Quantifying the rise of animals during the Ediacaran–Cambrian using ichnodissimilarity

Zekun Wang[1,*], Imran A. Rahman[1,2], Li-Jun Zhang[3]

[1] The Natural History Museum, London SW7 5BD, UK
[2] Oxford University Museum of Natural History, University of Oxford, Oxford OX1 3PW, UK
[3] Institute of Resources and Environment, Collaborative Innovation Center of Coalbed Methane and Shale Gas for Central Plains Economic Region, Henan Polytechnic University, Jiaozuo, China
Corresponding author *: E-mail: zekun.wang@nhm.ac.uk

Non-technical summary: The trace fossil record provides key insights into the evolution of early animals during the Ediacaran-Cambrian transition. By examining the diversity of these fossils, we can understand how early animal behaviors and body plans developed. We introduced a new mathematical method based on vectors to measure differences in trace fossil diversity. Using this method, we analyzed a large dataset of trace fossils and discovered the timings of important evolutionary events. Our findings show that early animals diversified with two stages, and more quickly in shallow marine environments and gradually specialized their ecological roles over time.

Abstract: The trace fossil record provides important insights into the evolution of early animals during the Ediacaran–Cambrian transition, with changes in ichnodiversity through time and between environments informing on the diversification of major body plans, behaviours and niches. To quantify variation in the diversity of trace fossils across this critical interval, we propose a measure of trace fossil dissimilarity (ichnodissimilarity) based on vector calculation. Furthermore, by comparing discrepancies between the angular bisector and mean vector of two sets of vectorized fossil data, we are able to weigh the relative importance of increases and decreases in the variation of occurrences of taxa. We used this metric to analyze an expansive dataset of Ediacaran–Cambrian trace fossils. The results allowed us to quantify the diversification of traces across this transition, informing on the timing of first appearance of different behaviours (e.g. foraging, grazing and resting) and functional groups. By interpreting the results in the context of environmental changes and advancements in motility and sensory capabilities, we were able to pinpoint the onset and sequence of the Fortunian Diversification Event, Cambrian Information Revolution and Agronomic Revolution, shedding light on the evolution of organismal body plans, behaviours and locomotion during the Ediacaran and Cambrian transition. We identified two phases of origination and expansion during the divergence of early animal traces. Furthermore, by analyzing shallow and deep marine trace fossils, we were able to uncover evidence for a more rapid diversification of traces in shallow marine environments, with progressive niche partitioning through the Ediacaran to Cambrian.

Keywords: Cambrian explosion, Ediacaran, Ichnology, Dissimilarity, Ichnodiversity, evolution

Introduction

The Ediacaran (~635–541 million years ago) to Cambrian (~541–485 million years ago) periods document critical steps in the earliest evolution of complex animal life. During this interval, almost all the major groups of modern animals appeared and diversified. This emergent phenomenon (Artime and Domenico 2022) is thought to reflect complex non-linear interactions between new macroscopic multicellular lifeforms and the environment. However, the body fossil record from this timespan (especially the Ediacaran) is patchy and depends on narrow preservational windows

(Mángano and Buatois 2014), which handicaps study of this fundamental evolutionary radiation. Therefore, trace fossils provide an alternative and complementary record of how early animals interacted with their environments. They are thought to document the first appearance of bilaterian animals (Gehling, Runnegar, and Droser 2014; Mángano and Buatois 2016; Chen et al. 2019), with some traces like *Cruziana* appearing earlier than their putative trace-makers (Antcliffe, Callow, and M.D. Brasier 2014). Moreover, *Treptichnus pedum* marks the GSSP for the Ediacaran–Cambrian boundary (Buatois 2018). Consequently, the ichnological record can provide very valuable insights into ancient ecosystems and environments during this critical interval, informing on major changes in biodiversity (Buatois and Mángano 2018), including evolutionary radiations and extinctions (Mángano and Buatois 2016).

Among these evolutionary events, the divergence of metazoans across Ediacaran and Cambrian is uniquely profound. It is believed that one of the important factors associated with the Cambrian explosion and the initial diversification of animal phyla is the fundamental change in the nature of the seafloor from Neoproterozoic-style substrates with microbial mats and limited bioturbation to Phanerozoic-style unconsolidated soft substrates with a well-developed mixed layer (Mángano and Buatois 2014, 2016). This shift in the complexity and heterogeneity of the substrate, termed the Agronomic Revolution (Seilacher and Pflüger 1994), is believed to have had a significant impact on the evolution of motility and feeding behaviours in early animals (i.e., the Cambrian Substrate Revolution), driving them to develop new strategies for moving across and through the seafloor and locating and capturing food, some of which are recorded in the trace fossil record. Consequently, studying Ediacaran and Cambrian trace fossils can help elucidate the pattern and process of this major evolutionary episode. However, to accurately quantify the diversification of

these early traces, an advanced mathematical tool that can effectively and precisely pinpoint changes in the ichnological record is first required.

A typical approach to quantify the diversification of traces produced by different behaviours and tracemakers on various substrates is ichnodiversity. This usually entails simply counting the number of ichnogenera that can be identified at a particular site (Mángano and Buatois 2016). However, this measure of 'alpha diversity' may be inadequate when comparing the differences between two sites over an environmental gradient or through time. As a result, the concept of 'beta diversity' (Whittaker 1960), which measures differences in diversity between sites, has also been used in ichnology (Mángano and Buatois 2016); in broader terms, beta diversity can be seen as a kind of dissimilarity. Although the dissimilarity of trace fossils (ichnodissimilarity) does not necessarily equate to differences in the diversity of the tracemakers, this measure can help us uncover how organism body plans and behaviours changed during major evolutionary radiations and mass extinction events. Ichnodissimilarity is therefore a potentially important tool for studying the early history of life.

Valuable though this metric is, quantitative definitions of dissimilarity are often simple and rough. The measure of beta diversity that is most commonly used in ichnology (Chao et al. 2005) is defined as:

$$\beta = \left(N_1 - S_{12}\right) + \left(N_2 - S_{12}\right), \tag{1}$$

where β is the beta diversity/dissimilarity, equivalent to the "absolute species turnover". N_1 and N_2 are the total numbers of species (or genera) at Site-1 and Site-2, respectively, and S_{12} denotes the number of shared species (genera) between the two sites.

This definition is unnormalized and, to some extent, case dependent. It is therefore difficult to compare different studies/sites. Alternative definitions of beta diversity proposed by Whittaker (Whittaker 1960; Jost 2007) and McArthur et al. (McArthur, Recher, and Cody 1966) that are widely used in ecology do not rely on simply counting numbers of species, but instead depend on alpha and gamma diversity (Ricotta 2017) and are incapable of taking details of each observation into account (e.g., weighting by the number of each observation). These are sometimes termed 'true' beta diversities (Beck et al. 2013). A third kind of measure is the pairwise dissimilarity calculated by comparing relative abundances species-by-species, such as Horn overlap and the Morisita-Horn index (Horn 1966). However, these indexes cannot establish which species diversity is larger between the two observations, nor do they allow us to identify whether dissimilarity is caused by presence or absence of new/more species. Moreover, there is also a computational bias in the dissimilarity calculated by Morisita-Horn index, which will be discussed later.

Orloci, 1967 proposed a vector-based method to calculate the dissimilarity between two communities, where each element in the vector represents a species, and the length of the chord between the two vectors is used to define dissimilarity. The chord distance can be scaled within the range between 0 and 1 for easier interpretation (Conde and Domínguez 2018). Similarly, taking the cosine of the angle between the two vectors is another simple way of defining this measure (Cheeyham and Hazel 1969). However, there is a disadvantage in using this approach when calculating dissimilarity because cosine does not obey the Law of Addition, which means it cannot be directly decomposed into components related to increase or decrease of taxa and their abundance.

112 Herein, we present an alternative measure of dissimilarity based on vector theory using the exact
113 angle between two normalized vectors instead of cosines. By comparing discrepancies between
114 the angular bisector and mean vector, we can weigh the relative importance of increases and
115 decreases in the variation of taxonomical occurrences. We can therefore define a ratio between the
116 split angles that describes the balance of turnovers, informing on the main driver underlying any
117 obtained dissimilarities. We use this metric to quantify the evolution of benthic communities
118 across the Ediacaran–Cambrian interval based on the trace fossil record. Traces representing
119 typical functional groups (e.g., epifaunal bioturbators, surficial modifiers, regenerators, conveyors
120 and biodiffusors) and behaviours (e.g., Agrichnia, Domichina, Pascichnia and Repichnia) are
121 studied, with their variation through time analysed. The distribution and evolution of traces across
122 environmental gradients is also investigated for this critical interval (Bottjer, Hagadorn, and
123 Dornbos 2000).

124 In the text below, we first introduce the definition of our measure of dissimilarity, including
125 both 1/0 based and probabilistic calculations, and propose the Balance Index for Occurrences, and
126 the Balance Index for Origination and Extinction. We then provide a comparison between the
127 dissimilarity index and existing measures and undertake a convergence study. Lastly, we apply the
128 proposed metric to the trace fossil record in order to quantify the variance of behaviours and
129 functional groups in response to environmental change during the Ediacaran and Cambrian periods.

130 ## Methods: Vector calculation and dissimilarity

131 ### *Basic formulation*

132 If we assume there exists an extremely large vector that can house all species, with each species
133 represented by a certain value, then this vector becomes a coordinate that can indicate the diversity

of a community in terms of the whole ecosystem. The direction of the vector is determined by both abundance and combination of the species.

Mathematically, the simplest way to estimate the difference between two vectors is to calculate the angle between them. Based on this, it is possible to define the dissimilarity as follows:

If one denotes the values in the vector as 1 for represented species (species found at the community/site) and 0 for non-represented species in the aforementioned coordinate, then the two coordinates representing each site ($\mathbf{V}_1$ and $\mathbf{V}_2$) can be expressed as:

$$\mathbf{V}_1 = (\underbrace{1,1,1,1,1}_{S_{12}}, \underbrace{1,1,1,1}_{N_1-S_{12}}, \underbrace{0,0,0}_{N_2-S_{12}}), \tag{2}$$

$$\mathbf{V}_2 = (\underbrace{1,1,1,1,1}_{S_{12}}, \underbrace{0,0,0,0}_{N_1-S_{12}}, \underbrace{1,1,1}_{N_2-S_{12}}). \tag{3}$$

The order of the numbers in these coordinates does not influence the value calculated through dot product. It is therefore recommended that each coordinate be divided into three sections for convenience of visualization, as in Equations (2) and (3): shared species, species only present in the first community, and species only present in the second community.

