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Longitudinal expansion fitness of brachiopod genera controlled by the Wilson cycle

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Abstract

The brachiopods constitute one of the major components of the marine metazoan fossil record. On the other hand their apparent decline in importance in forming benthic communities through the Phanerozoic is one of the most striking macroevolutionary and macroecological patterns. Here we analyzed changes in average latitudinal and longitudinal ranges – indices for success of spatial expansion of brachiopod genera – during post-Cambrian Phanerozoic, and compared their fluctuation and scaling behaviour to the changes in continental fragmentation. The results revealed that latitudinal ranges on the longest time scales were highly constrained, while longitudinal ranges shown persistent decrease. The scale-by-scale correlation analysis of Haar fluctuations revealed that there is positive functional dependence of longitudinal ranges at the longest time scales with continental fragmentation. Moreover the ratio of average longitudinal to latitudinal ranges was positively correlated to the continental fragmentation at all time scales. The long term minimum longitudinal ranges and the least elongated shapes in E-W direction of geographic ranges were found during the maximal amalgamation of the Pangaea during Triassic and Jurassic. The failure for brachiopods to regain the dominance in marine biosphere after P-Tr extinction should be related to the tectonic restrictions on their longitudinal ranges during the maximally supercontinental conditions of the planet. Therefore, the pattern exemplified by brachiopods shows that the spatial expansion success (fitness) of a major clade at an eon time scale could be a direct consequence of the multi-scale tectonic reconfigurations.

Keywords: tectonics, geographic ranges, brachiopods, macroevolution, scaling

Introduction

Spectacular fossil records show that the phylum Brachiopoda was both diverse and historically important component of marine biota (Carlson, 2016). The decline in global brachiopod diversity, and also of their local ecosystem dominance is a classical macroevolutionary and macroecological case study of the largest scale compositional and functional changes in marine communities (Gould and Calloway, 1980). Brachiopods reached their maximal genus richness in the Paleozoic, while the Meso-Cenozoic was characterized by low diversity (Carlson, 2016). Apparently, brachiopods were displaced by ‘modern evolutionary fauna’ (including bivalve molluscs) from most productive inner shelf habitats through geological time (Sepkoski and Miller, 1985).

There is a profound debate over the relative importance between two conceptually distinct factors in brachiopod decline. On the one hand it is argued that a random high magnitude P-Tr mass extinction event reset the dominance of the whole swath of clades including brachiopods (Alroy, 2010; Gould and Calloway, 1980). It is speculated that the failure to recover following an era-defining extinction could be related to a hypothesized loss of planktotrophic clades (Valentine and Jablonski, 1983). On the other hand it is argued that there was a systemic eon-scale displacement of brachiopods by their competitors, most likely bivalves which are similar in their ecomorphology and ecology (Gould and Calloway, 1980; Liow et al., 2015; Sepkoski, 1996) but more energy intensive and thus competitive in resource rich environments (Payne et al., 2014; Rhodes and Thompson, 1993). The post-Triassic decline in consistency of substrates due to intensified bioturbation as well general increase in predation is thought to contribute to the decline in competitiveness of sessile brachiopods that are characterized by low mobility (Donovan and Gale, 1990; Manojlovic and Clapham, 2021; Thayer, 1985). The hypothesis of a gradual displacement of brachiopods by other clades (the wedging out of a clade) suggests that there should be a monotonic decrease in clades' fitness metrics. Mass extinction, recoveries and mass originations in this model should appear as short transient fluctuations – essentially reversible i.e. as inconsequential perturbations (Sepkoski, 1996).

Little explored is the possibility of modulation of success of brachiopod clade by long-term (millions to hundreds of millions of years) geological processes, although there are some exemplary exceptions (Liow et al., 2015). There is growing evidence that the severity of extinctions is dependent on the long-term state of the biosphere (Mitchell et al., 2012), or continental amalgamation patterns (Saupe et al., 2019). The geometry of continental outlines have a potential to influence latitudinal as well as longitudinal patterns of the biodiversity (Jetz and Rahbek, 2001). The epoch of high continental dispersal and active mid-ocean spreading are simultaneously associated with high sea levels, and large extents of epeiric seas (Peters, 2007) – some of the most important habitats for benthic marine life. On the other hand, during the opposite phase of the Wilson cycle, when landmasses were aggregated into a single supercontinent, shallow marine areas decreased (thus decreasing potential for sequestration of carbon), leaving the Earth susceptible to prolonged hyperthermal episodes caused by, for example, of a large igneous province (Wignall, 2015). Brachiopod spatial and temporal diversity patterns were strongly influenced by the distribution and amount of shelfal areas (Powell, 2009) which are also strongly controlled by the tectonic interactions of continental land masses. It is therefore plausible that long time scale tectonic processes provide a major control on the changes in success of brachiopods at the global scale.

Here we present an analysis of the average per-stage brachiopod genus level latitudinal and longitudinal ranges. The geographical range is an important character of a taxon, it reflects a successful ability to cross an array of geographic barriers, to disperse, and ultimately invade and persist in new ecosystems (Stigall, 2019). At least during the background macroevolutionary regime (Foote et al., 2008; Jablonski, 1986; Payne and Finnegan, 2007), the geographical range is a significant factor positively influencing the survivorship component of taxon fitness (Jablonski, 2008, 2017). Additionally the duration of late Paleozoic brachiopod genera were strongly positively correlated with the extents of their (latitudinal as well as longitudinal) ranges, due to positive effects of the geographical range on the global abundance (Powell, 2007).

