0.47 in the Hirnantian, coincident with the homogenization of faunas during the Hirnantian mass extinction interval[27]. In sum, high β diversity developed during the early Cambrian, and showed a modest increase at the beginning of the Ordovician, before declining in the Hirnantian and failing to recover fully in the Silurian. The overall pattern is consistent with published geographic β diversity curves for the Phanerozoic[20]. We find no correlation between β diversity and the mean nearest-neighbour distance between grid cell centres in a time bin (Kendall's $\tau = 0.26$, $p = 0.25$, see Supplementary Information Table 1). Raw β diversity estimates are somewhat higher than the RAC (Relative Abundance Corrected) estimates, and show a relatively flattened signal through time (Extended Data Figure 1, see Methods for details on the RAC method).

Global γ diversity increases initially, from the Terreneuvian to Cambrian Series 2. After a small decline in the Miaolingian, γ diversity peaks in the Darriwilian (Figure 1a) and declines steeply in the Hirnantian, corresponding with the end-Ordovician mass extinction, before recovering somewhat in the early Silurian. γ diversity correlates moderately with α diversity over the Cambrian to Silurian (Kendall's $\tau = 0.46$, $p = 0.03$), and strongly with β diversity (Kendall's $\tau = 0.59$, $p < 0.01$).

Mean α diversity increases steadily from the Terreneuvian to the Sandbian, with a minimum of 5.6 in the Terreneuvian (Figure 1c). After peaking in the Sandbian, α diversity declines slightly after the Hirnantian, before peaking in the Sheinwoodian-Homerian. However, the end of the Silurian is marked by an α diversity decline. There is no correlation between α diversity and β diversity (Kendall's $\tau = 0.05$, $p = 0.86$).

Lithological variation within grid cells, represented by the mean number of formations within grid cells, shows no pronounced increase through time (Figure 2a). We find a moderate positive correlation between the number of formations within grid cells and α diversity (Kendall's $\tau = 0.43$, $p = 0.04$; Figure 3).

We also calculated lithological heterogeneity between grid cells. We treated the lithological units within grid cells as taxa and calculated the raw Sørensen dissimilarity, since this is a presence-absence measure and we do not expect incomplete sampling to affect the numbers of formations recorded. While there is no clear trend in lithological β diversity through time and values are high, we find a moderate positive correlation between taxonomic and lithological β diversity (Kendall's $\tau = 0.39$, $p = 0.08$).

Nestedness is very low in the Cambrian and Ordovician, with almost all β diversity reflecting turnover (Figure 2b). However, in the Silurian, nestedness increases somewhat, accounting for up to 16 % of geographic β diversity.

While the number of grid cells containing sufficient data for analysis varies between time bins, there is no statistically significant correlation between α, β or γ diversity and the number of grid cells (Kendall's $\tau = 0.10$, $p = 0.67$; Kendall's $\tau = 0.18$, $p = 0.44$; Kendall's $\tau = 0.33$, $p = 0.16$). We infer that the number of samples is not a major influence on the diversity patterns recovered.

Discussion

Our results confirm that geographic β diversity is an important component of γ diversity increase over the Cambrian – Ordovician. This is consistent with published data[13], which suggest that the CE occurred under conditions of continental fragmentation and, in the early Cambrian, involved animals with low dispersal abilities, leading to a global assemblage of relatively low-diversity but highly spatially differentiated communities. We also find that incomplete sampling flattens raw geographic β diversity fluctuations throughout the Cambrian-Silurian, making null models and correction methods valuable for β diversity studies over this interval (See Extended Data Figure 1).

The results of our γ diversity calculations are consistent with previous curves at stage level[28]. The Middle Ordovician peak in γ diversity appears decoupled from β diversity, and instead rises with α diversity (Figure 1). After the Floian, Ordovician increases in α and γ diversity were not matched by any corresponding increase in β diversity, and as the GOBE proceeded in the Darriwilian-Katian, β diversity began to decline, suggesting faunal homogenisation. In the Silurian, α diversity continues to increase while geographic β diversity declines, suggesting that enhanced α diversity may be related to the expansion of taxa into new areas.

The recovery of γ diversity after the Hirnantian involves an initial increase in β diversity, after which α diversity continues to rise as β diversity declines. This may correspond to the high-competition scenario of Hautmann (2014)[19], in which increases in β diversity during diversifications are transient, and cease when habitat contraction cannot continue. We find a strong correlation between γ and β diversity over the whole time interval, but the curves suggest a decoupling of γ and β diversity in the Middle-Late Ordovician and Silurian. This is consistent with the conclusions of Hofmann et al. (2019)[14], who found that within formations, β diversity is only a major driver of γ diversity in the early stages of diversifications, particularly in the early Palaeozoic. A similar pattern may apply to diversity patterns over spatially defined areas.