Based on this, it is possible to calculate the angle between the two vectors (θ):

$$\theta = \langle \mathbf{V}_1, \mathbf{V}_2 \rangle = \cos^{-1} \frac{\mathbf{V}_1 \cdot \mathbf{V}_2}{|\mathbf{V}_1||\mathbf{V}_2|} = \cos^{-1} \left(\sum_{n=1}^{N_1+N_2-S_{12}} \frac{V_{1,n} V_{2,n}}{|\mathbf{V}_1||\mathbf{V}_2|} \right) = \cos^{-1} \frac{S_{12}}{\sqrt{N_1 N_2}}, \tag{4}$$

where n is the nth component of the vectors, magnitude of $\mathbf{V}_1$, $|\mathbf{V}_1| = \sqrt{N_1 \cdot 1^2} = \sqrt{N_1}$, and $|\mathbf{V}_2| = \sqrt{N_2}$. Since no components of the coordinate can be negative ($V_{1,n} \geq 0$, $V_{2,n} \geq 0$), naturally, $\frac{S_{12}}{\sqrt{N_1 N_2}} \in [0,1]$, and especially for two identical communities ($S_{12} = N_1 = N_2$), $\frac{S_{12}}{\sqrt{N_1 N_2}} = 1$. This

coefficient within inverse trigonometric function is termed the Otsuka Coefficient (Peters 1968), and when it falls in the interval [0,1], the range of this inverse trigonometric function should be $[0,\pi/2]$, that is, $\theta \in [0,\pi/2]$. To make this concept more readily understandable, the angle is further normalized by $\pi/2$, and we define this parameter as a new dissimilarity *D*:

$$D = \frac{2\theta}{\pi} = \frac{2}{\pi}\cos^{-1}\frac{S_{12}}{\sqrt{N_1 N_2}}. \quad (5)$$

Therefore, for two communities with adequate numbers of represented taxa (e.g., totaling at least at the order of ten), if there are no shared species between the communities, the two vectors are orthometric and $D = 1$. In contrast, if all the species from the two sites are identical, then $S_{12} = N_1 = N_2$ and $D = 0$. In other words, dissimilarity becomes evident as the value of *D* approaches 1, whereas similarity manifests as it approaches 0. However, great care should be exercised if the two vectors are extremely sparse (i.e., if the total number of observations is very small, or many species are underrepresented) as their orthogonality ($D = 1$) might be a false indicator. This holds true for any kind of definition of dissimilarity. Nevertheless, in normal cases with sufficient number of samples *D* can genuinely reflect the variation in species diversity along an environmental or spatial gradient.

A statistical expression with consideration of species abundance

In the above definition, whether a species exists or not is only roughly defined by 1 or 0. For improved accuracy, we can define the values in a coordinate with the statistical parameter p_i, taking into account the abundance of each species. Under different scenarios, this statistical parameter can have different meanings (but comparisons must be made at the same scale). For example, p_i could be:

(1) The number of times n_i (or frequencies $f_i = n_i/N$, where N is the total number of observations) that species *i* is represented in the case. Due to the normalization process involved in our calculation of dissimilarity (i.e., Equations (4) and (5)), the results calculated with n_i and f_i are the same (direction of the coordinate stays unchanged during normalization). In this way, the abundance of the species is considered.

(2) The number of species belonging to genus *i* that exist at a certain site (n_i). Similarly, one could also use its frequency f_i to compute the dissimilarity, where $f_i = n_i/N_i$, with N_i the total number of species that this genus has within a certain large-scale scenario (e.g., a continent or geological time period).

This statistical parameter can also be endued with a probability of existence within a hierarchical relation (i.e., the diversity of existing species within the same genus or the diversity of existing genera within the same family). Based on this, for two different sites, the coordinates can be written as:

$$\mathbf{V}_1 = (\underbrace{p_{1,1}, p_{1,2}, \dots, p_{1,S_{12}-1}, p_{1,S_{12}}}_{S_{12}}, \underbrace{p_{1,S_{12}+1}, \dots, p_{1,N_1}}_{N_1-S_{12}}, \underbrace{0,0,0}_{N_2-S_{12}}), \tag{6}$$

$$\mathbf{V}_2 = (\underbrace{p_{2,1}, p_{2,2}, \dots, p_{2,S_{12}-1}, p_{2,S_{12}}}_{S_{12}}, \underbrace{0,0,0}_{N_1-S_{12}}, \underbrace{p_{2,S_{12}+1}, \dots, p_{2,N_2}}_{N_2-S_{12}}), \tag{7}$$

where $p_{1,i}$ and $p_{2,i}$ are the parameters obtained with data from the first and second sites, respectively, and N_1 and N_2 are the total numbers of observations at each site. Hence, the dissimilarity can be defined as:

$$D = \frac{2\theta}{\pi} = \frac{2}{\pi}\cos^{-1}\frac{\mathbf{V}_1 \cdot \mathbf{V}_2}{|\mathbf{V}_1||\mathbf{V}_2|} = \frac{2}{\pi}\cos^{-1}\frac{\sum_{i=1}^{S_{12}} p_{1,i}p_{2,i}}{\sqrt{\left(\sum_{j=1}^{N_1} p_{1,j}^2\right)\left(\sum_{k=1}^{N_2} p_{2,k}^2\right)}}, \quad (8)$$

where j and k are the jth and kth parameter of Site-1 and Site-2. If there is significant similarity between the two sites, D will be close to 0, and if the difference is strong, then D will approach 1.

Balance Index for Occurrences / Origination–Extinction

An advantage of using angles instead of cosine values to characterize dissimilarity is that they obey the Associative Law of Addition. That is to say, Angle A plus Angle B equals Angle (A+B), whereas cos(A) plus cos(B) does not equal cos(A+B). This means we can split the angle (or a normalized angle) denoting dissimilarity into two parts to quantify the relative contribution of increases and decreases in the abundance of taxa.

Herein, a mean vector ($\mathbf{V}_{\mathrm{m}}$) is employed to split the angle (θ) into two parts:

$$\mathbf{V}_{\mathrm{m}} = \frac{\mathbf{V}_1 + \mathbf{V}_2}{2}. \quad (9)$$

The angle between the mean vector and Vector 1 (V_1) is θ_1 and the angle between the mean vector and Vector 2 (V_2) is θ_2, defined as:

$$\theta_1 = \left\langle \mathbf{V}_1, \frac{\mathbf{V}_1 + \mathbf{V}_2}{2} \right\rangle = \cos^{-1}\left(\frac{|\mathbf{V}_1|}{2|\mathbf{V}_2|} + \frac{\mathbf{V}_1 \cdot \mathbf{V}_2}{2|\mathbf{V}_1||\mathbf{V}_2|}\right), \quad (10)$$

$$\theta_2 = \left\langle \mathbf{V}_2, \frac{\mathbf{V}_1 + \mathbf{V}_2}{2} \right\rangle = \cos^{-1}\left(\frac{|\mathbf{V}_2|}{2|\mathbf{V}_1|} + \frac{\mathbf{V}_1 \cdot \mathbf{V}_2}{2|\mathbf{V}_1||\mathbf{V}_2|}\right), \quad (11)$$

196 and therefore,

$$\theta = \theta_1 + \theta_2 . \quad (12)$$

197 As shown in **Fig. 1A**, only when the increase is identical to the decrease can Triangle *Oca* and
198 Triangle *Ocb* be said to be congruent, with θ_1 equal to θ_2 and the mean vector being the angular
199 bisector of θ (Angle *bOa*). If the increasing rate is much higher (i.e., larger vector magnitude with
200 larger Angle *aOx*), the mean vector becomes closer to Vector 2, with a larger θ_1 (**Fig. 1B**).

201 The Law of Addition holds true if the angles are normalized with $\pi/2$:

$$D_1 = \frac{2\theta_1}{\pi}, \quad D_2 = \frac{2\theta_2}{\pi}, \quad \text{and } D = D_1 + D_2, \quad (13)$$

202 where D_1 and D_2 are partial dissimilarities. Since D_1 increases with the number of occurrences,
203 we can define a Balance Index for Occurrences (γ):

$$\gamma = \frac{D_1}{D} = 1 - \frac{D_2}{D} . \quad (14)$$

204 When the increase in the number of occurrences is equal to the decrease, $D_1 = D_2$ and
205 $\gamma = \frac{D_1}{2D_1} = 0.5$, and the taxonomic flux is balanced. When the rate of increase is higher,
206 $D_1 \in (0.5, 1]$, and when the rate of decrease is higher, $D_1 \in [0, 0.5)$. When using "1/0" based
207 descriptions (i.e. "1" for presence and "0" for absence, as in Equations (2) and (3)), the obtained
208 result will inform on the balance between the origination and extinction components of
209 dissimilarity (the Balance Index for Origination and Extinction), similar to that in(Bush et al. 2019).

However, it should be noted that this Balance Indices only work when $\mathbf{V}_1 \neq \mathbf{V}_2$. If the two vectors are equal, they are overlapped, we therefore by default consider $\gamma = 0.5$.

Simple demonstration and convergence study

In this section, we present a simple case study illustrating the difference between the absolute species turnover in Equation (1) and the metric proposed herein. Table 1 shows observations from four different sites:

If one calculates beta diversities for Site-1 versus Site-2 and Site-3 versus Site-4 using Equation (1), the same value of 3 is obtained. However, the community from Site-1 only shows small differences from that at Site-2, while the community from Site-3 is very different to the one at Site-4, with only one shared species.

In contrast, using the measure proposed herein, we can compute the dissimilarity (beta diversity here as well) between Site-2 versus Site-1 as: $\beta_{2-1} = \frac{2}{\pi}\cos^{-1}\frac{11\cdot 1+3\cdot 0}{\sqrt{12\cdot 13}} = 0.314$, and that between Site-4 and Site-3 as $\beta_{4-3} = \frac{2}{\pi}\cos^{-1}\frac{1\cdot 1+13\cdot 0}{\sqrt{2\cdot 3}} = 0.732$, indicating that the communities from Site-2 and Site-1 are similar, while those communities from Site-4 and Site-3 are dissimilar. This provides a better explanation of the data presented in Table 1.