Latitudinal range mostly reflects the range of temperatures; it co-varies with the climatic temperature conditions tolerated by a taxon. The longitudinal distribution of a taxon should be less constrained, and should mostly be affected by the taxon's intrinsic capacity to invade new (climatically similar) ecosystems, to cross geographical barriers, and the internal organismal dispersal ability. The fitness of an organism or taxon depends on the interaction of their internal properties and environmental conditions (Levins and Lewontin, 1987) over a range of time scales. In this way, longitudinal ranges should more faithfully reflect the expansion fitness (Van Valen, 1989) of a genus in a given physiographical and biospheric condition than latitudinal ranges. Species and higher taxa, are composed of many spatially distributed populations which occupy varied ecosystems, where they fulfil diverse context dependant roles (or "niches") which can be enabled by their internal characteristics (Eldredge, 1995). Therefore geographic spread is also related to the taxons' capacity for functional adaptability.

Based on these theoretical premises, here we investigate the temporal evolution and temporal scaling of brachiopod geographic ranges. We also test the hypothesis of their hierarchical control by plate tectonics as measured by continental fragmentation index (Zaffos et al., 2017) – the major factor reflecting physiography of the Earth. The fluctuation patterns of brachiopod genus level latitudinal and longitudinal ranges were studied using Haar fluctuation analysis (Lovejoy and Schertzer, 2012), and tested for multi-scale correlation with continental fragmentation index using cross-Haar fluctuation analysis (Spiridonov and Lovejoy, 2022). We also analysed the scaling behaviours of given metrics, which revealed qualitative differences between dynamics of longitudinal and latitudinal ranges as well as their ratios (shapes of ranges) as a function of time scale.

Methods

Data

Estimation of brachiopod geographic ranges and supercontinental cycle proxy data

In order to examine the temporal changes of brachiopod genus level longitudinal and latitudinal ranges we used data from the Paleobiology Database (PaleoDB, <https://paleobiodb.org/> downloaded on November 18, 2021). The genus level was chosen because it is the closest in the Linnean hierarchy to the species level, and in many studies it was shown that it reflects species level processes reasonably well even if genera are paraphyletic (Sepkoski and Kendrick, 1993). The species level is preferable, but given sparseness of even genus level records in many stages, the analysis at the species level would have made many data points unused (for example in a genus known from three location, and each location represented by a separate species). The dataset includes all occurrences of Brachiopoda, excluding uncertain genera, which were filtered out during

the download. In total data on 171,545 genus occurrences were downloaded. *ArcGIS Pro 2.5.0* software in combination with *Python 2.7.16* was used for the following data pre-processing. The data were binned to international stages from the Tremadocian to the Holocene. All fossil occurrences that were not uniquely binned at the stage level, as well as ones with missing paleocoordinates, and genus information were eliminated. Samples collected from unlithified sediments were eliminated too, since later factor could induce much more complete spatial coverage, and possibly systematically different compositions of marine taxa in more recent time periods (Hendy, 2009). Only one occurrence was kept per genus, per unique paleolocation, and per stage following approach of Foote and others, 2016(Foote et al., 2016). The final dataset consisted of 36,838 unique brachiopod genus/stage/location records. The downloaded dataset could be found as a Supplementary Information to the article.

As a geographic range metric we used the average geodetic distance in latitudinal and longitudinal directions between GPlates(Müller et al., 2018), paleolocations (available in the Paleodb record) of each pair of occurrences in the current genus/stage combination. Only genera which had ≥ 3 occurrences were used for the calculation of average ranges. Only time bins which had ≥ 3 genera, and satisfying all previous conditions were used in calculating per stage average longitudinal and latitudinal range sizes of brachiopod genera.

As a proxy for a state of a Wilson (supercontinental) cycle we used so called continental fragmentation index (Zaffos et al., 2017) obtained from the Zaffos and others, (2017). The index quantifies the standardized proportion of continental plate boundaries which touch each other to a situation where all plates are totally separated. The maximal value of the index is “1” where all continental plates are fully dispersed. The value of “0” corresponds to the maximal aggregation of continental plates into a single supercontinent. This continental fragmentation index was calculated by the cited authors from EarthByte tectonic paleoreconstruction model (Zaffos et al., 2017) - <https://www.earthbyte.org/>.

It should be mentioned that the quality of tectonic reconstructions, which are used both – for the estimation of geographic ranges of genera, and also continental fragmentation indices, are variable in quality, and this quality decreases with the geological age of formations. The latitudinal reconstructions are less constrained, since only magnetic paleo-longitudes can be estimated from polarity of magnetic field in minerals. In the case of Meso-Cenozoic, the positions of continents can be estimated by using the age maps of oceanic crust, with very high accuracy. On the other hand, the distribution of taxa, climatically sensitive minerals, and the continuity of geological formations, currently allows the estimation of relatively robust models of paleocontinental configurations (Torsvik and Cocks, 2013). The use of fossil taxa for the inference of paleogeographical reconstructions is a bit circular in current context. On the other hand, here we analysing only one large clade, while the paleogeographic reconstructions are usually based on multi-taxa information, in combination with all other geophysical and geological evidence.

