Supplemental Material, Text 1 and Supplemental Figures Captions.

Supplementary material for

Small-world dynamics drove Phanerozoic divergence of burrowing behaviors

Andrea Baucon^{1,2*}, Carlos Neto de Carvalho^{2,3}, Fabrizio Felletti⁴, Gabriele Tosadori⁵, Alexandre Antonelli^{6,7,8}

¹ DISTAV, University of Genova, Corso Europa 52, Genova, 16132, Italy.

² Geology Office, Naturtejo UNESCO Global Geopark, Avenida Zona Nova de Expansão, 6060-101, Idanha-a-Nova, Portugal.

³ Instituto D. Luiz, University of Lisbon. Faculdade de Ciências da Universidade de Lisboa, Campo Grande Edifício C1, Piso 1, 1749-016 Lisbon, Portugal.

⁴ Università degli Studi di Milano, Dipartimento di Scienze della Terra, Via Mangiagalli 34, 20133-Milano, Italy

⁵ Dipartimento di Medicina, University of Verona, Policlinico GB Rossi, Piazzale L.A. Scuro 10, 37134 Verona

⁶ Royal Botanic Gardens, Kew, TW9 3AE, Richmond, UK

⁷ Gothenburg Global Biodiversity Centre, Department of Biological and Environmental Sciences, University of Gothenburg, Carl Skottsbergs gata 22 B, 413 19 Göteborg, Sweden

⁸ Department of Plant Sciences, University of Oxford, South Parks Road, OX1 3RB Oxford, U.K.

* Corresponding author: andrea@tracemaker.com

DETAILED METHODS

Overview

The source data for this study is the table compiled by Adolf Seilacher in the 1950s for the Exxon company and successively released on a variety of publications (Seilacher, 1967, 1978, 2007). The most recent version of the table is used (Seilacher, 2007).

In the source table rows correspond to paleontological sites ($n=45$), columns represent trace fossil taxa and paleoenvironmental proxies ($n=34$). As such, the table is a presence-absence matrix in which each cell represents the presence or absence of a particular taxon/proxy in a given locality. The PAST and Gephi software (Bastian et al., 2009) are used to translate this source table as an undirected, unweighted network (ichnofossil network), following an approach used to model individual trace-bearing sites (Baucon and Felletti, 2013; Baucon et al., 2014b, 2015). The process for building the network consists of drawing a link between those ichnotaxa that co-occur in one (or more) paleontological sites. The resulting network is used to test the Phanerozoic divergence hypothesis, stating that deep-sea associations of trace fossils have retained their distinctiveness from shallow marine ones. The divergence hypothesis holds at least from the Ordovician since highly-patterned traces (graphoglyptids) have begun to migrate to the deep-sea after the Middle Cambrian (Crimes and Fedonkin, 1994; McIlroy and Brasier, 2017). To this aim, it is first compared the ichnofossil network with null models; then subgroups are searched and the correlation between subgroups and environmental proxies is tested. Finally, an algorithm capable of generating networks topologically similar to the ichnofossil network is developed. The hypothesis-testing framework is thoroughly discussed in the following lines ('hypothesis-testing framework' section).

Stratigraphic ranges of ichnotaxa are based on literature (Häntzschel, 1975; Tchoumatchenco and Uchman, 2001; Uchman, 2004; Jensen et al., 2006; Seilacher, 2007; Desai et al., 2010; Buatois and Mángano, 2011; Stachacz, 2012; Baucon et al., 2014a, 2020; Zhang et al., 2015; Knaust and Neumann, 2016; Knaust, 2017; McIlroy and Brasier, 2017; Chen et al., 2018).

Definitions of terms are based on previous works (Davitashvili, 1945; Pickerill and Brenchley, 1975; Ekdale *et al.*, 1984; Wassermann and Faust, 1994; Wuchty and Stadler, 2003; Caporossi *et al.*, 2003; McIlroy, 2004; Legendre, 2005; Newman, 2006; Bhadra *et al.*, 2009; Fortunato, 2010; Danovaro *et al.*, 2014; Baucon *et al.*, 2015) and provided in SM Tab. 3.