Our measure of dissimilarity shows little bias compared to Morisita-Horn (M-H) dissimilarity (Horn 1966): $D_{\mathrm{mh}} = 1 - \frac{2\sum V_{1,i}V_{2,i}}{\left(\frac{\sum V_{1,i}^2}{N_1^2} + \frac{\sum V_{2,i}^2}{N_2^2}\right)N_1 N_2}$. For example, the following benchmark case has 10000 random integers ranging from 1 to 20, and we have 21 testing cases (for comparison) where the *M*th case has *M* integers ranging from 1 to *M* ($M \leq 20$, 0th case has all-zero components, and

20th case shall be equivalent to the benchmark, with its integers ranging from 1 to 20). As such, the proposed dissimilarity of the benchmark case versus the 10th cases (as shown in Table 2, which share 10 elements with the benchmark case) should analytically be $D=\frac{2}{\pi}\cos^{-1}\frac{500\cdot1000\cdot10+500\cdot0\cdot10}{500\sqrt{20}\cdot1000\sqrt{10}}=0.5$, which is exactly "half the same", as it should be. On the other hand, the Morisita-Horn dissimilarity should analytically be $D_{\mathrm{mh}}=1-\frac{2\cdot(500\cdot1000\cdot10)}{\left(\frac{20\cdot500^2}{10000^2}+\frac{10\cdot1000^2}{10000^2}\right)10000^2}=\frac{1}{3}$, which demonstrates severe computational bias. This computational bias is shown in **Fig. 2**, where the proposed measure of dissimilarity is an antisymmetrical odd function about (10,0.5) with better linearity between the metrics and number of non-shared observations, whereas the M-H dissimilarity is a convex function that exhibits no symmetry over "half-similarity". In other words, one shared sample among 20 (~0.856) is complementary to 19 shared samples among 20 (~0.144), and these two values add up to 1 in the proposed metrics.

In addition to computationally bias-free accuracy, convergence and robustness are also important features for evaluating our newly proposed measure of dissimilarity. To assess this, we created two datasets containing 2000 integral numbers. The first dataset has 10 different numbers (1 to 10), while the second dataset has 20 different numbers (1 to 20). These numbers are evenly and randomly distributed in the datasets. Dissimilarities between the two datasets were then calculated with certain numbers of observations extracted from the datasets (from 50 to 2000, at intervals of 50). Seven data series were generated in this way. The estimated beta diversities versus the number of observations used in the calculations are shown in **Fig. 3**.

As shown in **Fig. 3**, as the number of observations increases, the obtained dissimilarity between the two datasets converges on the analytical result of 0.5. The mean absolute error is 5% for 100 observations, which is 5 times the number of features (20). The mean absolute error decreases to 2.5% at around 260 observations, which is 13 times the number of features. This indicates that the proposed measure of dissimilarity will perform well (2.5% error) as long as the total number of the observations in the dataset exceeds around 13 times the number of data features (e.g., taxa).

From the above analyses, it is evident that our proposed measure of vector-based dissimilarity functions well at different observation sizes and abundances and can accurately determine the dissimilarity between two datasets. It is not biased by the number of overlapping features and readily converges on the analytical result.

To evaluate the Balance Index for Occurrences, we set up a test case with the following vectors. Partial dissimilarities and Balance Indices were computed with comparisons between $\mathbf{V}_2 \sim \mathbf{V}_7$ and $\mathbf{V}_1$:

$$
\begin{aligned}
&\mathbf{V}_1 = [1,1,1,1,1,0,0,0,0,0], \\
&\mathbf{V}_2 = [1,1,1,1,0,1,0,0,0,0], \quad D_{1\_2-1} = D_{2\_2-1} = 0.2048, \quad \gamma_{2-1} = 0.5; \\
&\mathbf{V}_3 = [1,1,1,0,0,1,1,0,0,0], \quad D_{1\_3-1} = D_{2\_3-1} = 0.2952, \quad \gamma_{3-1} = 0.5; \\
&\mathbf{V}_4 = [1,1,1,1,0,1,1,1,0,0], \quad D_{1\_4-1} = 0.2871, \quad D_{2\_4-1} = 0.2402, \quad \gamma_{4-1} = 0.5445; \\
&\mathbf{V}_5 = [1,1,0,0,0,1,0,0,0,0], \quad D_{1\_5-1} = 0.2871, \quad D_{2\_5-1} = 0.3729, \quad \gamma_{5-1} = 0.4304; \\
&\mathbf{V}_6 = [1,1,1,1,2,0,0,0,0,0], \quad D_{1\_6-1} = 0.1145, \quad D_{2\_6-1} = 0.0903, \quad \gamma_{6-1} = 0.559; \\
&\mathbf{V}_7 = [1,1,1,1,0,30,0,0,0,0], \quad D_{1\_7-1} = 0.8434, \quad D_{2\_7-1} = 0.1187, \quad \gamma_{7-1} = 0.877.
\end{aligned}
\tag{15}
$$

This shows that, if the increase of taxa is equal to the decrease compared to $\mathbf{V}_1$ (i.e., $\mathbf{V}_2$ and $\mathbf{V}_3$), the Balance Index is 0.5, and the magnitudes of partial dissimilarities increase with the magnitude of taxonomic flux. However, if the magnitude of increase is higher than that of the

decreases ones (i.e., $\mathbf{V}_4$, one extinction, three originations), the balance is broken and the index exceeds 0.5, and vice versa for $\mathbf{V}_5$. An increase in species abundance (i.e., $\mathbf{V}_6$ and $\mathbf{V}_7$) also leads to an increase in the Balance Index.

Materials

Under present ichnological practice, diagnostics of trace fossils experiences unavoidable uncertainties from behavioural diversity, taphonomic effects and observer biases, leading to synonyms and problematica taxa. Therefore, the authors employed a well-tuned but conservative dataset containing widely-accepted trace fossils taxa from the Ediacaran and Cambrian periods mainly from (Mángano and Buatois 2016), with putative body fossils like *Nenoxites* (*Shaanxilithes*) (Zhu et al. 2017; Mángano and Buatois 2020; Luo and Miao 2020) removed, and supplemented with new data from other relevant studies. This included *Cochlichnus* (Webby 1970; Darroch, Cribb, Buatois, and al. 2021) from shallow marine (i.e.**,** wave-influenced region in this paper**)** deposits of the latest Ediacaran Torrowangee Group of western New South Wales and the Nama Group of southern Namibia, as well as *Diplichnites* from the Shibantan Member of the upper Dengying Formation in the Yangtse Gorges area in South China (Chen et al. 2018), which may represent the earliest trackways made by bilaterian animals with paired appendages. Additionally, *Radulichnus* (Seilacher and Hagadorn 2010) and *Lockeia* (Crimes and Fedonkin 1994; Pandey et al. 2014; Kaur et al. 2021) from Ediacaran and Cambrian shallow marine deposits, *Bergaueria* (Alpert 1973) and *Torrowangea* (Zhuravlev and Riding 2000) from Ediacaran and Cambrian shallow and deep marine deposits, *Thalassinoides* (Zhang et al. 2017), *Gordia* (Buatois et al. 2014), *Parapsammichnites* and *Streptichnus* from Ediacaran shallow seas (Buatois et al. 2018; Darroch, Cribb, Buatois, Germs, et al. 2021), *Archaeonassa* (Hofmann et al. 2012), *Didymaulichnus* (Jensen

and Mens 2001) and *Trypanites* (James, Kobluk, and Pemberton 1977) from Cambrian shallow marine deposits, *Saerichnites* from Cambrian deep marine deposits (Buatois and Mángano 2004), and *Protopaleodictyon* (Zhuravlev and Riding 2000) from Cambrian shallow and deep marine deposits were added to the dataset. *Treptichnids* from Nama group is tentatively combined into *Treptichnus* due to possible variations from behaviours or taphonomy. The occurrences are recorded at the 'Member' scale, unless the formation has not been subdivided into members. The full dataset is shown in Table 3.

There may be uncertainties related to the age, behavioural categorization and taxonomic identifications of some of the trace fossils in our dataset, as well as possible sampling biases to contend with. However, bounded by the Central Limit Theorem (Kwak and Kim 2017), the distribution of these data approximates a Gaussian distribution around the "true value". Consequently, background noise will be minimized so long as the number of observations is sufficiently large and the computational algorithm is converged, as demonstrated in the previous section.

Results and Discussion

Ediacaran–Cambrian trace fossil dissimilarity, origination and extinction

The Ediacaran preserves the oldest evidence of large and morphologically complex multicellular organisms, including some of Earth's earliest animals, which documents the first appearance of convincing bilaterian traces (Gehling, Runnegar, and Droser 2014; Mángano and Buatois 2016; Chen et al. 2019; Evans et al. 2022). As the sensory and locomotory capabilities of early metazoans evolved, they started to have a bigger impact on their environment by disturbing the substrate and creating vertical burrows (Cribb et al. 2019), enhancing the exchange of nutrients between pelagic

and benthic realms (Erwin and Tweedt 2012; Buatois et al. 2018). When the substrate became increasingly bioturbated and heterogeneous during the early part of the Cambrian (i.e., the Agronomic Revolution), it posed challenges to organisms grazing on microbial mats (which had served to stabilize substrates during much of the Proterozoic), which are thought to have driven changes in animal morphology, function and behaviour. This evolutionary divergence in response to changes in the nature of the substrate is referred to as the Cambrian Substrate Revolution (Bottjer, Hagadorn, and Dornbos 2000). To help decipher the evolution of early metazoans during this interval, we analyzed the dissimilarity and Balance Index of trace fossils from the Ediacaran–Cambrian.

Using the data in Table 3, we obtained six vectors for the corresponding six time periods. For example, after removing columns with all-zero elements, the vectors for the White Sea and Nama group are (3,1,0,0,0,2,3,9,6,1,0,0,8,3,0,1,0) and (1,1,2,1,2,0,5,14,4,0,1,1,10,0,1,7,4), respectively. We used these to calculate dissimilarity and the Balance Index for Ocurrences for each pair of time bins and plotted these against time, with the results shown in **Fig. 4**. Based on this, we found that dissimilarity (**Fig. 4 A**) and both Balance Indices (**Fig. 4 B, C**) peaked across the interval between the Ediacaran Nama Group and the Cambrian Fortunian Stage, associated with a dramatic increase in global diversity and abundance of trace fossils (Mángano and Buatois 2016). These include simple horizontal traces like *Gordia*, *Helminthopsis* and *Helminthoidichnites*, thought to be made by vermiform primary consumers (mat grazers) that lived on Ediacaran-style microbial substrates. Such traces tend to have limited curvature with simple geometries, and no specific ethological taxis can be identified from them. These simple traces persisted into the Cambrian (Buatois et al. 2014). However, by the Fortunian, more morphologically complex traces like *Cruziana* and *Rusophycus*, which are thought to have been produced by arthropods, pentaradially symmetrical

Asteriacites (a putative asterozoan resting trace (Knaust and Neumann 2016)), *Teichichnus* (a passively filled sub-vertical spreite burrow thought to be created by arthropods or annelid worms (Knaust 2018)) and *Dactyloidites* (thought to be made by polychaetes or worms with a suspension-feeding life mode (Curran and Glumac 2022)) started to appear. Evidence of sharp turnings, self-crossing or avoidance of self-crossing, displacement of sediment and taxis can be observed in several of these traces. This increase in the abundance and complexity of traces across the Ediacaran–Cambrian boundary also informs on the evolution of the trace makers, implying the emergence of ecosystem engineers, secondary consumers, detritivores and scavengers with morphologically varied body plans and feeding strategies. Based on study of the trace fossil record, major new animal body plans and feeding modes seem to have appeared across the boundary between the Ediacaran and Cambrian periods, and this event has been termed the Fortunian Diversification Event (FDE) (Mángano and Buatois 2016). This is thought to be an expression of the Cambrian Information Revolution (CIR) (Plotnick, Dornbos, and Chen 2010; Hsieh, Plotnick, and Bush 2022), which was characterized by the development of more advanced sensory, cognitive and locomotory capabilities. As ecological niches were progressively filled during this evolutionary radiation, the diversification of traces slowed, with the magnitude of dissimilarity steadily decreasing through the Cambrian (**Fig. 4A**). Ichnodissimiliarity dropped to a low point of 0.161 across the boundary between the third and fourth stages of the Cambrian, indicating an evident similarity in ichnotaxa from these two stages.