The distribution of taxa on the globe could be in principle affected by geometric constraints of spherical coordinate system and circular distribution of climatic zones. First of all the maximal possible range in the E-W direction can in principle be two time longer that the maximal range in N-S direction. Therefore, we can expect that the taxa in principle can have larger range in

E-W than in N-S direction. Additionally, climate sensitive taxa occupying higher latitudes due to geometric constraint have fewer possibilities to expand in the E-W direction, with polar taxa affected most. Therefore, possible the bias is a complex one. On the other hand, average per-stage brachiopod ranges are much smaller than the maximal possible ranges – some early Paleozoic average longitudinal ranges reach 4 to 6 thousand km, and latitudinal average ranges reach up to ≈ 4 thousand km; numbers which are much smaller than circumference ($\approx 40,075$ km) or even half circumference ($\approx 20,037$ km) of the Earth. Moreover the geometric bias due to spherical coordinates and climate zones is working at all times equally and therefore the dynamics of geographic ranges (which are of interest here), and time scale characteristics of dynamics, should not be affected much by it. It could be argued, that the movement of continents and their concentration in specific latitudes can affect the potential for brachiopods to disperse between regions, as a kind of geometric bias. Although, since this effect would be of tectonic origin it cannot be called a bias per se but should be treated as a separate causal geodynamics related factor, which is of interest here.

Haar fluctuations, multiscale correlations and fluctuation exponents

Haar fluctuation analysis (Lovejoy and Schertzer, 2013) is a convenient method for the determination of structure functions (scaling relations) of dynamic processes with fluctuation exponents in a range of $-1 < H < 1$. Therefore it is suitable for the description of both differences and anomalies (Lovejoy and Schertzer, 2012). A more traditional approach uses first difference wavelet, which is valid for “wandering” processes (Lovejoy and Schertzer, 2013; Spiridonov and Lovejoy, 2022) with fluctuation exponent H between 0 and 1 (exemplar studies using this approach (Cornette and Lieberman, 2006; McKinney and Oyen, 1989; Spiridonov et al., 2016)). Therefore Haar fluctuation can be seen as a more generalized multiscale approach, which can be used also for stabilizing processes which are characterized by $H < 0$.

For a given time series, such as $T(t)$ the Haar fluctuation at a given time scale Δt is defined as the difference between the average of the first and second halves of the interval Δt :

$$\Delta T(\Delta t)_{Haar} = \frac{2}{\Delta t} \int_{t-\Delta t/2}^t T(s) ds - \frac{2}{\Delta t} \int_{t-\Delta t}^{t_0+\Delta t/2} T(s) ds$$

Then the fluctuation exponent H is defined with respect to the mean absolute fluctuation:

$$\langle |\Delta T|_{Haar} \rangle \propto \Delta t^H$$

Fluctuations in the **Fig. 2** are multiplied by the factor of 2 in order to make fluctuations closer to anomaly ($-1 < H < 0$) or difference ($0 < H < 1$) fluctuations. Although other exponents are needed to fully characterize scaling series, (especially when these are intermittent), the value of H is often the important determinant of the qualitative behaviour of the system. If it is < 0 , then successive fluctuations tend to cancel, average fluctuations tend to diminish with scale, the

behaviour appears stable. If $H > 0$, then fluctuations grow with scale, the series tends to “wander”, with apparently unstable, diverging behaviour (Lovejoy and Schertzer, 2013).

Paleontological and paleoclimatological studies commonly use variograms, (and their averages, structure functions) based on fluctuations defined instead by first difference (or “poor man’s” wavelet) for the correlation (McKinney and Oyen, 1989) and scaling analyses of time series. However, at a time scale Δt , such variograms will only reflect the typical fluctuations at scale Δt when $0 < H < 1$: when $H < 0$ they will instead be artefacts being dominated by the lowest frequencies in the series. In contrast structure functions based on Haar fluctuations are useful over the much wider range $-1 < H < 1$ that includes the “cancelling”, stable regime, overall it is adequate for the great majority of geosignals (Lovejoy and Schertzer, 2012). The fluctuations which are determined using Haar wavelet can also be used for multiscale correlation analysis of two time series (so called cross-Haar analysis (Spiridonov and Lovejoy, 2022), a convenient real-space analogue of cross-spectral analysis). The ensembles of fluctuations that are calculated using Haar fluctuations at each time scale can be used for the calculation of correlation coefficients and their statistical significance at each time scale. Here we calculated in the *Mathematica* environment, Pearson product moment correlation coefficients between average longitudinal ranges, average latitudinal ranges, ratios of average latitudinal and longitudinal ranges, and continental fragmentation index fluctuation time series at all available time scales (plotted in **Fig. 4**). For the in-depth explanation of applied Haar fluctuation and cross-Haar analysis methodologies reader is directed to read (Spiridonov and Lovejoy, 2022).