The decline in β diversity during the Floian-Katian, in the main pulse of the GOBE, suggests that the geographic range expansion of Ordovician marine invertebrates may have begun a gradual, global faunal homogenization, a process both predicted and measured in the early Palaeozoic[23,29,30]. The slight increase in nestedness reported here, particularly over the Ordovician and Silurian, suggests that over this interval, assemblages within grid cells are increasingly structured by patterns of colonisation followed by taxon loss[31]. The RAC β diversity curve also emphasizes the profound impact of the Hirnantian mass extinction interval on geographic β diversity, which almost halved over this time. Global faunal homogenization during the Hirnantian has been documented in studies of between-formation β diversity (e.g.[27]), but its impact appears to have been more severe than previously recognized. Furthermore, we find that the Hirnantian extinctions had a proportionally greater impact on geographic β diversity than on mean α diversity, emphasising their geographically heterogeneous effects.

The positive correlation between lithological and taxonomic β diversity likely illustrates the role played by habitat differentiation in β diversity; pairs of grids containing occurrences from different lithological formations are more taxonomically distinct, and pairs containing occurrences from the same formation are more taxonomically similar, though there is no clear trend in lithological β diversity over time. While lithological formations often comprise multiple distinct habitats[14], we have chosen to average the habitats recorded in a single lithological formation and compare the number of formations occurring within grid cells. The positive correlation between α diversity and the number of formations in a grid cell suggests that the more formations occur within a grid, the higher its α diversity is likely to be. Although this heterogeneity has both spatial and temporal components, the same effects are also present in the diversity data, so we treat them as comparable. We suggest that in addition to community differentiation between habitats, increased spatial environmental heterogeneity may have been linked to increased α diversity over the Cambrian-Silurian.

α diversity is highest during the Silurian, but this is not solely due to the *in situ* origination of new taxa, since β diversity declined at this time, and γ diversity peaked during the Middle Ordovician. Here, we will first address the implications of the decline in β diversity, and then go on to discuss the implications of the disjunct between α and β diversity for the mechanisms driving α diversity.

At the large spatial scales used in this study, β diversity patterns are affected by large-scale physical features such geographic barriers and the development of a latitudinal diversity gradient[26,32–34], and our results suggest that they are also linked to changes in the spatial distribution of environments and in the ease of dispersal. The gradual decline in β diversity from the Middle Ordovician to the Silurian implies enhanced dispersal of genera between grid cells. Geographic and environmental range expansion of taxa is expected as taxa age, and has been documented in the Ordovician rock record[23]. This dispersal may have been enhanced from the Ordovician onwards after the stepwise event known as the Ordovician Plankton Revolution[3], a diversification of planktic organisms from the late Cambrian onwards. In particular, both molecular clock estimates and evidence from molluscan protoconchs suggest a Cambrian-Silurian increase in the diversity of larval phases capable of feeding (planktotrophy), particularly in the late Cambrian-early Ordovician[35,36]. Planktotrophic larvae can typically disperse for longer than non-planktotrophic larvae and can be produced in larger numbers, since they do not require an energetically expensive yolk as a food source[37]. The dispersal of planktic larvae over longer distances provides a possible evolutionary mechanism for early Palaeozoic β diversity decline.

Enhanced dispersal is also consistent with the slight increase in nestedness in the late Ordovician and Silurian, which suggests that assemblages are increasingly constructed by the dispersal of taxa into new areas followed by taxon loss[31], rather than the isolation which leads to taxon replacement (turnover). A quantitative examination of the role of dispersal in Ordovician genus range expansion is outside the scope of this study, because of the general lack of preservation of motile larval stages. However, widespread dispersal of brachiopod and trilobite taxa has been documented through the Middle and Late Ordovician, and has been implicated as a driver for speciation[22,38].