The general profile of ichnodissimilarity over the Ediacaran–Cambrian (**Fig. 4A**) closely matches estimates of diversification rates for marine animals based on sampling-standardized analyses (Na and Kiessling 2015), which show a peak in the Fortunian, followed by a decline through the Cambrian. However, comparing ichnodissimilarity to the global and beta diversities

of marine animals, which peaked at around the Cambrian Stage 3 (Sepkoski 1998; Na and Kiessling 2015; Fan et al. 2020), reveals a stronger asynchrony between the trace and body fossil records. This asynchrony suggests that the overall dissimilarity of trace fossils more closely corresponds to the diversification of major animal body plans and behaviours at higher taxonomic levels (Zhang and Shu 2021) than it does to genus or species level diversity.

Unlike ichnodissimilarity, the Balance Index for Occurrences shows a second peak at the start of the Cambrian Stage 3 (**Fig. 4 B**). The Balance Index for Origination and Extinction is only slightly above 0.5, demonstrating that this peak indicates an increase in the abundance of existing ichnotaxa, rather than the origination of new trace fossils. This could be associated with the diversification and expansion of existing animals in a stable ecological system, as well as the divergence of crown group animals with similar body plans and ethological tendencies (Na and Kiessling 2015), consistent with suggestions of a two-phase model for the evolution of stem group and expansion and divergence of crown group animals during the Cambrian (Zhuravlev and Wood 2018; Zhang and Shu 2021).

Across the boundary between the Cambrian Stages 3 and 4, the decrease in the occurrences of trace fossils exceeded the increased ones for the first time, resulting in the Balance Indices less than 0.5 (**Fig. 4 B**). A decline in marine bioturbation at this time was also noted by (Buatois and Mángano 2016). This could reflect a reduction in the abundance and diversity of marine animals during this interval, corresponding to regional disappearance/extinction of some groups (Na and Kiessling 2015). This may be related to the Sinsk Event, an episode of widespread shallow marine anoxia (Zhuravlev and Wood 2018; Na and Kiessling 2015).

Behavioural activities

Our analyses of ichnodissimilarity also shed light on the evolution of animal behaviours during the Ediacaran–Cambrian. For those traces fossils that have been interpreted as the result of two different behaviours, such as the funnel-shaped vertical concentric burrow *Rosselia*, which could be the product of both dwelling and feeding behaviours, the number of occurrences in each time interval was halved in the corresponding ichnological matrix; for example, the occurrence of *Rosselia* as a Domichnia or Repichnia during the Ediacaran and Cambrian periods is denoted as (0, 0, 0, 1, 3.5, 2.5). In this way, the matrix for each behavioural (ethological) category was estimated. For example, Cubichnia gives the following matrix:

$$\begin{array}{c} \\ \textit{Asteriacites} \\ \textit{Cheiichnus} \\ \textit{Conichnus} \\ \textit{Elingua} \\ \textit{Epibaion} \\ \textit{Lockeia} \\ \textit{Parapsammichnites} \\ \textit{Rusophycus} \end{array} \begin{array}{c} \begin{array}{cccccc} W & N & F & S2 & S3 & S4 \end{array} \\ \begin{bmatrix} 0 & 0 & 1 & 1 & 0 & 1 \\ 0 & 0 & 0 & 1 & 4 & 1 \\ 0 & 0.5 & 0.5 & 0.5 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 1 \\ 2 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 1 & 1 & 2 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 10 & 19 & 31 & 23 \end{bmatrix} \end{array}, \quad (16)$$

where the eight rows correspond to ichnogenera representing different resting behaviours and the six columns denote the six time periods. *Parapsammichnites* is interpreted as a resting/struggling trace of segmented worms in response to environmental stress for its abundant but short and frequent loops on the same surface. The dissimilarity between two intervals was calculated using the corresponding columns of vectors.

We selected four ethological categories (Agrichnia, Domichnia, Pascichnia and Repichnia) and reconstructed matrices for each of these based on the data in **Table 3**. The ichnodissimilarity and Balance Indices calculated for each behaviour across this interval are shown in **Fig. 5**.

The global ichnodiversity and frequencies of occurrence of grazing traces (Pascichnia) increased during the Fortunian Stage (**Table 3**), resulting in a peak in dissimilarity of 0.615 at the Ediacaran–Cambrian boundary (**Fig. 5A**). This evident change was a result of origination, as evidenced by the peak of the Balance Index for Origination and Extinction (**Fig. 5C)**. Grazing traces increased in size during the Cambrian, and began to exhibit more complex behaviours (Mitchell et al. 2022) like space-filling patterns reflecting phobotaxis (i.e. avoiding crossovers of previous trails), thigmotaxis (i.e. staying close to the original trails) and strophotaxis (i.e. periodic 180-degree turns), as evidenced by trace fossils such as *Psammichnites* and *Oldhamia* (Seilacher, Buatois, and Mángano 2005; Mángano and Buatois 2016; Gougeon, Néraudeau, et al. 2018) (**Fig. 6A, B)**. This indicates that Cambrian grazers, e.g., molluscs (Wang and Rahman 2023), were better at exploring the substrate than Ediacaran forms, and strongly implies changes to their cognitive, sensory, and navigational capabilities (Hsieh, Plotnick, and Bush 2022). This evolutionary event is referred to as the Cambrian Information Revolution (Plotnick, Dornbos, and Chen 2010). With the enhanced capacities for motility that animals evolved following the Fortunian, the microbial matground became more and more patchy and, as a result, the diversification rate of grazing behaviours slowed down after the Fortunian. In contrast, the Balance Index for Occurrences at this interval is very close to 0.5 (**Fig. 5B**), meaning the occurrence of new grazing behaviours and body plans was balanced by a reduction in abundance of existing ones, possibly due to the crowded niche at water-substrate interface.

For dwelling traces (Domichnia), peak dissimilarity (0.487) was reached at the boundary between the Fortunian and the Cambrian Stage 2 (**Fig. 5A**), associated with increases in their frequency of occurrences (**Fig. 5B**), as well as behavioural/bauplan innovations (**Fig. 5C**), rooted from Fortunian and prospered during Cambrian Stage 2. This process was characterised by the appearance and abundance of vertical burrows like *Skolithos*, *Arenicolites*, *Gyrolithes* and *Rosselia*, as well as U-shaped burrows with spreites, like *Diplocraterion* (**Fig. 6C–E**). Oblique to sub-vertical burrows with actively filled spreites (Knaust 2013), like *Teichichnus* and *Rhizocorallium*, were also abundant during this interval. These vertical or sub-vertical burrows may indicate the evolution of new and more active feeding strategies (Zamora et al. 2017), biomineralized hard parts (Roy and Purohit 2018) (to remove or displace sediment), and/or possible predation pressure (Wilson, Rayburn, and Edwards 2012). The diversification of these dwelling traces, thought to be created by crustaceans and other suspension-feeding animals (Buatois et al. 2020), coincided with a shift in organism–substrate interactions (i.e., the displacement of sediment particles) from a diffusion-dominated stage to an advection-dominated stage (Tarhan 2018), which enhanced the exchange of nutrients particles between the water column, benthic and infaunal communities. After the Fortunian, the origination rate of new Domichnia dropped, evidenced by reductions in the Balance Index for Origination and Extinction (**Fig. 5C**), perhaps reflecting the occupation of the associated living strategies and niches. Nevertheless, an increase in the frequency of occurrences (**Fig. 5B**) can be seen at the boundary between Cambrian Stages 2 and 3, potentially suggesting the presence of increasingly habitable environments, especially in high-energy shallow waters.

Locomotory traces (Repichnia) show similar tends to domichnia, with a major peak in dissimilarity at the boundary between the Fortunian and the Cambrian Stage 2 (**Fig. 5A**). This reflects the appearance of complex new body plans and behaviours, such as *Cruziana*, *Diplichnites*

435 (**Fig. 6F**) and *Curvolithus* during the Fortunian Diversification, evidenced by a peak in the Balance
436 Index for Origination and Extinction at the Ediacaran–Cambrian boundary (**Fig. 5C**). This
437 evolutionary radiation continued into the Cambrian Stage 2, albeit at a relatively slower rate
438 (shown by the lower magnitudes in both the Balance Indices), at which time existing locomotory
439 traces like *Diplichnites* became more abundant, and new complex trackways like *Petalichnus*,
440 *Protovirgularia* and *Tasmanadia* first appeared (Mángano and Buatois 2016). These trackways
441 from Fortunian and Cambrian Stage 2 provide evidence for more enhanced mobility (e.g., stronger
442 muscles attached to exoskeletons with joints) and maneuverability of primary and secondary
443 consumers, producing stronger and deeper impressions in the substrate and more laterally
444 extensive sediment displacement than grazing traces. Together with the aforementioned increase
445 in vertical dwelling burrows, this contributed to the transformation of the substrate from a
446 primarily two-dimensional matground to a three-dimensional mixground inhabited by diverse
447 benthic animals during the Cambrian Stage 2. Due to the heterogenous nature of this mixground,
448 feeding strategies shifted from slowly grazing the surface of the matground (i.e., Pascichnia) to
449 searching for food across long distances (i.e., Repichnia). This transition marks the onset of the
450 Agronomic Revolution (AR) (Ichaso et al. 2022), with Repichnia increasing in abundance during
451 Cambrian Stage 3 (as illustrated by the high Balance Index for Occurrences, alongside low Balance
452 Index for Origination & Extinction, **Fig. 5B-C**).