RESULTS

Ordinary least square regression was performed on brachiopod longitudinal and latitudinal average ranges (**Fig. 1, A**) using R 4.0.3 statistical program fitting `lm` function in the base R (R Development Core Team, 2015). The analysis revealed that the hypothesis of a linear decrease in average per stage longitudinal ranges of brachiopod genera is strongly supported ($r = 0.4$, $r^2 = 0.17$, $p = 0.0003$, $n = 69$). At the same time there is weak evidence for the decrease in average per stage latitudinal ranges of brachiopod genera through the post-Cambrian Phanerozoic ($r = 0.2$, $r^2 = 0.037$, $p = 0.059$, $n = 69$). The omission of a large positive Ypresian (Paleogene) outlier, strongly increases the model performance by increasing the effective size and significance of the decrease in average per stage longitudinal ranges of brachiopod genera ($r = 0.5$, $r^2 = 0.25$, $p = 8.35 \times 10^{-6}$, $n = 68$). The decrease in latitudinal ranges while of a weak correlation also becomes significant ($r = 0.32$, $r^2 = 0.104$, $p = 0.004$, $n = 68$).

As a first approximation, average longitudinal brachiopod ranges significantly decreased, while latitudinal ranges approximately stayed the same during the Phanerozoic. On closer inspection, a more nuanced picture emerges. The ratio of average longitudinal to latitudinal

ranges, especially at longer time scales show remarkable resemblance (**Fig 1 B, C**) to the changes in continental fragmentation index (Zaffos et al., 2017). The smoothed ratios of average longitudinal to average latitudinal ranges apparently show 2nd order periodic oscillations (**Fig 1, C**). If the long-term non-linear trend is subtracted from this smoothed record, then the REDFIT spectral analysis (Schulz and Mudelsee, 2002) shows that there is a statistically significant (at 99 %) quasi-periodicity with the period length of 75 Myrs.

The performed analyses are of the absolute geographic ranges, ratios, and tectonic indices. It is illuminating to consider the corresponding fluctuations between the corresponding quantities. This is conveniently done using Haar fluctuation analysis of the mean fluctuations of longitudinal and latitudinal ranges. **Fig 2 B** shows that longitudinal ranges (top) are systematically more variable than latitudinal ones (bottom) at all time scales. To understand this behaviour better, if over a range of scales, the typical size of fluctuations (ΔF) changes in power law manner $\Delta F \approx \Delta t^H$ as a function of time scale (Δt), then the pattern is said to be scaling, and H is the fluctuation exponent. Although at scales less than about 20 Myrs. the uncertainties are strong, it seems that both latitudinal and longitudinal range fluctuations show two regimes: positive scaling exponents up to the time scales of 20 Myrs and at longer time scales show strong negative exponents, i.e. a decrease of variability or stabilization ($H \approx -0.5$) - if the process is Gaussian (low intermittency), then $H=0.5$ is Brownian motion and $H = -0.5$ is white noise. Longitudinal ranges show a scaling with roughly $H \approx 0.0$ with high variability at short as well as at long time scales. **Fig. 2A** shows the (logarithms) of the ratios of the mean fluctuations (the differences in **Fig. 2B**). This shows that the starkest (and significant) difference appears at the longest time scales > 100 Myrs. Differences in magnitudes of longitudinal fluctuations to latitudinal fluctuations monotonically grow at the longest time scales. The continental fragmentation index (**Fig. 2 C**) shows very strong and consistent positive scaling exponent ($H \approx +0.75$). The same pattern of positive exponent is observed for the ratio (**Fig. 2 D**) of average per stage longitudinal and latitudinal ranges ($H \approx +0.17$), suggesting that continental fragmentation could be a driving force behind the changes in average shapes of geographic ranges. The comparison of average relative shapes and sizes of ranges of brachiopod genera (**Fig. 3**) as a function of time scale clearly shows that at all scales, fluctuations in geographic ranges are on average larger in the E-W direction. At time scales longer than approximately >100 Myrs the variability is completely dominated by longitudinal range changes.

Analysis of the scale-by-scale Haar fluctuation correlations revealed that longitudinal ranges have statistically significant and consistent correlations with the continental fragmentation index (**Fig. 4 A**) on the longest time scales (>60 Myrs). In addition, at short time scales, the latitudinal ranges show generally small negative correlations with fragmentation index (**Fig. 4 B**) but display increasingly negative correlations at time scales >100 Myrs. Despite these differences in correlations with the continental fragmentation index, longitudinal and latitudinal ranges are highly correlated at most time scales (**Fig. 4 C**) except the longest time scales with no correlation at a scale of 200 Myrs. The scale by scale analysis of ratios of longitudinal to latitudinal ranges show that the ellipticity (in E-W direction) of brachiopod ranges is positively correlated with continental fragmentation over a wide scale range (**Fig. 4 D**), with consistently positive high ($r \approx 0.8$) and statistically significant values observed at the longest time scales (time scales > 100 Myrs). Apparently at the longest time scales positive fluctuations in the continental fragmentation are

associated with the longitudinal expansions and latitudinal (much smaller) contractions which result in formation of highly elliptic in E-W direction geographic ranges. Conversely the increase in continental aggregation in to a supercontinent results in long-term states of small and almost isometric geographic ranges.