Extent and resolution of the study

The patterns that we observe in nature, and the processes that cause these patterns, change with the scale of observation (Cooper *et al.*, 1998). It is therefore important to define the observation scale of this study by characterizing its major components, that are, extent and resolution. The major advantage of the Seilacher dataset is its wide spatial, temporal and environmental extent. Seilacher's table is the only published dataset that (1) covers shallow and deep-sea environments, (2) spans the Cambrian-Neogene interval, (3) has a global extent. In addition, it provides information about both physical and biogenic structures, which is the prerequisite for a rigorous testing of the divergence hypothesis. While the extent of the dataset is wide, its spatial, temporal and stratigraphic resolution is coarse. Seilacher dataset includes, on average, 4.5 sites per geological period. It comprises sites from three present continents, *i.e.*, Europe (27 sites), Asia (3 sites) and America (15 sites). The stratigraphical resolution is that of the formation, *i.e.*, presence/absence data are referred to geological formations.

The scale of interpretation necessarily depends upon the scale of the dataset. Because the Seilacher's table presents a wide extent but a coarse resolution, its interpretation should be conducted at the biome level, which is one of the eight fundamental levels of organization in ecology: (1) cell, (2) organism, (3) population, (4) community, (5) ecosystem, (6) landscape, (7) biome and (8) biosphere (Allen and Hoekstra, 1990). The biome level typically comprises large spaces at least at the (sub)continental scale (Mucina, 2019). The biome-level scale of interpretation is primarily required by the stratigraphical resolution of the dataset. In fact, each row of the table

represents a trace fossil assemblage encompassing all the trace fossils occurring within a single locality, which corresponds to a geological formation. Consequently, assemblages of the dataset do not necessarily represent ichnocoenoses, i.e. groups of traces that have been formed by the action of what approximates to a single benthic community (Davitashvili, 1945; McIlroy, 2004; Baucon *et al.*, 2015). Rather, each of the trace fossil assemblages is a time-averaged group of traces from a specific biome, that is, shallow- or deep-marine. The biome-specificity is demonstrated by the fact that no assemblage of the dataset is associated with both shallow- and deep-marine proxies.

The coarse resolution of the dataset is not necessarily a limitation, since there is no single natural scale at which ecological phenomena should be studied (Levin, 1992). As recognized by previous studies (Valentine, 1973), processes that regulate life at fine spatiotemporal scales may differ from those that control large-scale patterns. It should also be noted that at present there are no higher-resolution datasets published depicting Phanerozoic bioturbation patterns at a global extent. Although there are more recent trace fossil datasets, these cover single depositional environments (Uchman, 2004) and/or narrow stratigraphic intervals (Buatois and Mángano, 2016). By contrast, Seilacher's dataset covers marine environments at a global scale, from the Cambrian to the Neogene. To our knowledge, no other trace fossil datasets cover a wider environmental and temporal extent. An alternative approach would be aggregating different datasets, but this would have introduced bias due to differing taxonomic approaches and sampling resolutions. For the same reason, we keep the ichnotaxa names described in the most recent version of the dataset (Seilacher, 2007), although some of them have been successively lumped in the same ichnogenus (i.e., *Helminthoida* has been included in *Nereites*; scollicids and *Scolicia* meanders). In addition, keeping the original taxa names allow a direct comparison with the seminal ichnofacies model, as it was archetypally proposed (Seilacher, 1967, 1978, 2007).

The dataset was compiled by Seilacher for the Exxon company and was successively released on a variety of publications (Seilacher, 1978, 2007). Since these publications were not

peer-reviewed, they may raise concerns about the coherence of the dataset itself. The lack of peer-review is clearly a reflection of the times when the dataset was first released. For instance, the influential journal *Nature* introduced formal peer review only in 1967, e.g. the 1953 publication by Watson and Crick on the structure of DNA was not peer-reviewed (Siegel, 2008; Tan, 2018). In addition, the source data table reflects the work for the hydrocarbon industry, which often prevents the full disclosure of scientific data of commercial value. It should also be added that the source data underwent an indirect, partial peer-review process. In fact, the source data table presents several ichnoassociations of the classic ‘Bathymetry of Trace Fossils’ paper (Seilacher, 1967). Here, Seilacher discusses several sites of the 1978 data table, citing source literature for most of them: localities in Northern Iraq (Seilacher, 1963), the Oslo region (Seilacher and Meischner, 1964), Kulm Shales (Huckriede, 1952), the Taconics (Neuman, 1962) and Ouachita Mountains. Based on these observations, the lack of a full peer-review is a limitation of Seilacher’s dataset, which however meets the minimum requirements for data analysis.