453 With the development of enhanced sensory, mobility and maneuverability capabilities, benthic
454 animals started to explore new feeding strategies, like farming of bacteria within a designed
455 substrate topology, or new parenting strategies. This is termed Agrichnia, and typical ichnotaxa
456 include *Saerichnites* and *Paleodictyon* (**Fig. 6G**) and *Protopaleodictyon* (Morgan, Henderson, and
457 Pratt 2019). Though some of these behaviours can be traced to earlier stages in the Cambrian, the

biggest increase in the abundance of such trace fossils occurred during the Cambrian Stage 3, giving the greatest dissimilarity and Balance Index for Occurrences (**Fig. 5A-B**) at the boundary between the Cambrian Stages 2 and 3. The taxonomical turnovers during this period was, however, basically balanced (**Fig. 5C**).

After the Cambrian Stage 3, the dissimilarity of grazing, dwelling, locomotion and farming traces all decreased (**Fig. 5A**), with all Balance Index for Occurrences lower than 0.5 (**Fig. 5B**), and domichnia and pascichnia even experienced a higher extinction rate (**Fig. 5C**). This indicates the decrease in frequency of occurrences and even loss of taxa during this Cambrian Stage 4. This could be interpreted as an outcome of animals reaching an over-crowded niche conditions, but might also be related to the decrease in global genus-level diversity of marine animals at this time due to anoxia events (Na and Kiessling 2015).

The Balance Indices for Occurrences for Domichnia and Repichinia, and the Balance Indices for Origination and Extinction for Pascichnia and Repichinia all show two distinct peaks (**Fig. 5B, C**), which parallel the patterns in the overall Balance Indices of Ediacaran–Cambrian trace fossils (**Fig. 4B**). This informs on the two-phase evolutionary pattern during this critical interval: a major evolutionary radiation occurred during the Fortunian Diversification Event, with the appearance of novel body plans and behaviours, as well as high frequency of occurrences among different localities. There is also a smaller second peak in the Balance Indices at the boundary between Cambrian Stages 2 and 3 (**Fig. 4 B**), which was the result of an increase in occurrences, rather than origination (albeit origination was still higher than extinction). But Agrichnia hadn't come onto the stage by the first round of overall divergence of behavirous.

Functional groups

Facilitated by the evolution of more sophisticated sensory, cognitive and locomotory capabilities during the Ediacaran–Cambrian, early animals began to explore deeper tiers within the substrate. Based on their impacts on sedimentary ecosystems, these organisms can be classified into six categories (Francois et al. 2002; Solan and Wigham 2005). (1) Epifaunal bioturbators living on substrates without penetrating the sediment–water interface (e.g., arthropods and gastropods), which can produce surficial traces like *Rusophycus*, *Cruziana* and *Curvolithus*; (2) Surficial modifiers living within the uppermost layers of the sediments (e.g., some meiofauna), which tend to create shallow horizontal burrows like *Gordia*. (3) Biodiffusive bioturbators disturbing deeper mixed layers (e.g., bivalves), which leave deep horizontal or plug-shaped burrows, such as *Psammichnites*. (4) Regenerators creating semi-permanent vertical/oblique burrows that serve to extend the water column downwards, e.g., crustaceans and *Skolithos*. (5) Conveyors transporting sediment particles between the surface and the bottom of a vertical or oblique burrow (e.g., polychaetes), which produce traces that tend to have backfills and spreites, like *Rhizocorallium* and *Diplocraterion*. (6) Gallery biodiffusors creating inter-connected burrow systems with one or more openings to the surface (e.g., polychaetes), like *Trichophycus and Palaeodictyon*.

Using the data in Table 3, we calculated dissimilarities and Balance Indices for these different functional groups. The number of occurrences of traces with two different interpretations (e.g., *Gordia* produced by meiofauna (e.g., foraminifera) as a surficial modifier or produced by small arthropods as epifaunal bioturbators) were halved for each functional group, similar to Equation (16). The results are shown in **Fig. 7**.

501 The dissimilarities of epifaunal bioturbators (E) and surficial modifiers (SM) show very similar
502 profiles, with dissimilarity reaching a peak at the boundary between the Ediacaran and the
503 Cambrian, before decreasing steadily through the Cambrian (**Fig. 7A**). This indicates these two
504 functional groups were the dominant bioengineers during the Ediacaran and earliest Cambrian, at
505 which time early mobile animals were largely restricted to the surface of the substrate and the
506 upmost layers of sediment. To be precise, the dissimilarities of traces left by epifaunal bioturbators
507 over different intervals are all larger than those of surficial modifying traces which penetrates
508 shallowly into the substrates. This means there are even more animals living upon the substrate
509 surfaces compared to those in shallow sedimentary layers. Interestingly, the profile of epifaunal
510 bioengineer's evolutionary dissimilarities also shows common features with that of Pascichnia in
511 **Fig. 5**, indicating that the main approach through which these epifaunal benthos transformed the
512 substrate during the Ediacaran was grazing, and these bioengineers were important components of
513 the Fortunian Diversification Event, as shown by the evident origination components shown in
514 **Fig. 7C**. Following the Fortunian, as the matground became more disturbed (Mángano and Buatois
515 2020), the diversification rate of grazing epifaunal animals (and their traces) decreased.

516 The traces left by regenerators (R) and conveyors (C), which produced vertical, subvertical or
517 oblique burrows, reached peaks in dissimilarity at the boundary between the Fortunian and the
518 Cambrian Stage 2 (**Fig. 7A**), corresponding to the profile of Domichnia (**Fig. 5**), which are also
519 dominated by vertical burrows. This again highlights that although the exploration of deeper tiers
520 by animals started in the Fortunian, this became more prominent (as evidenced by the high Balance
521 Index for Origination and Extinction between the Fortunian and the Cambrian Stage 2, see **Fig.**
522 **7C**) during the second stage of the Cambrian (Buatois et al. 2020), perhaps due to the greater
523 maneuverability, presence of a mineralized exoskeleton and/or predation pressure in these early

524 animals. These Regenerators and conveyors extended the lower boundary of the water column to
525 the burrow bottom, thereby enhancing nutrient exchange between the water column and the
526 substrate. As a result, they can be seen as pioneering ecosystem engineers that transformed the
527 substrate from a 2D stabilized matground into a 3D heterogenous mixground, ushering in the so-
528 called Agronomic Revolution (Buatois et al. 2014).

529 Biodiffusive bioturbators (B) and gallery biodiffusors (G) diversified slightly later in the
530 Cambrian, and peaked in ichnodissimilarity at the interface between Cambrian Stage 2 and 3 (**Fig.**
531 **7A**), showing certain similarities to Agrichnia (**Fig. 5**). This change in the dissimilarity of traces
532 produced by gallery biodiffusors is a result of the appearance of new ichnotaxa (bauplans or
533 behaviours), evidenced by the high origination of gallery biodiffusors after Cambrian Stage 3 (**Fig.**
534 **7C**), while the peak of traces left by biodiffusive bioturbators was the result of both origination in
535 Cambrian Stage 2 and increased occurrences of existing taxa (mainly those that originated in the
536 Stage 2, as shown in **Fig. 7**B, **C**). In many cases, these trace makers would have had to
537 simultaneously move their body forwards while also removing sediments, and hence would likely
538 have required more advanced mobility, maneuverability, sensibility and even cognition (especially
539 for burrow systems). These biodiffusors would have further enhanced the mixing rate and nutrient
540 exchange within the substrate by creating complex burrow systems. The existence of a better
541 developed sedimentary mixed layer would have reduced the chances of preserving surficial and
542 semi-infaunal trace fossils (Tarhan, 2018). This is also one possible explanation for the persistent
543 decrease in the dissimilarity of the traces left by epifaunal bioturbators and surficial modifiers after
544 the Fortunian (**Fig. 7A**), when regenerators, conveyors, biodiffusive bioturbators and gallery
545 biodiffusors started to flourish.

546 The patterns of dissimilarity in functional groups across the Ediacaran and the Cambrian (**Fig.**
547 **7A**) indicate a progressive and expansive exploration of substrates or niches through this interval,
548 from surface, shallow surface, vertical burrows to burrow systems, with stronger and stronger
549 ability to maneuver sediments. However, Balance Indices (**Fig. 7B-C**) generally show that all the
550 functional groups underwent a similar two-phase diversification of origination and expansion,
551 which is consistent with the full ichnological dataset (**Fig. 4 B**). The first peak occurred at the
552 Ediacaran–Cambrian boundary, when earliest complex animals underwent phylum-level
553 diversification. The number of occurrences for some functional groups (e.g., conveyors) were not
554 particularly high at this time, despite the evidence for considerable innovation. The second peak
555 occurred at the boundary between the Cambrian Stages 2 and 3, corresponding to global genus-
556 level diversification (Na and Kiessling 2015) with similar body plans and behaviours causing an
557 increased abundance within the same ichnogenus. By the Cambrian Stage 4, animals from different
558 functional groups were all experiencing more loss of occurrences or even taxa, which may have
559 been the result of local extinctions of stem group taxa (Zhuravlev and Wood 2018) and limited
560 possibilities for innovations.

561 *Shallow and deep marine environments*

562 In addition to the aforementioned analyses of the diversification of traces, behaviours and
563 functional groups, the proposed measure of ichnodissimilarity can also be used to compare traces
564 from different environments. As illustrated in **Fig. 8**, dissimilarity, the Balance Index for
565 Occurrences and the Balance Index for Origination and Extinction can be used to determine
566 differences between successive stages across Ediacaran and Cambrian deep/shallow seas, as well
567 as the beta diversity between deep and shallow seas during the same stage.

Fig. 8 shows that all the dissimilarities and more than half Balance Indices of traces across Ediacaran and Cambrian shallow-sea facies (top rippled) were higher than those of deep-sea facies (bottom dotty). This suggests that more substantial evolutionary changes in mobile animals occurred in shallow marine settings during this interval (Gougeon, Mángano, et al. 2018), both in terms of their abundance and origination. This is coincident with the diversification of major animal groups and ethological innovation from trace fossil record: e.g., the appearance of the resting trace *Rusophycus* in shallow marine, which is thought to have been produced by trilobites; the vertical tube burrows in nearshore high-energy facies produced by dwelling behaviours.