DISCUSSION

Previous studies have shown that global marine diversity levels are positively correlated with continental fragmentation (Zaffos et al., 2017). Therefore, the multiscale correlation patterns of geographic ranges and shapes with the fragmentation of continents described here, as exemplified by brachiopods, provides a plausible mechanistic explanation of the former pattern. The increasing fragmentation of continents at the longer time scales (> 100 Myrs) creates the opportunity for marine taxa to effectively expand in climatically similar epicontinental habitats – thus promoting expansion in the latitudinal direction, and increasingly buffering it from extinctions caused by local environmental perturbations. Given restricted and almost unchanging long-term (>100 Myrs) average potential of brachiopod genera to expand in latitudinal directions (climate zones) through the Phanerozoic, temperatures should have worked as formidable barriers. The fragmentation of landmasses into smaller disjoint continents should have alleviated barriers for migration, dispersal, and general range shifts of marine taxa in E-W direction, and consequently resulted increase in the geographical genus level fitness.

Brachiopod genera extinction rates in the Triassic to early Cretaceous (Powell et al., 2015; Reitan and Liow, 2017) were some of the highest in the whole Phanerozoic. This time interval coincides with maximal continental aggregation, lowest long-term E-W ellipticity geographic ranges, and low long-term longitudinal ranges (**Fig. 1**). The modulation of the latitudinal geographic ranges (or latitudinal expansion fitness) of brachiopod genera, and of the shapes of their ranges induced by plate tectonics provides a mechanism which could account for the variability of the long-term clade macroevolutionary rates. The variability in longitudinal ranges at time scales > 100 Myrs is much higher than in latitudinal ranges. It could be argued that this relation could appear due to quicker saturation of latitudinal variability due to geometric constraints on the sphere (2 times larger maximally possible range in E-W direction). Although if we look at the **Fig. 1 A** we can see that the typical (long-term average) latitudinal ranges through the Phanerozoic are somewhere around 1.5 thousand km. If only geometric constraint was at work there, we could have expected much greater wandering in average values which in principle could approach up to 20 thousands km in N-S direction.

It should be noted that at the longer time scales, also there is a consistently high correlation with continental fragmentation. Additionally, it appears that the strength of the correlation of longitudinal ranges with the fragmentation of continents has a positive scaling exponent (**Fig. 4**). The probable reason of this increasing correlation with time scale is that the continental fragmentation index has a very steep positive scaling exponent, implying that at longer and longer time scales we expect much larger fluctuations than at short scales. Therefore since there

is linear correlation between evolutionary rates and fragmentation, and since the continental cycle directly affects range dynamics, then we expect stronger correlations on longer and longer time scales. The variability in range shapes (**Figs. 2 D**, and **3**), as expected also has $H > 0$ over a wide range of time scales. Increasingly positive correlations with the time scale are also observed between range shapes (ellipticity in E-W direction) and the continental fragmentation (**Fig. 4 D**).

Separate attention should be given to the scaling pattern of latitudinal ranges. Up to time scales of 25-30 Myrs, latitudinal ranges scale positively – at these time scales, their fluctuation amplitudes are the largest (**Fig. 2B**). Beyond this time scale there is a scaling regime with large negative exponent, with variability falling off very quickly at longer and longer time scales, returning to its long term average. A possible explanation for this pattern could be, that climate at time scales longer than 1 Myrs also scales positively, forming the “megaclimate” regime (Lovejoy, 2015). Increasing with time scale variability in megaclimate is then matched by variability in brachiopod latitudinal ranges up to a certain point. Apparently further growth in average temperature variability doesn't translate into equal variability in N-S dispersal of genera. It could be speculated that this could stem from some sort of constraint for latitudinal dispersion. One explanation could be related to the zonal geometry of climate belts. During hyperthermal conditions, tropical regions could achieve lethal temperatures (Benton, 2018; Wignall, 2015), therefore zones with tolerable temperatures south or north of the equator would be inaccessible for biota living in opposite hemispheres during the long durations of the hot periods. In the case of the fluctuation with the opposite sign – during icehouse conditions, steep pole-equator temperature gradients are expected (Scotese et al., 2021), which should act as important barriers for geodispersal (Stanley, 2010). In any case the brachiopods should have had quite similar and restricted average temperature tolerances through the whole Phanerozoic to yield this stochastically constant pattern.

The current finding of scaling and significant correlations between geographic ranges, their shapes and the continental fragmentation confirms the important and precise role of the multiscale dynamics of the Wilson cycle of dispersal and amalgamation of supercontinents on the evolution of spatial biodiversity structure. The restricted latitudinal range variability on the longest time scales in combination with high levels of variability in longitudinal ranges ensures that the systemic changes in average ranges is mostly determined by the E-W variability component (**Fig. 3**). Since longitudinal range variation is connected tightly to the state of fragmentation of continental plates on the longest time scales, range size evolution is mostly determined by the state of the supercontinental cycle. Therefore this study shows that range restriction of brachiopod genera, which was modulated by tectonic configurational changes, is expected to significantly contribute to restricting the success of this clade during the Triassic and Jurassic in the aftermath of the P-Tr extinction event. Longitude restriction of brachiopod genera was also determined earlier in the case of transition from Carboniferous to the Permian (Powell, 2007), reflecting temporally longer trend related to the formation of Pangaea described here.