Dispersal could also explain the rise in α diversity at a time when β was declining. One mechanism for increasingly close spatial packing of taxa is the rise of environmental spatial heterogeneity at increasingly small scales, for example through the expansion of complex environments such as reefs. This creates ever-smaller environmental niches for species to occupy, increasing niche packing and consequently α diversity[1,39]. According to this model, taxa cannot persist in environments where they are outcompeted in all niches; the more specialised the niche, the less likely it is that an individual will find its niche when colonising a new area. Enhanced dispersal abilities may have allowed genera to disperse over large distances and sustain high mortality in search of patchy habitats which fit increasingly narrow environmental preferences[37]. This would facilitate the development of α diversity in areas with enhanced environmental heterogeneity by allowing animals to adopt narrower niches and coexist at higher diversities, a prediction which may be supported by the positive correlation between α diversity and the number of formations within grids.

However, easy dispersal also allows the development of a metacommunity from which populations can be replenished after local extinction. This allows 'transient' taxa to persist and contribute to α diversity over long timescales, despite lacking a competitive advantage in any particular niche[40–42]. Where dispersal is easy, increased niche packing and an increase in the prevalence of transient genera leave the same spatial diversity patterns (increased α diversity and reduced β diversity), and are not mutually exclusive processes, so we cannot directly quantify their contributions in this case. However, the niche packing interpretation implies the ongoing origination of new taxa with increasingly specialised habitat preferences, and the extinction of pre-existing taxa, and so should be accompanied by high origination and extinction rates. Instead, origination and extinction rates fell rapidly during the Late Cambrian-Early

Ordovician[43], suggesting that niche packing was not a dominant driver of increasing α diversity after this time. Instead, we tentatively interpret the Ordovician-Silurian disjunct between β and α diversity as a consequence of a major increase in transient species within grid cells, facilitated by the increasing ease of dispersal after the evolution of planktotrophic larvae.

In sum, our results suggest a combination of mechanisms for the reported early Palaeozoic shift from rising γ diversity driven by β diversity, to α diversity[14]. As expected, γ diversity correlates positively with both α and β diversity over the Cambrian-Silurian, though the influence of β diversity may have declined after the Ordovician, when γ and α both rise while β falls. Environmental heterogeneity and faunal differentiation between environments appears to be an important driver of both α and β diversity, illustrated by positive correlations with the number of formations within grids and lithological β diversity, respectively. Our data are also consistent with an important role for dispersal in driving both α and β diversity patterns, with increased dispersal from the late Cambrian leading to declining β diversity and enhanced α diversity. This combination of mechanisms may have altered global diversity dynamics and ecosystem complexity by allowing taxa to adopt narrower niches, and, from the early Ordovician onwards, allowing taxa with no competitive advantage to persist more easily. The result was a shift in the mechanisms driving global diversification, from the maintenance of geographic β diversity through origination of young taxa with low dispersal abilities, to enhanced α diversity driven by environmental and faunal differentiation at smaller spatial scales, geographic range expansion, and an increase in the prevalence of transient genera.

Ongoing work is required to evaluate the relative impacts of palaeogeographic, palaeoenvironmental and evolutionary drivers on global diversity. α and β diversity estimates at varying scales and using a variety of approaches (spatial, environmental, and using indices which focus on different aspects of faunal difference), can complement each other to clarify possible drivers for global diversification in the early Palaeozoic. Furthermore, more studies of the sedimentology and geochemistry of early Palaeozoic environments, and their interaction with niche occupation in early Palaeozoic communities, are needed to unpick the smaller-scale mechanisms driving community differentiation, niche packing, and taxon persistence over this critical time interval.

Methods

We calculated α, β and γ diversity for all time bins which contained at least four grid cells containing ten fossil occurrences or more, of which at least two had to reach the coverage for standardization (set to 0.4). We set the minimum number of occurrences to ten to reduce the chance that null models would be built based on data which represented the abundance distribution of their original populations poorly. Along with diversity measures, we also used additive β diversity partitioning to assess the contributions of nestedness and turnover to β diversity, and calculated the mean nearest-neighbour great-circle distances between grid cell centres using the R package icosa[44].

We based our analysis on fossil occurrences of brachiopods, echinoderms, molluscs and trilobites from the Paleobiology Database (PaleoBioDB), identified to genus level (downloaded 18th January 2019, www.paleobiodb.org). Additional data were input to the database before this study, and the PaleoBioDB is the most comprehensive fossil occurrence dataset available.

Lagerstätten were removed, to minimize the impact of varying preservation quality between time bins. All PaleoBioDB collections are linked to paleogeographic latitudinal and longitudinal coordinates based on GPlates (https://www.gplates.org/) rotations[45]. We used the R package icosa[44] to assign fossil occurrences to equal-area hexagonal grid cells of side 111 km, and treated each grid cell as a single sample. Consequently, samples for α diversity calculation are composed of fossils from an undifferentiated mix of depositional environments, and are also time-averaged within time bins (see Supplementary Information Tables 2 and 3 for time bin boundaries). Grids of side 222 km and 55 km gave similar β diversity results (See Extended Data Figure 2).