Ediacaran and Cambrian deep marine environments had relatively low dissimilarities and abundance (**Fig. 8**) across time intervals, with the trace fossils mostly simple horizontal locomotory/grazing traces like *Helminthoidichnites* or *Helminthopsis*, as well as the resting or dwelling traces *Bergaueria* which are thought to have been made by sea anemones (as shown in Table 3). These simple traces, which mostly are indicative of grazing feeding strategies, imply the persistence of a mat-ground ecology from the Ediacaran into the earliest part of the Phanerozoic (Buatois and Mángano 2003; Buatois et al. 2014). This discrepancy in the rate of evolution of animals in shallow and deep marine environments reflected by differences in their dissimilarity and the Balance Index for Origination and Extinction could be a result of the higher energy conditions in shallow seas: turbulent flow in neritic regions accelerated water, nutrient and oxygen exchange between the water column and the sediment, and thus would have increased the heterogeneity and oxygen content of the substrate (Li et al. 2020). This heterogeneous mixground may have driven benthic animals to develop stronger cognition, detectability and maneuverability capabilities to survive. And in turn, the bioturbation caused by these more complex behaviours could have further heterogenized the substrate (Gougeon, Mángano, et al. 2018), promoting the

591 evolution of functional morphology and ethology (i.e., the 'Savannah' hypothesis for early
592 bilaterian evolution) (Budd and Jensen 2015; Mitchell et al. 2020). All these processes would have
593 been facilitated by the abundance of oxygen and warmer temperature in shallow marine settings
594 during this time interval. Additionally, the decayed dead metazoans and the organic matters
595 brought by the tides and transgression in the late Ediacaran and early Cambrian would ultimately
596 rejoin this active carbon cycle (Herringshaw, Callow, and McIlroy 2017) in turbulent shallow
597 marines. Such changes in carbon availability and organism–environment co-evolution culminated
598 in a major evolutionary radiation of mobile animals in shallow marine settings during the
599 Cambrian. Traces (and the trace makers) that were mainly found in deep marine settings in later
600 geological periods, like *Paleodictyon*, *Protovirgularia*, *Zoophycos*, *Helminthoida*, *Nereites*, are
601 thought to have actually originated and migrated from Cambrian shallow marine environments
602 (Crimes and Fedonkin 1994; Zhang, Fan, and Gong 2015; Hammersburg, Hasiotis, and Robison
603 2018).

604 Dissimilarities and Balance Indices of both shallow marine and deep marine show similar
605 profiles to the overall trend for the trace fossil record (**Fig. 4**), with a maximum dissimilarity at the
606 Fortunian linked to the origination of taxa with fairish abundance, and a smaller second peak in
607 Balance Indices at the Cambrian Stage 3 due to increased abundance of existing taxa, with limit
608 originations. The loss of taxa and abundance exceeded the gained ones later in the Cambrian Stage
609 4.

610 Dissimilarity (or beta diversity) between contemporaneous shallow and deep marine benthic
611 communities (middle in **Fig. 8**) has lower value for the Ediacaran period (0.217 and 0.231)
612 compared to the Cambrian (~0.6). This implies a greater (triple) niche overlap between shallow
613 and deep marine mobile communities during the Ediacaran (Mángano and Buatois 2016), which

could indicate that shallow and deep marine ecosystems were relatively similar at this time, or the animals has yet experienced evident divergence across bathymetry. However, as the substrate became heterogenized due to bioturbation and high-energy flow, especially in the neritic region, stronger niche partitioning occurred, and dissimilarity between shallow and deep marine mobile communities increased to 0.6 during the Cambrian. Ecological specialization during this period is also observed when looking at the body fossil record (Eden, Manica, and Mitchel 2022).

All the Balance Indices between contemporary shallow and marine seas, as shown in the middle lines in **Fig. 8**, are smaller than 0.5. This suggests that, in addition to overlapping niches/ichnogenera, there were more ichnogenera existing in shallow marine environments than in deep marine ones across the Ediacaran and Cambrian. Particularly in the Ediacaran, all the trace fossils in deep marine setting can also be found in shallow marine settings. This suggest that complex mobile animals (i.e. bilaterians) might have evolved in shallow marine (e.g., traces from Dengying Formation (Chen et al. 2018)), whereas earlier sessile forms (e.g. frondose representatives of the Ediacara biota) originated in deeper, cold and stenothermal environments (Boag et al. 2018; Darroch, Cribb, Buatois, et al. 2021; Turk et al. 2022), with higher inter-site beta diversity (Finnegan, Gehling, and Droser 2019).

Conclusions

The measure for estimating dissimilarity proposed herein has great potential for estimating differences between communities across environmental gradients (e.g., shallow to deep marine) and geological timespans. Using this approach, we were able to quantify trace fossil diversity across major evolutionary events during the Ediacaran–Cambrian.

635 The results demonstrate that there was a sudden increase in both the diversity and frequency of
636 occurrences of traces at the beginning of the Phanerozoic, associated with the Cambrian
637 Information Revolution during the Fortunian. Peaks in ichnodissimilarity and the high Balance
638 Indices during this period signal the onset of the Fortunian Diversification Event.

639 The evolution of more complex animal behaviours and the exploration of deeper tiers/broader
640 territories rooted in Fortunian, but prospered later in the Cambrian Stage 2. This ethological
641 diversification and the establishment of conveyors and regenerators was characterized by the
642 appearance of new and more efficient feeding strategies and deep vertical burrow systems with
643 passive and active infills. This also served to shift the dominant mode of bioturbation from
644 diffusion to advection of solid sediment/nutrient particles (but this was not necessarily true for
645 oxygen, see e.g. (Cribb et al. 2023)), which may have been associated with an increase in the extent
646 of the mixed layer. These novel three-dimensional organism–substrate interactions became
647 dominant in the Cambrian Stage 2, marked the onset of the Agronomic Revolution, and paved the
648 way for the later, more vigorous diversification of animal crown groups and the Cambrian
649 Substrate Revolution. Many trace makers also experienced a second, but lower, peak in the
650 Cambrian Stage 3, mainly due to increases in abundance, but also with limited diversification. This
651 corresponds with the expanded global genus-level body fossil record, where bauplans and
652 behaviours are more conserved and could lead to similar trace morphologies. But later on during
653 Stage 4, a loss of abundance or even extinction was observed. The lowest ichnodissimilarity at
654 Cambrian Stage 4 is also believed to be a result of fully-exploited living strategies (e.g., feeding,
655 moving) and niches. The Origination (Fortunian) – Expansion (Cambrian Stage 3) two-phase
656 pattern is identified through analyses.

Furthermore, we find evidence for asynchrony of evolution in shallow and deep marine environments, indicating a more rapid evolutionary radiation in benthic regions during the Ediacaran–Cambrian interval. The lower dissimilarity of trace records during Ediacaran also indicates an overlapped niche, which then became more specialized during Cambrian Explosion.

Our measure of ichnodissimilarity could also be used to analyze diverse aspects of trace fossil diversity and abundance, such as the evolution of architectural designs, which might provide a more objective insight into the divergence of organismal body plan and mobility. Vectorizing trace fossil data could also help reveal hierarchical relationships by assigning different dimensions or positions to taxonomic units, and could be seamlessly integrated into various multivariate statistical techniques such as Ordination Methods, Multivariate Regression and Dimensionality Reduction, as well as Deep Learning approaches. We therefore believe that the proposed metrics represent powerful tools to investigate how evolution took place during critical events in Earth's history. This could provide new insights into how body plans, behaviours and niche diversified in different environments during the emergence of complex animal life. Methodologically, the proposed metrics are also applicable to body fossil and extant animals database.

Acknowledgements

This work was supported by funding from the Royal Society and the K.C. Wong Education Foundation to Z. Wang (NIF R1 221871). We thank A. Bush, A. Cribb and anonymous reviewers for helpful comments on an earlier version of this manuscript.

Declaration of Competing Interests

The authors declare none.

Cited Literature

Alpert, S. 1973. 'Bergaueria Prantl (Cambrian and Ordovician), a probable actinian trace fossil ', *J. Paleontol.*, 47: 919-24.

Antcliffe, J.B, R.H.T. Callow, and M.D. Brasier. 2014. 'Giving the early fossil record of sponges a squeeze', *Biol. Rev. Camb. Philos. Soc.*, 89: 972-1004.

Artime, O., and M. De Domenico. 2022. 'From the origin of life to pandemics: emergent phenomena in complex systems', *Philos. T. R. Soc. A*, 380: 20200410.

Beck, J., J.D. Holloway, W. Schwanghart, and D. Orme. 2013. 'Undersampling and the measurement of beta diversity', *Methods Ecol. Evol.*, 4: 370-82.

Boag, T.H., R.G. Stockey, L.E. Elder, P.M. Hull, and E.A. Sperling. 2018. 'Oxygen, temperature and the deep-marine stenothermal cradle of Ediacaran evolution', *Proc. Biol Sci.*, 285: 20181724.

Bottjer, D.J., J.W. Hagadorn, and S.Q. Dornbos. 2000. 'The Cambrian Substrate evolution', *GSA Today*, 10: 1-8.

Buatois, L. A., and M. G. Mángano. 2004. 'Terminal Proterozoic–Early Cambrian ecosystems: ichnology of the Puncoviscana Formation, northwest Argentina', *Fossils and Strata*, 51: 1-16.

Buatois, L.A. 2018. '*Treptichnus pedum* and the Ediacaran–Cambrian boundary: significance and caveats', *Geol. Mag.*, 155: 174-80.

Buatois, L.A., J. Almond, M.G. Mángano, S. Jensen, and G.J.B. Germs. 2018. 'Sediment disturbance by Ediacaran bulldozers and the roots of the Cambrian explosion', *Sci. Rep.*, 8: 4514.

Buatois, L.A., and M.G. Mángano. 2016. 'Recurrent Patterns and Processes: The Significance of Ichnology in Evolutionary Paleoecology.' in M.G. Mángano and L.A. Buatois (eds.), *The Trace-Fossil Record of Major Evolutionary Events. Topics in Geobiology* (Springer, Dordrecht).

Buatois, L.A., and M.G. Mángano. 2018. 'The other biodiversity record: Innovations in animal-substrate interactions through geologic time', *GSA Today*, 28: 4-10.

Buatois, L.A., M.G. Mángano, N.J. Minter, and et al. 2020. 'Quantifying ecospace utilization and ecosystem engineering during the early Phanerozoic—The role of bioturbation and bioerosion', *Sci. Adv.*, 6: eabb0618.

Buatois, L.A., G.M. Narbonne, M.G. Mángano, N.B. Carmona, and P Myrow. 2014. 'Ediacaran matground ecology persisted into the earliest Cambrian', *Nature Commu.*, 5: 3544.

Budd, G.E., and S. Jensen. 2015. 'The origin of the animals and a 'Savannah' hypothesis for early bilaterian evolution', *Biol. Rev.*, 92: 446-73.

Bush, A.M., S.C. Wang, J.L. Payne, and N.A. Heim. 2019. 'A framework for the integrated analysis of the magnitude, selectivity, and biotic effects of extinction and origination', *Paleobiology*, 46: 1-22.