The biodiversity is repeatedly shown to exhibit cyclic and quasi-cyclic behaviour on multi-million time scales (Lieberman and Melott, 2007). The putative quasi-periodicity with the period length of ≈ 75 Myrs, could be related to the similar in period length ($\approx 56 - 60$ Myrs) cycles in tectonics, geochemistry, and biodiversity which were reported earlier (Meyers and Peters, 2011; Melott et al., 2012). If the shapes and sizes of ranges at least partially determine the rates of

macroevolution, then the quasi-periodic changes in ranges, probably caused by tectonics, could be a significant driver of quasi-periodic changes in diversity. The presented hypothesis needs separate analyses. It should be mentioned, that the tectonic activity, as reflected by continental fragmentation index, shows almost perfect positive scaling similar to that of megacclimate regime (Lovejoy, 2015). Therefore, any cyclic tectonic processes (and biogeographic processes which are enabled by them) should be dominated by variability of the stochastic continuum of ever increasing in magnitude fluctuations with the measured time scale.

The geographic range expansion is a crucial element in biodiversity generation by means of geodispersal of allopatric speciation which plays a major role (alongside vicariance) in cyclic biodiversity generation (Stigall, 2019; Stigall et al., 2017). Therefore, the inability of genera to expand in suitable climate zones due to the tectonic constraints, should induce both a higher extinction risk as well as a slowdown in the overall dispersal of innovations at the global scale. Conversely, periods of intensive fragmentation and ocean spreading are expected to be conducive to the preservation and spread of diversity.

Conclusions

The scaling and scale-by-scale correlation analysis of dynamics of brachiopod geographic ranges revealed that:

- i) Average latitudinal ranges of brachiopods were relatively constant on long time scales (>100 Myrs) during the post-Cambrian Phanerozoic, while longitudinal ranges experienced a significant decline.
- ii) The longitudinal ranges are statistically significantly positively correlated with the fragmentation of continents on the longest time scales (> 100 Myrs).
- iii) The shape of brachiopod geographic ranges (their elongation in E-W direction) is significantly positively correlated with the fragmentation of continents on a wide range of time scales.
- iv) The wide geographical ranges (mostly in longitudinal direction) are related to the dispersed phase of the Wilson cycle, while the aggregational global state of the cycle (formation of a supercontinent) induces small and isometric average geographic ranges of brachiopods.
- v) The decline of brachiopod spatial ranges or spatial fitness, and thus their significance in forming marine biosphere, during the Paleozoic to Jurassic is significantly influenced by the formation of Pangaea.

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FIGURES

Fig. 1. A Average per-stage longitudinal (black) and latitudinal (red) ranges of brachiopod genera through post-Cambrian Phanerozoic, straight lines are ordinary least square linear regressions; **B** average per stage longitude and average latitude range ratios, and their 2 (brown) and 4 (red) point Gaussian smoothed curves; **C** Continental fragmentation index(Zaffos et al., 2017) (black, n=463 data points) and smoothed 5 point moving average ratios (red) of average per-stage longitudinal and latitudinal ranges of brachiopod genera; both normalized by dividing by the largest value in a range. Here and in other figures, all brachiopod time series analyses were based on n=69 points (time bins).

Fig. 2. A Divergence between average fluctuations in longitudinal and latitudinal per-stage brachiopod ranges $D = \log_{10}\left(\frac{RMS_{long}}{RMS_{lat}}\right)$ as a function of time scale; RMS – root mean square fluctuations. RMS fluctuations as a function of time scale (lag Δt): **B** average longitudinal and latitudinal ranges (measured in m) with 95 % confidence intervals of typical magnitudes of fluctuations; **C** continental fragmentation; **D** ratios of average per-stage longitudinal to average per-stage latitudinal brachiopod generic ranges. Dashed lines show reference lines for scaling functions H. Time scale lags Δt separated by 0.1 units on the \log_{10} scale in Myrs.

Fig. 3. Relative sizes and shapes of brachiopod geographic range fluctuations as a function of time scale. Characteristic magnitudes of fluctuations are obtained from **Fig. 2B**. For ease of the interpretation, the average longitudinal (E-W) and latitudinal (N-S) time specific fluctuations organized into four time scale classes. The shortest time scales Δt in each group are green, then

follows orange, then blue, and the longest are red. Time scale lags Δt separated by 0.1 units on the \log_{10} scale in Myrs (i.e. steps of $10^{0.1} \approx 1.26$).

Fig. 4. Scale-by-scale Pearson correlations between Haar fluctuations: **A** Average per-stage longitudinal ranges and continental fragmentation index; **B** Average per-stage latitudinal ranges and continental fragmentation index; **C** Average per-stage longitudinal ranges and average per-stage latitudinal ranges; **D** Ratio of average longitudinal and latitudinal ranges and continental fragmentation index. Mean in purple and standard deviations confidence limits in red dashed lines. Time scale lags Δt separated by 0.1 units on the \log_{10} scale in Myrs.