Hypothesis-testing framework

Three steps are carried out. First, the primary null hypothesis (trace fossil taxa are randomly or regularly associated) is tested. To do so, the ichnofossil network is compared with random and regular null models that are equivalent. Second, subgroups are searched in the ichnofossil network and the correlation between the detected subgroups and environmental proxies is tested. Third, an algorithm generating networks with topological features comparable to those of the ichnofossil network is developed. The mentioned topological features are: high clustering, short distance (small-world effect) and community structure. By analogy with social networks, the average clustering coefficient of the ichnofossil network measures the probability that two ichnotaxa co-occurring with a third one are associated themselves (Girvan and Newman, 2002; Baucon and Felletti, 2013). Distance measures the shortest path of connection between two nodes (Wassermann and Faust, 1994) therefore, in the ichnofossil network, it represents proximity of trace fossil taxa via

co-occurrence relationships . Community structure does not refer to the concept of biological community, but it is the property of presenting high concentrations of links within special groups of nodes, and low concentrations between these groups (Fortunato, 2010).

Comparison with equivalent networks

Metrics of the ichnofossil network are compared to those of equivalent random and regular networks (Latora and Marchiori, 2001; Fronczak et al., 2004). To this aim, the topology of the ichnofossil network is analyzed using NetworkX, a Python package for the creation, manipulation, and study of the structure, dynamics, and functions of complex networks (Bastian et al., 2009) . We develop Python code that empirically generates 1000 networks for each of the following network models:

- *Erdős–Rényi model*, in which each pair of nodes is connected with a given probability (Erdős and Rényi, 1959). In the Python code the probability is set to 0.62 in order to get the same average degree of the ichnofossil network (19.8);
- *Regular graph*, generated according to the algorithm of Steger and Wormwald (Steger and Wormald, 1999). In the code the degree of each node is set to 20 in order to get an average degree similar to that of the ichnofossil network (20).
- *Watts–Strogatz model*, in which each node is joined to a number of nearest neighbors, and then links are rewired according to given rewiring probability (Watts and Strogatz, 1998). In the code, the number of nearest neighbors is set to 20 and the rewiring probability is set to 0.5. This allows to get an average degree of 20, i.e., similar to that of the ichnofossil network.

To evaluate whether the ichnofossil network is a small-world, the small-worldness index S is calculated, which compares clustering and distance of a given network to an equivalent random network. A network is said to be a small-world if $S > 1$ (Humphries and Gurney, 2008). It is also

calculated the small-world measure ω , which compares clustering of a given network to an equivalent lattice network and its distance to an equivalent random network (Telesford et al., 2011). Values of ω close to zero are considered small-world (Telesford et al., 2011). The Python code uses the NetworkX package. All code developed for this study is provided in SI 1-4 and is based on the NetworkRandomizer plugin for Cytoscape (Tosadori et al., 2017).

Subgroup detection

Subgroups of nodes are searched using the modularity optimization algorithm (Blondel et al., 2008) and then the correlation between network subgroups and environmental proxies is tested. The relationship between taxa of the ichnofossil network and environmental proxies is evaluated by calculating the Jaccard index and by performing the chi-square test. The Jaccard index (Jaccard, 1912) is defined as the number of shared occurrences divided by the total number of occurrences (Hammer and Harper, 2006). The software PAST is used for these calculations. Results are visualized as a network layout in which the coordinates of nodes represent the Jaccard-based probability of association with shallow (x coordinate) and deep marine (y coordinate) proxies (Fig. 3). The Jaccard similarity for absence-presence data quantifies the probability of association between two elements, if at least one of them is present in the sample (Hammer and Harper, 2006). Accordingly, the closer a node is to the upper left corner ($x=0$, $y=1$) of the plot, the higher is the probability of a taxon to be specific of deep-sea settings. Conversely, closeness to the upper right corner ($x=1$, $y=0$) implies shallow-marine specificity. The diagonal segment that connects these corners contains the points for which the probability of co-occurring in the shallow sea equals that of co-occurring in the deep-sea. Consequently, the diagonal segment separates the deep-sea biome from the shallow-marine one. The small-worldness index S (Humphries and Gurney, 2008) and the small-world measure ω (Telesford et al., 2011) are calculated with NetworkX.