Chao, A., R.L. Chazdon, R.K. Colwell, and T. Shen. 2005. 'A new statistical approach for assessing similarity of species composition with incidence and abundance data', *Ecol. Letters*, 8: 148-59.

Cheeyham, A.H., and J.E. Hazel. 1969. 'Binary (Presence-Absence) Similarity Coefficient', *J. Paleontol.*, 43: 1130-36.

Chen, Z., X. Chen, C.M. Zhou, X.L. Yuan, and S.H. Xiao. 2018. 'Late Ediacaran trackways produced by bilaterian animals with paired appendages', *Sci. Adv.*, 4: eaao6691.

Chen, Z., C.M. Zhou, X.L. Yuan, and S.H. Xiao. 2019. 'Death march of a segmented and trilobate bilaterian elucidates early animal evolution', *Nature*, 573: 412-15.

Conde, A., and J. Domínguez. 2018. 'Scaling the chord and Hellinger distances in the range [0,1]: An option to consider', *J. Asia-Pac. Biodivers.*, 11: 161-66.

Cribb, A.T., C.G. Kenchington, B.Koester, B.M. Gibson, T.H. Boag, R.A. Racicot, H.Mocke, M. Laflamme, and S.A.F. Darroch. 2019. 'Increase in metazoan ecosystem engineering prior to the Ediacaran–Cambrian boundary in the Nama Group, Namibia', *Roy. Soc. Open Sci.*, 6: 190548.

Cribb, A.T., S.J. van de Velde, W.M. Berelson, D.J. Bottjer, and F.A. Corsetti. 2023. 'Ediacaran–Cambrian bioturbation did not extensively oxygenate sediments in shallow marine ecosystems', *Geobiology*, 21: 435-53.

Crimes, T. P., and M. A. Fedonkin. 1994. 'Evolution and Dispersal of Deepsea Traces', *PALAIOS*, 9: 74-83.

Curran, H.A., and B. Glumac. 2022. 'Dactyloidites ottoi (Geinitz, 1849) in Bahamian Pleistocene carbonates: a shallowest-marine indicator', *Geological Society, London, Special Publications* 522: 1.

Darroch, S. A.F., A.T. Cribb, L.A. Buatois, G.J.B. Germs, C.G. Kenchington, E.F. Smith, H. Mocke, G.R. O'Neil, J.D. Schiffbauer, K.M. Maloney, R.A. Racicot, K.A. Turk, B.M. Gibson, J. Almond, B. Koester, T.H. Boag,

S.M. Tweedt, and M. Laflamme. 2021. 'The trace fossil record of the Nama Group, Namibia: Exploring the terminal Ediacaran roots of the Cambrian explosion', *Earth Sci. Rev.*, 212: 103435.

Darroch, S.A.F., A.T. Cribb, L.A. Buatois, and et al. 2021. 'The trace fossil record of the Nama Group, Namibia: Exploring the terminal Ediacaran roots of the Cambrian explosion', *Earth Sci. Rev.*, 212: 103482.

Eden, R., A. Manica, and E.G. Mitchel. 2022. 'Metacommunity analyses show an increase in ecological specialisation throughout the Ediacaran period', *Plos biol.*, 20: e3001289.

Erwin, D.H., and S. Tweedt. 2012. 'Ecological drivers of the Ediacaran-Cambrian diversification of Metazoa', *Evol. Ecol.*, 26: 417-33.

Evans, S.D., C. Tu, A. Rizzo, R.L. Surprenant, P.C. Boan, H. McCandless, N. Marshall, S. Xiao, and M.L. Droser. 2022. 'Environmental drivers of the first major animal extinction across the Ediacaran White Sea-Nama transition', *PNAS*, 119: e2207475119.

Fan, J.X., S.Z. Shen, D.H. Erwin, and et al. 2020. 'A high-resolution summary of Cambrian to Early Triassic marine invertebrate biodiversity', *Science*, 367: 272-77.

Finnegan, S., G. Gehling, and M.L. Droser. 2019. 'Unusually variable paleocommunity composition in the oldest metazoan fossil assemblages', *Paleobiology*, 45: 235–45.

Francois, F., M. Gerino, G. Stora, J.P. Durbec, and J.C. Poggiale. 2002. 'A functional approach to sediment reworking by gallery-forming macrobenthic organisms: modelling and application with the polychaete Nereis diversicolor', *Mar. Ecol.-Prog. Ser.*, 229: 127–36.

Gehling, J.G., B.N. Runnegar, and M.L. Droser. 2014. 'Scratch Traces of Large Ediacara Bilaterian Animals', *J. Paleontol.*, 88: 284-98.

Gougeon, R., D. Néraudeau, M. Dabard, A. Pierson-Wickmann, F. Polette, M. Poujol, and J. Saint-Martin. 2018. 'Trace Fossils from the Brioverian (Ediacaran–Fortunian) in Brittany (NW France)', *Ichnos* 25: 11-24.

Gougeon, R.C., M.G. Mángano, L.A. Buatois, G.M. Narbonne, and B.A. Laing. 2018. 'Early Cambrian origin of the shelf sediment mixed layer', *Nature Commu.*, 9: 1909.

Hammersburg, S.R., S.T. Hasiotis, and R.A. Robison. 2018. 'Ichnotaxonomy of the Cambrian Spence Shale Member of the Langston Formation, Wellsville Mountains, Northern Utah, Usa', *Paleontol. Contri.*, 20: 1-66.

Herringshaw, L.G., R.H.T. Callow, and D. McIlroy. 2017. 'Engineering the Cambrian explosion: the earliest bioturbators as ecosystem engineers', *Geological Society, London, Special Publications*, 448: 369 - 82.

Hofmann, R., M.G. Mángano, Elicki O., and Shinaq R. 2012. 'Paleoecologic and Biostratigraphic Significance of Trace Fossils From Shallow- to Marginal-Marine Environments From the Middle Cambrian (Stage 5) of Jordan', *J. Paleontol.*, 86: 931 - 55.

Horn, H.S. 1966. 'Measurement of "overlap" in comparative ecological studies', *Am. Nat.*, 100: 419-24.

Hsieh, S., R. E. Plotnick, and A.M. Bush. 2022. 'The Phanerozoic aftermath of the Cambrian information revolution: sensory and cognitive complexity in marine faunas', *Paleobiology*, 48: 397-419.

Ichaso, A., L.A. Buatois, M.G. Mángano, P. Thomas, and D. Marion. 2022. 'Assessing the expansion of the Cambrian Agronomic Revolution into fan-delta environments', *Sci Rep.*, 12: 14431.

James, N.P., D.R. Kobluk, and S.G. Pemberton. 1977. 'The Oldest Macroborers: Lower Cambrian of Labrador', *Science*, 197: 980-83.

Jensen, S., and K. Mens. 2001. 'Trace fossils Didymaulichnus cf. tirasesnsis Monomorphichnusisp. from the Estonian Lower Cambrian, with a discussion on the early Cambrian Ichnocoenoses of Baltica', *Proc. Estonian Acad. Sci. Geol.*, 50: 75–85.

Jost, L. 2007. 'Partitioning diversity into independent alpha and beta components', *Ecology*, 88: 2427-39.

Kaur, R., B.P. Singh, O.N. Bhargava, R. Mikuláš, G. Singla, S.K. Prasad, and S. Stopden. 2021. 'Ichnology and biostratigraphic significance of Cambrian trace fossils from the lowest stratigraphic level of Kunzam La Formation, Chandra Valley, Lahaul and Spiti, India.', *Ichnos*, 28: 176–207.

Knaust, D. 2013. 'The ichnogenus Rhizocorallium: Classification, trace makers, palaeoenvironments and evolution', *Earth Sci. Rev.*, 126: 1-47.

Knaust, D. 2018. 'The ichnogenus Teichichnus Seilacher, 1955', *Earth Sci. Rev.*, 177: 386-403.

Knaust, D., and C. Neumann. 2016. 'Asteriacites von Schlotheim, 1820 – the oldest valid ichnogenus name – and other asterozoan-produced trace fossils', *Earth Sci. Rev.*, 157: 111-20.

Kwak, S.G., and J.H. Kim. 2017. 'Central limit theorem: the cornerstone of modern statistics', *Korean J Anesthesiol.*, 70.