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Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Journal Pre-proof

Highlights

- Average longitudinal ranges of brachiopods declined through the Phanerozoic
- Sizes of longitudinal ranges are directly determined by fragmentation of continents
- The formation of the Pangaea supercontinent was a significant factor restricting the brachiopod success

Journal Pre-proof

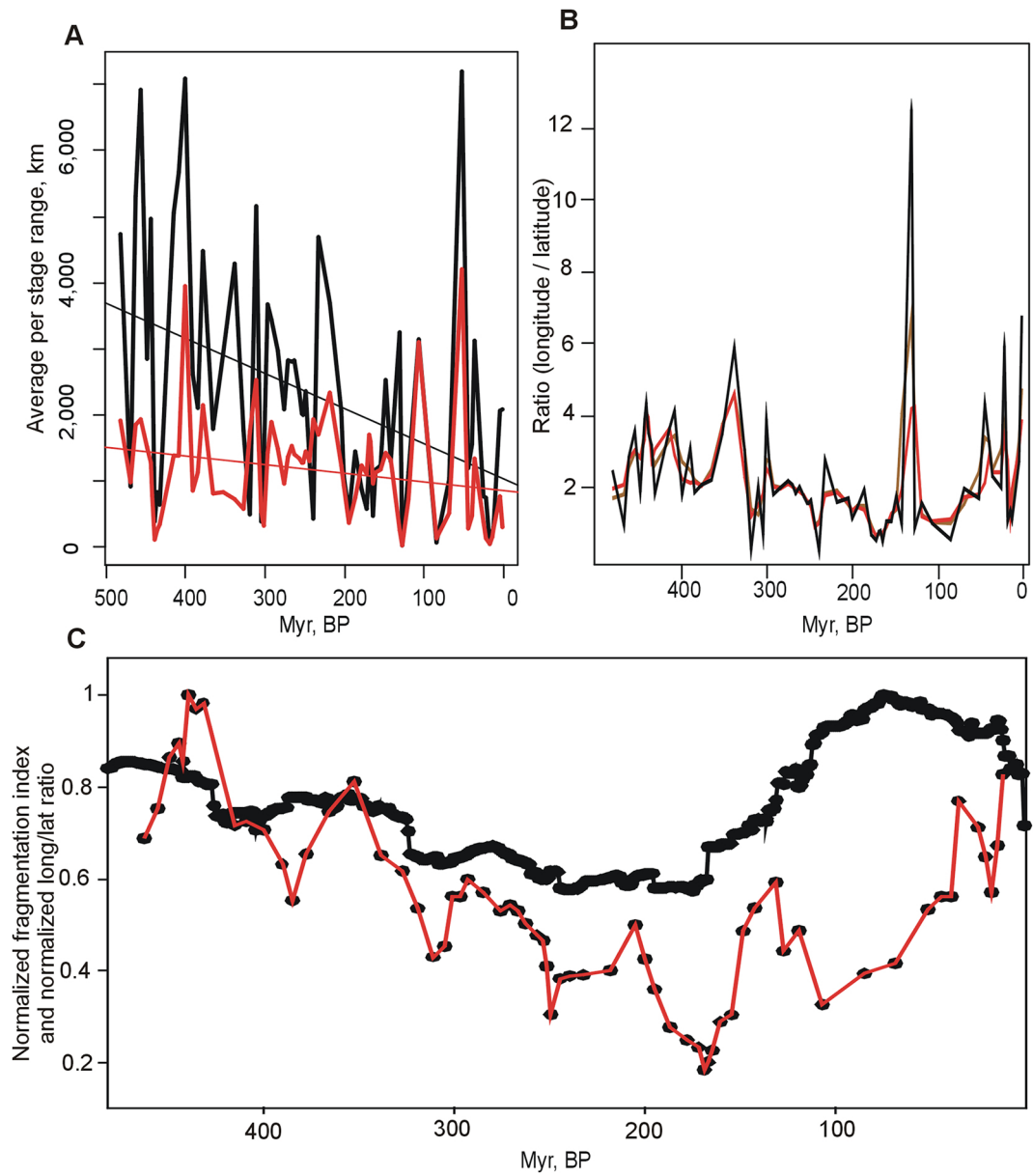


Figure 1

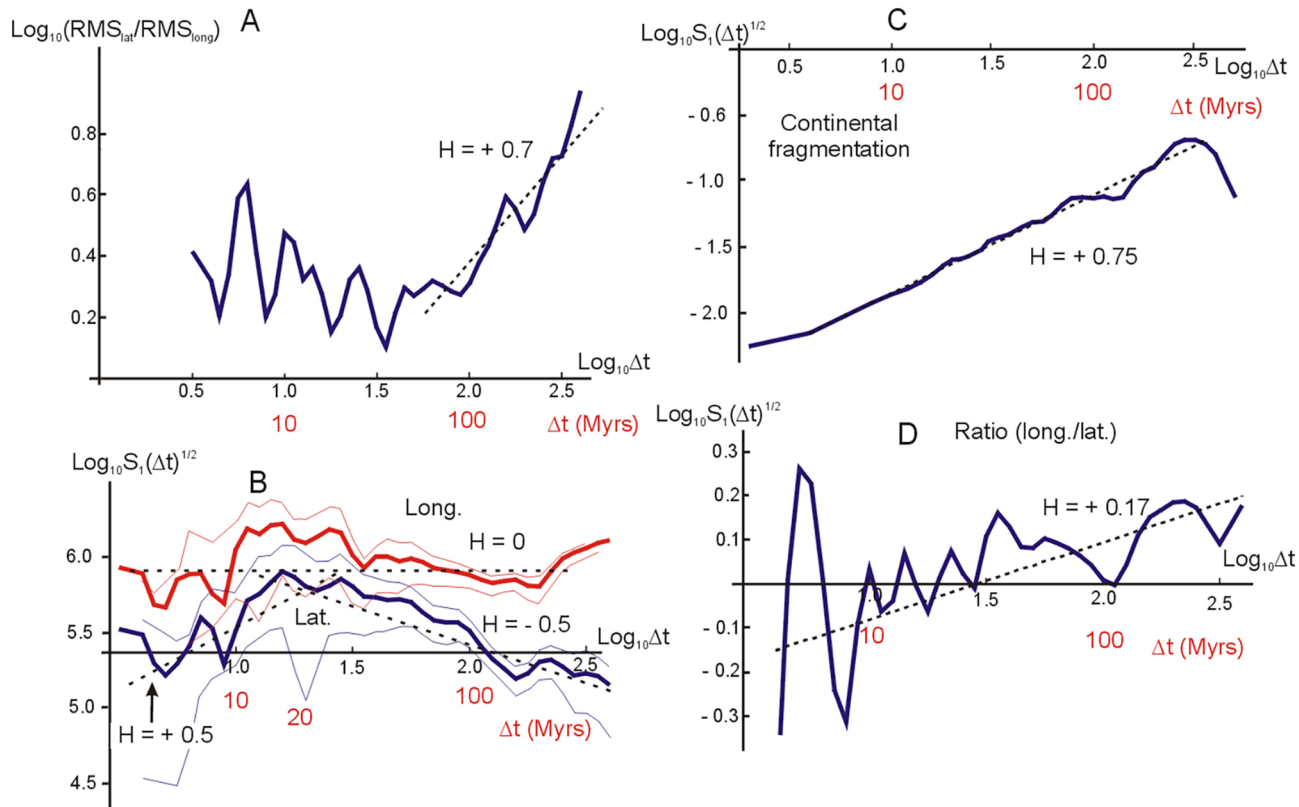
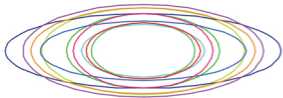
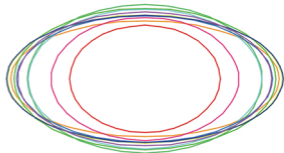


Figure 2

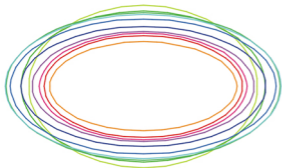
3 - 10 Myrs



12 - 40 Myrs



40 - 125 Myrs



125 - 400 Myrs



Figure 3

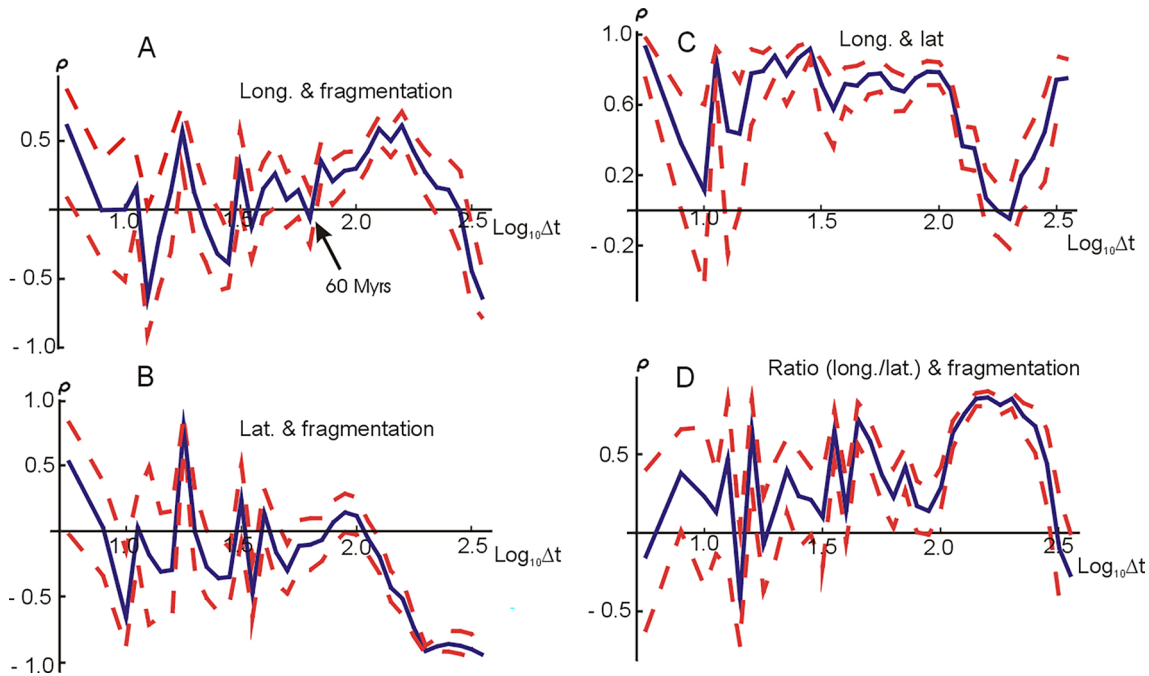


Figure 4