The time bins are based on chronostratigraphic stages from the International Chronostratigraphic Chart (v2018/08)[46]. The current PaleoBioDB chronostratigraphic binning scheme is less precise and based on Gradstein et al. (2012)[47], which caused some data loss during binning (such as the data from Cambrian Stage 4 and the three Furongian stages). All PaleoBioDB occurrences that have absolute time and/or chronostratigraphic stage assignments that fit within our time bin scheme were taken into consideration for our analysis. However, time bin duration can influence α, β and γ diversity patterns, because the temporal turnover of species can artificially inflate diversity in longer time bins[20]. Cambrian to Silurian stages in the PaleoBioDB binning scheme range in duration from 11 Myr in the Terreneuvian, to 1.4 Myr in the Hirnantian. Mean time bin durations in the Cambrian and Ordovician are similar to each other (5.8 and 5.9 Myr, respectively), while Silurian time bins are shorter (3.1 Myr). To ensure that diversity measurements were comparable between time periods, we amalgamated the shortest Silurian time bins with their neighbouring bins (revised mean Silurian time bin length = 6.2 Myr), reducing our number of time bins to 16 but limiting the impact of time bin length on results. This leaves the Silurian divided into four time bins: Rhuddanian-Aeronian, Telychian, Sheinwoodian-Homerian and Gorstian-Ludfordian-Pridoli. Neither α, β nor γ diversity shows a significant correlation with revised time bin length (See Extended Data Table 1).

Coverage standardisation was used to reduce the impact of sampling effort and exposed rock volume on the results[48]. This effect is especially pronounced in α and γ diversity, but there is no correlation between mean coverage and β diversity, when no coverage standardisation is applied (Kendall's $\tau = 0.08$, $p = 0.77$). However, because the relationship between α and β is of interest, we chose to coverage-standardise β diversity for comparability with α diversity. Coverage standardisation for γ diversity estimates was done over whole time bins, rather than standardising each grid cell separately. The standardisation coverage was set to 0.4 because this permitted β diversity calculations for most of the time bins which met the minimum number of grid cells; sensitivity analyses demonstrate that a standardization coverage of 0.2 or 0.5 does not significantly change the results (See Extended Data Figure 3). Time bins were pre-screened in an attempt to ensure that there would be enough data in the time bin for simulated datasets to pass coverage standardization. When coverage for standardization is set to 0.5, several additional time bins do not contain enough data for analysis. The minimum number of grid cells for time bins to be analysed was arbitrarily set to 4, to remove data from time bins containing very few grid cells which would have low spatial coverage.

'β diversity' may refer to any one of over twenty mathematical treatments of faunal difference, with distinct sensitivities, biases and data types, and there are also conceptual differences in the definition of β diversity between studies[49–53]. For example, β-diversity can be measured across depositional environments[1,38,54], between or within lithostratigraphic units[14,27], or across pre-defined sampling areas[13,20]. Here, we estimated global geographic β diversity[13] by calculating pairwise Sørensen dissimilarities between equal-area grid cells using the R package vegan[55].

β diversity can be subdivided into turnover and nestedness components[31]. Nestedness reflects the extent to which less diverse assemblages are subsets of more diverse ones, while turnover reflects the extent to which taxa are replaced when assemblages are compared[31]. Because nestedness and turnover result from differing processes (taxon loss and taxon replacement, respectively), partitioning β diversity into turnover and nestedness components can reveal underlying drivers of assemblage difference, which are not obvious from a single β diversity measure[56]. The Sørensen dissimilarity incorporates both turnover and nestedness components of β diversity; the nestedness component is calculated by subtracting the Simpson dissimilarity[51,57,58], which only measures turnover, from the Sørensen dissimilarity[31,51,59]. While the R package betapart is designed for performing this procedure, we implemented it using RACB.Diversity()[60], which has an option to calculate the Simpson dissimilarity as re-expressed by Lennon et al. (2001)[57]. Presence-absence diversity indices may be excessively influenced by the presence of rare taxa, so we also calculated the abundance-based RAC Bray-Curtis dissimilarity[51,61], which was not significantly different from the Sørensen dissimilarity curve, demonstrating that rare taxa are not a major influence on our results (See Extended Data Figure 4). The β diversity between two communities ranges from 0 to 1, where a value of 0 indicates that the assemblages are identical, while a value of 1 indicates that the assemblages contain no shared taxa.