782 L.A., Buatois, and Mángano M.G. 2003. 'Early colonization of the deep sea: ichnologic evidence of deep-marine
783 benthic ecology from the Early Cambrian of northwest Argentina', *PALAIOS*, 18: 572-81
784 Li, C., W. Shi, M. Cheng, C. Jin, and T.J. Algeo. 2020. 'The redox structure of Ediacaran and early Cambrian oceans
785 and its controls', *Sci. Bull.*, 65: 2141-49.
786 Luo, C., and L.Y. Miao. 2020. 'A Horodyskia-Nenoxites-dominated fossil assemblage from the Ediacaran-Cambrian
787 transition (Liuchapo Formation, Hunan Province): Its paleontological implications and stratigraphic
788 potential', *Paleogeogr. Paleoecl.*, 545: 109635.
789 Mángano, M.G., and L.A. Buatois. 2014. 'Decoupling', *Proc. Biol. Sci.*, 281: 20140038.
790 Mángano, M.G., and L.A. Buatois. 2016. *The Trace-Fossil Record of Major Evolutionary Events* (Springer Dordrecht).
791 Mángano, M.G., and L.A. Buatois. 2020. 'The rise and early evolution of animals: where do we stand from a trace-
792 fossil perspective?', *Interface Focus*, 10: 20190103.
793 McArthur, R.H., H. Recher, and M. Cody. 1966. 'On the relation between habitat selection and species diversity', *Am.
794 Nat.*, 100: 319–32.
795 Mcilroy, D. 2017. 'Ichnological evidence for the Cambrian explosion in the Ediacaran to Cambrian succession of
796 Tanafjord, Finnmark, northern Norway', *Geological Society London Special Publications*: 351-68.
797 Mitchell, E.G, N. Bobkov, N. Bykova, and et al. 2020. 'The influence of environmental setting on the community
798 ecology of Ediacaran organisms', *Interface Focus*, 10: 20190109.
799 Mitchell, E.G., S.D. Evans, Z. Chen, and S. Xiao. 2022. 'A new approach for investigating spatial relationships of
800 ichnofossils: a case study of Ediacaran–Cambrian animal traces', *Palaeobiology*, 48: 557-75.
801 Morgan, C.A., C. Henderson, and B. Pratt. 2019. 'A Giant Protopaleodictyon from the Middle Cambrian of Western
802 Canada', *Ichnos*, 26: 216-23.
803 Na, L., and W. Kiessling. 2015. 'Diversity partitioning during the Cambrian radiation', *PNAS*, 112: 4702-06.
804 Orloci, L. 1967. 'An agglomerative method for classification of Plant communities', *J. Ecol.*, 55: 193-206.
805 Pandey, D.K., A. Uchman, V. Kumar, and R.S. Shekhawat. 2014. 'Cambrian trace fossils of the Cruziana ichnofacies
806 from the Bikaner-Nagaur Basin, north western Indian Craton', *J. Asian Earth Sci.*, 81: 129-41.
807 Peters, J.A. 1968. 'A computer program for calculating degree of biogeographical resemblance between areas', *Syst.
808 Zoology*, 17: 64-69.
809 Pickerill, R.K., and J.D. Keppie. 1981. 'Observations on the Ichnology of the Meguma Group (?Cambro–Ordovician)
810 of Nova Scotia', *Maritime Sediments and Atlantic Geology*, 17: 130–38.
811 Plotnick, R.E., S.Q. Dornbos, and J.Y. Chen. 2010. 'Information landscapes and sensory ecology of the Cambrian
812 Radiation', *Paleobiology*, 36: 303-17.
813 Ricotta, C. 2017. 'Of beta diversity, variance, evenness, and dissimilarity', *Ecol. Evol.*, 7: 4835-43.
814 Roy, A.B., and R. Purohit. 2018. 'Palaeozoic Geological History.' in R. Purohit and A.B. Roy (eds.), *Indian Shield:
815 Precambrian Evolution and Phanerozoic Reconstitution* (Elsevier).
816 Seilacher, A., L.A. Buatois, and M.G. Mángano. 2005. 'Trace fossils in the Ediacaran–Cambrian transition: Behavior
817 diversification, ecological turnover and environmental shift', *Paleogeogr. Paleoecl.*, 227: 323-56.
818 Seilacher, A., and J. W. Hagadorn. 2010. 'Early molluscan evolution: evidence from the trace fossil record', *PALAIOS*,
819 25: 565-75.
820 Seilacher, A., and F. Pflüger. 1994. 'From biomats to benthic agriculture: A biohistoric revolution.' in W.E. Krumbein,
821 D. M. Peterson and L.J. Stal (eds.), *Biostabilization of Sediments.* (Bibliotheks-und Informationssystem der
822 Carl von Ossietzky Universität Oldenburg).
823 Sepkoski, Jr J.J. 1998. 'Rates of speciation in the fossil record', *P. Trans. R. Soc. B*, 353: 315–26.
824 Solan, M., and B.D. Wigham. 2005. 'Biogenic particle reworking and bacterial-invertebrate interactions in marine
825 sediments.' in E. Kristensen, R.R. Haese and J.E. Kostka (eds.), *Macro- and Micro-organisms in Marine
826 Sediments. Coastal and Estuarine Studies* (American Geophysical Union,).
827 Tarhan, L.G. 2018. 'The early Paleozoic development of bioturbation—Evolutionary and geobiological consequences',
828 *Earth Sci. Rev.*, 178: 177-207.
829 Turk, K.A., K.M. Maloney, M. Laflamme, and S.A.F. Darroch. 2022. 'Paleontology and ichnology of the late
830 Ediacaran Nasep–Huns transition (Nama Group, southern Namibia)', *J. Paleontol.*, 96: 753-69.

831 Wang, Z.K., and I. Rahman. 2023. 'Quantitative ichnology: A novel framework to determine the producers of
832 locomotory trace fossils – the ichnogenus *Gordia* as a case study', *Palaeontology*, 66: e12686.
833 Webby, B.D. 1970. 'Late Precambrian trace fossils from New South Wales', *Lethaia*, 3: 79-109.
834 Whittaker, R.H. 1960. 'Vegetation of the Siskiyou Mountains, Oregon and California', *Ecol. Monogr.*, 30: 279-338.

Wilson, T.L., A.P. Rayburn, and Jr T.C. Edwards. 2012. 'Spatial ecology of refuge selection by an herbivore under risk of predation', *Ecosphere*, 3: 1-18.
Zamora, S., B. Deline, J.J Álvaro, and I.A. Rahman. 2017. 'The Cambrian Substrate Revolution and the early evolution of attachment in suspension-feeding echinoderms', *Earth Sci. Rev.*, 171: 478-91.
Zhang, L.J., R.Y. Fan, and Y.M. Gong. 2015. 'Zoophycos macroevolution since 541 Ma', *Sci. Rep.*, 5: 14954.
Zhang, L.J., Y.A. Qi, L.A. Buatois, M.G. Mángano, Y. Meng, D. Li, and R.F. Tang. 2017. 'The impact of deep-tier burrow systems in sediment mixing and ecosystem engineering in early Cambrian carbonate settings. ', *Sci. Rep.*, 7: 45773.
Zhang, X.L., and D.G. Shu. 2021. 'Current understanding on the Cambrian Explosion: questions and answers', *palZ*, 95: 641-60.
Zhu, M., A. Zhuravlev, R. Wood, F. Zhao, and S. Sokhov. 2017. 'A deep root for the Cambrian Explosion: implications of new bioand chemostratigraphy from the Siberian PlatformZ', *Geology*, 45: 459-62.
Zhuravlev, A., and R. Riding. 2000. *The Ecology of the Cambrian Radiation* (Columbia University Press: New York).
Zhuravlev, A.Y., and R.A. Wood. 2018. 'The two phases of the Cambrian Explosion', *Sci. Rep.*, 8: 16656.

List of Figures and Tables

Fig. 1. Diagram showing how the angle representing the dissimilarity between two vectors can be divided into increased (In) and decreased (De) components of occurrences. Only when the gained and loss of occurrences are balanced (1A), can the two angles split by the mean vector be equal. If the loss of occurrences is higher (1B), the mean vector becomes closer to Vector 1.

Fig. 2. Variation in dissimilarity (*D*) across a number of shared elements (*M*th case) compared to the benchmark: proposed vector-based dissimilarity versus M-H dissimilarity.

Fig. 3. Convergence study. The obtained dissimilarity (*D*) converges on 0.5 with increasing numbers of observations.

Fig. 4. Ichnological dissimilarity (A) and Balance Indices (B) across the Ediacaran–Cambrian. (A) Dissimilarity is most evident at the Ediacaran–Cambrian boundary, decreasing through the Cambrian. (B) Balance Indices for Occurrences (line) and Origination & Extinction (dashed line) across the Ediacaran–Cambrian. Values above 0.5 indicate that the contribution from increasing numbers of taxa is greatest and values below 0.5 are when the contribution from the loss of taxa or abundance are greatest. The Balance Index for Occurrences peaks at the boundaries between the Ediacaran and the Cambrian and between the Cambrian Stages 2 and 3, before declining

868 at the boundary between the Cambrian Stages 3 and 4. The second peak is a result of increased occurrences
869 rather than the origination of new body plans, as shown by the low value of the Balance Index for Origination
870 and Extinction.
871
872 Fig. 5. Evolution of animal behaviours across the Ediacaran–Cambrian. (A) Dissimilarity. Grazing traces
873 (Pascichnia) peak at the Ediacaran–Cambrian interface, while dwelling traces (Domichnia) and locomotion
874 traces (Repichnia) peak later on after the Fortunian Stage. Complicated behaviours like parenting and farming
875 (Agrichnia) experienced a later divergence at the end of the Cambrian Stage 2. In all cases, dissimilarity
876 decreased after the Cambrian Stage 3. (B) Balance Index for Occurrences. Pascichnia and Agrichnia reached the
877 peak of diversity and abundance at the interface between the Cambrian Stages 2 and 3, while Repichnia and
878 Domichnia had another peak at the Ediacaran–Cambrian interface. All the behaviours experienced reductions in
879 abundance or even taxa at Cambrian Stage 4. (C) Balance Index for Origination and Extinction. All the categories
880 but Agrichnia peaked at the Ediacaran–Cambrian boundary, with Repichnia and Pascichnia experiencing a
881 second smaller peak at the boundary between the Cambrian Stages 2 and 3.
882
883 Fig. 6. Typical Cambrian grazing trace fossils: *Oldhamia* (A) shows evidence of phobotaxis and thigmotaxis,
884 *Psammichnites* (B) shows evidence of strophotaxis. These complex grazing traces first appeared in the Fortunian
885 stage, with photos adopted from (Seilacher, Buatois, and Mángano 2005; Mángano and Buatois 2020). Typical
886 field photos of the vertical and sub-vertical dwelling burrows *Skolithos* (C), two opening of U-shape *Arenicolites*
887 (D), and *Diplocraterion* (E), which first appeared during Cambrian Stage 2, photos adopted from (Mcilroy 2017)
888 and our collections from Shiyantou Formation, Yunan, China, and Hardeberga Formation, Bornholm, Denmark
889 (Cambrian Stage 2); Arthropod trackway *Diplichnites* (F) from the Cambrian Stage 2 (Pandey et al. 2014), and
890 Putative farming traces *Paleodictyon* cf. *imperfectum* (G) from the Goldenville Group, Nova Scotia (Pickerill
891 and Keppie 1981). All scale bars are 1cm.
892
893 Fig. 7. Exploration of function groups and niches across the Ediacaran–Cambrian interval. E: Epifaunal
894 bioturbators, SM: Surficial modifiers, B: Biodiffusive bioturbators, R: Regenerators, C: Conveyors, G: Gallery

biodiffusors. (A) Dissimilarity: Epifaunal bioturbators and surficial modifiers experienced massive divergence at Ediacaran–Cambrian interface, Regenerators and conveyors came to stage after Fortunian, while gallery biodiffusors and Biodiffusive bioturbator reached their peak at the interface between the Cambrian Stages 2 and 3. (B) Balance Index for Occurrences: Almost all functional groups experienced a two-peak increase in diversity and occurrences at Ediacaran–Cambrian interface and the interface between the Cambrian Stages 2 and 3. (C) Balance Index for Origination and Extinction: Shallow niches experienced origination earlier than deeper niches, and a small origination happened during the Cambrian Stage 3.

Fig. 8. Ichnological dissimilarity (first-line green values), Balance Index for Occurrences (second-line black values) and Balance Index for Origination and Extinction (third-line blue values) in different environments across the Ediacaran–Cambrian interval. The dissimilarities between geological intervals at shallow marine (wavy background) is higher than those of the deep marine (dotted background), with slightly higher Balance Indices especially at Ediacaran-Cambrian transition. Dissimilarity (beta diversity) is low between contemporaneous shallow and deep marine during Ediacaran, while higher during Cambrian, but shallow marine always has more abundance and taxa than deep marine.

Table 1. Observations from four 4 sites, where A–N represent different species

Table 2. Theoretical probability of occurrence of each element in the benchmark and the 10th testing case

Table 3. Dataset of marine trace fossils from the Ediacaran to Cambrian Series 2.