Modelling the ichnofossil network

A model to generate networks with topological features (high clustering, short average distance) is proposed and comparable to those of the ichnofossil network. Among the existing models, the Watts and Strogatz (1998) and the Newman and Watts (Newman, 2000) models show both clustering and short distances, but they lack an explicit spatial component which is required by the concept of trace association itself. For this reason, the model of network evolution is inspired by these models but simultaneously considers the concept of spatial co-occurrence. The model is implemented using the programming language Python, the package NetworkX, and its fundamental package for scientific computing, NumPy (Walt et al., 2011) (Supplemental Material Code 4). In the spatial model of this study, the seafloor is simulated by a unidimensional domain across which burrows are distributed (Supplemental Material Fig. 4). The spatial ranges of n taxa of burrows are modelled by segments arranged within this domain and can change at discrete points in time ($t=0\dots t_{\max}$) according to a defined set of rules, which are described in the following lines. At the end of the simulation, a network is produced based on co-occurrence relationships between ichnotaxa, i.e., nodes are linked if the ranges of the corresponding ichnotaxa intersect at any given time. Accordingly, the topology of this simulation network depends on the rules properly to which taxon ranges change at each time step of the simulation. Two simple rules result in complex patterns of trace fossil association that are comparable to those observed in the real-world ichnofossil network. The first is a ‘specialist-rule’, i.e., having a narrow and changing spatial range across time. At the start of the simulation, g specialist ichnotaxa are randomly distributed within the seafloor domain and present a small range width, which is randomly selected between 0 and a maximum value ($w_{\max}$). At any of the successive time steps, the ranges of specialist ichnotaxa (s) vary of a small amount, which is randomly selected between 0 and a maximum value ($r_{\max}$). The second rule is a ‘generalist-rule’, i.e., keeping a wide range across time. Accordingly, a number of ichnotaxa (g : generalist taxa) maintain a range that is as wide as the entire seafloor domain for the

entire duration of the simulation. It should be noted that these rules are an oversimplification of real-world processes but are inspired by known facies-breaking taxa for generalists (e.g. *Chondrites*) and facies-specific ones (e.g. *Paleodictyon*) for specialists, although exceptions exist for individual occurrences (e.g. Malekzadeh and Wetzel, 2020).

SUPPLEMENTARY DISCUSSION

The source dataset contains several ichnogenera that are known to occur in different depositional environments. For instance, *Taenidium* has been found in both marine and terrestrial deposits (Keighley and Pickerill, 1994), whereas *Chondrites* is associated with either shelf or deep-sea deposits (Baucon *et al.*, 2020). Seilacher himself referred to these environment-crossing ichnotaxa as ‘facies-breaking ichnogenera’ (Seilacher, 1978, 2007) when interpreting the source dataset. A question might therefore arise: are these environment-crossing ichnogenera captured by network topology?

Apparently, the ichnofossil network does not capture environment-crossing ichnotaxa because it is partitioned in a shallow-sea (group A) and a deep-sea (group B) group of traces. Environment-crossing ichnotaxa would be expected to pertain to both groups. However, the modularity optimization algorithm cannot tackle overlapping community structure, in which one node may belong to more than one group (Shen *et al.*, 2009). The tendency to cross different environments is quantified by network betweenness, a centrality measure that quantifies ‘how between’ a given node is (Wassermann and Faust, 1994) by considering the number of shortest paths that run through it (Wuchty and Stadler, 2003). High-betweenness nodes lie between many others, acting as a bridge between different groups of ichnotaxa and potentially connecting different ichnoassociations and/or environments (Baucon and Felletti, 2013). Intriguingly, all the “facies-breaking ichnogenera” of Seilacher (1978, 2007) (*Chondrites*, scolichids, *Taenidium*, *Neonereites*, *Phycosiphon*, *Fucusopsis*) are high-betweenness nodes in the ichnofossil network. Specifically, the