Many suggested drivers for early Palaeozoic diversifications involve an increased supply of resources such as oxygen, nutrients, or chemical energy[10,62], which may increase the abundance of organisms[63]. Abundance influences diversity patterns because abundant taxa are more likely to be preserved and sampled than rare ones[64], and with incomplete sampling, abundance distributions can alter apparent β diversity[60]. Because of this, we used the Relative Abundance Corrected (RAC) β diversity between grid cells within time bins as a β diversity measure, because it corrects for spuriously high β diversities caused by incomplete sampling, and because it reduces the impact of changing abundance distributions on β diversity[60]. Raw β diversity values recovered are considerably higher than the RAC values, which suggests that incomplete sampling may increase apparent β diversity values in the early Palaeozoic (See Extended Data Figure 1). We used 100 replicates for simulations within RACB.Diversity(), and coverage-standardised to Good's u = 0.4, to reduce the impact of uneven sampling on diversity estimates and to ensure that α and β diversity estimates are based on the same data.

Coverage-standardised α (within grid cell) and γ diversities were calculated using the function estimateD() in the R package iNEXT[65], which calculates taxonomic diversity with a pre-defined level of sample coverage (set to 0.4, for comparability with β diversity analyses). We excluded extrapolations with suspected large biases from the means for each time bin. We used the mean within-grid α diversity as a proxy for spatial niche packing[1,17], based on the principle that two taxa cannot coexist if they occupy the same ecological niche (Gause's principle of competitive exclusion[66]), and we extend this principle to the genus level.

The effects of sampling may be especially hard to interpret for β diversity. The effect of exposed sedimentary rock volume on global diversity curves is well documented, though may have a ‘common cause’ with diversification[67–69]. Similarly, we might expect declining β diversity values in time bins with increasingly closely spaced samples. Therefore, we checked for correlations between β diversity and the number of grids in a time bin, and also between β diversity and the mean nearest-neighbour great circle distance between grid cell centres in a time bin (See Extended Data Table 1).

The heterogeneity of environments within grid cells was evaluated using the mean number of formations within grid cells, which we calculated after removing grid cells containing fewer than ten fossil occurrences.

We checked for autocorrelation in all variables before calculating correlations between them using the acf() function in R[70]. No variable showed autocorrelation (See Extended Data Figure 5), so we have not detrended data before checking for correlations. We used Kendall’s τ as a measure of correlation, and we set the critical value for significance at 0.1, given the relatively small sample size ($n = 13$, once time bins with insufficient data are filtered out).

Code Availability

The complete code and relevant results are recorded in R-code and can be downloaded at zenodo.org (DOI: 10.5281/zenodo.3463219).

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Author Contributions

AP and BK devised this research, agreed on analytical techniques, and wrote the paper together. AP calculated β diversity and checked correlations. BK downloaded and formatted data from the Paleobiology Database, calculated α and γ diversity, and drew the figures.

Data Availability

All data used in this work can be downloaded from the Paleobiology Database (https://paleobiodb.org/#/). URLs for retrieving the data used to generate these results are available in the accompanying code (see ‘Code Availability’).

Competing Interests

The authors declare no competing interests.

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Figure Captions

Figure 1. Gamma, beta, and alpha diversity curves from 540-419 Ma

The following abbreviations are used for stratigraphic names: Terr = Terreneuvian, Se2 = Cambrian Series 2, Mia = Miaolingian, Fu = Furongian, Tr = Tremadocian, Fl = Floian, Dp = Dapingian, Dw = Darriwilian, Sb = Sandbian, Ka = Katian, Hi = Hirnantian, Rh = Rhuddanian, Ae = Aeronian, Tl = Telychian, Sh = Sheinwoodian, Ho = Homerian, Go= Gorstian, Lu = Ludfordian, Pr = Pridoli, Lo = Lochkovian.

a. Global (γ) diversity, showing a peak during the Darriwilian, during the main pulse of the GOBE.

b. Geographic β diversity measured using the RAC Sørensen dissimilarity.

c. Mean α diversity.

In all figures, 95% confidence intervals are shown in orange. All metrics are coverage-standardised to Good's u = 0.4. The Cambrian Explosion (CE) extends from approximately 530-520 Ma[11], while the Great Ordovician Biodiversification Event (GOBE) extends throughout the Ordovician[8].

Figure 2. Heterogeneity of lithological units within grids, and nestedness from 540-419 Ma

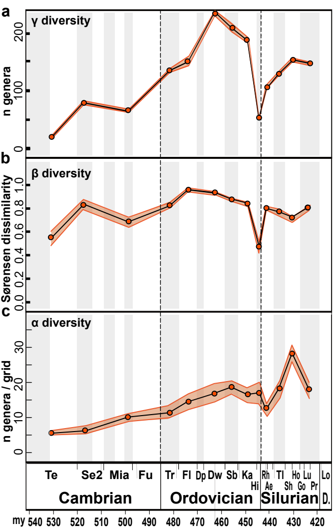
The following abbreviations are used for stratigraphic names: Terr = Terreneuvian, Se2 = Cambrian Series 2, Mia = Miaolingian, Fu = Furongian, Tr = Tremadocian, Fl = Floian, Dp = Dapingian, Dw = Darriwilian, Sb = Sandbian, Ka = Katian, Hi = Hirnantian, Rh = Rhuddanian, Ae = Aeronian, Tl = Telychian, Sh = Sheinwoodian, Ho = Homerian, Go= Gorstian, Lu = Ludfordian, Pr = Pridoli, Lo = Lochkovian.

a. Mean number of formation within grids, used as a measure of environmental heterogeneity.

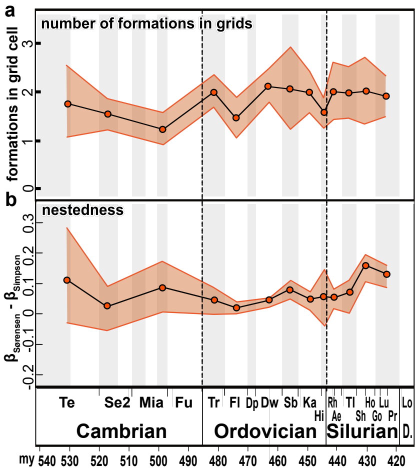
b. Nestedness, calculated by subtracting the RAC Simpson dissimilarity from the RAC Sørensen dissimilarity.

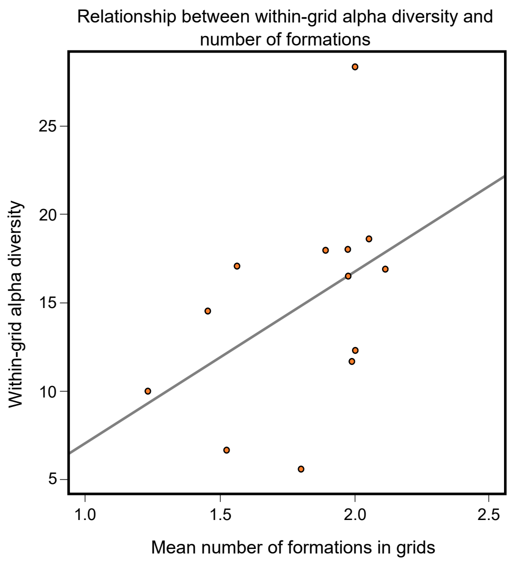
Figure 3. Relationship between within-grid alpha diversity and within-grid number of formations.

Kendall's $\tau = 0.53$, $p = 0.01$



a
γ diversity
n genera
200
100
0
b
β diversity
Sørensen dissimilarity
1.0
0.8
0.6
0.4
0.2
0.0
c
α diversity
n genera / grid
30
20
10
0
Te
Se2
Mia
Fu
Tr
Fl
Dp
Dw
Sb
Ka
Hi
Rh
Ae
Tl
Sh
Ho
Go
Lu
Pr
Lo
Cambrian
Ordovician
Silurian
D.
my
540
530
520
510
500
490
480
470
460
450
440
430
420


a
number of formations in grids
formations in grid cell
b
nestedness
$\beta_{Sorensen} - \beta_{Simpson}$
Te
Se2
Mia
Fu
Tr
Fl
Dp
Dw
Sb
Ka
Hi
Rh
Ae
Tl
Ho
Sh
Go
Lu
Pr
Lo
Cambrian
Ordovician
Silurian
D.
my 540 530 520 510 500 490 480 470 460 450 440 430 420


Relationship between within-grid alpha diversity and number of formations
Within-grid alpha diversity
Mean number of formations in grids
25
20
15
10
5
1.0
1.5
2.0
2.5