betweenness of these ichnogenera is above the network average, with *Chondrites*, *Taenidium* and *scolicids* being the highest-betweenness ichnotaxa of the whole network. Except for *Fucusopsis*, the betweenness values of facies-breaking ichnogenera are above the upper quartile, implying that they pertain to the 25% highest-betweenness nodes. It should be noted that the upper quartile nodes comprise *Paleodictyon* and *Nereites*, which are typically associated with deep-sea deposits. These outliers are explained by the fact that the *Paleodictyon* and *Nereites* nodes are central for the deep-sea group of nodes, i.e., they separate fine-scale sub-groups within the deep-sea group of traces. This observation is confirmed by field studies (Uchman, 2009), highlighting the fact that the *Nereites* ichnofacies comprise different ichnosubfacies (e.g., *Nereites* ichnosubfacies, *Paleodictyon* ichnosubfacies). The distribution of betweenness show another important difference between the ichnofossil network and regular networks. The distribution of betweenness (SM Fig. 2b) is bimodal, indicating that the ichnofossil network topology is characterized by low-betweenness nodes and shortcuts running through high-betweenness nodes. Shortcuts are not compatible with a regular network topology.

An independent line of evidence is provided by considering the correlation with environmental proxies. It is expected that Seilacher's "facies-breaking taxa" should be strongly correlated with both shallow- and deep-sea proxies. This prediction can be tested by considering the node layout of Fig. 3, in which the position of each node corresponds to the probability of association with shallow (x coordinate) and deep marine (y coordinate) proxies. This is the case of most facies-breaking taxa, e.g. *Taenidium* ($x_{Ta}=0.13$; $y_{Ta}=0.15$), *Neonereites* ($x_{Ne}=0.26$; $y_{Ne}=0.30$) and *Chondrites* ($x_{Ch}=0.41$; $y_{Ch}=0.42$).

Supplementary information code

Supplementary Information Code 1. Python code for generating multiple networks with *Erdős–Rényi* model.

Supplementary Information Code 2. Python code for generating multiple networks with regular model.

Supplementary Information Code 3. Python code for generating multiple networks with *Watts–Strogatz* model.

Supplementary Information Code 4. Python code for generating networks according to the model of ichnotaxa distribution proposed in this paper.

Contributions

A.B. designed the research project, wrote the initial drafts of the manuscript, figures and supplementary material. A.B. wrote the Python code for analysing the ichnofossil network and for generating networks according to the proposed model of taxa distribution. A.B. and C.N.C. compiled the presence/absence dataset for the ichnofossil network. G.T. wrote the Python code for generating random, regular and small-world networks. C.N.C., F.F., G.T., A.A., contributed to the interpretation of data and to the final version of the manuscript.

Corresponding author

Correspondence to Andrea Baucon.

Ethics declarations

Competing interests

The authors declare no competing interests.

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Supplemental Material Figure Captions

Supplemental Material Fig. 1. Topological properties of the ichnofossil network compared to equivalent regular, small-world and random networks. Equivalent networks present the same number of nodes ($n=32$) and comparable average degree (≈ 20) with respect to the ichnofossil network. a. Average clustering coefficient-distance scatterplot. Each dot represents a single network. b. Degree range-maximum betweenness scatterplot. Degree range is intended as the difference between the maximum and the minimum degree in a network.

Supplemental Material Fig. 2. Histograms of topological parameters of the ichnofossil network. a. Histogram of degree, which is the number of taxa associated with a given one. b. Histogram of betweenness, which measures the numbers of shortest paths passing through a node. The distribution of betweenness (SM 2B) is bimodal, indicating the presence of low-betweenness nodes and shortcuts running through high-betweenness nodes. The presence of shortcuts is not compatible with a regular network topology.

Supplemental Material Fig. 3. Network layout showing results of the chi-squared test. The chi-squared test evaluates the correlation between network-based subgroups and environmental proxies. Each datapoint is a node and corresponds to a taxon; its coordinates are the p values of the chi-squared test. Results show that most (8/15) taxa of subgroup A are significantly associated to shallow-marine proxies at a significance level of 0.1. In parallel, the correlation between traces of subgroup B and deep-marine proxies is statistically significant for most (12/17) taxa of the subgroup. Links have not been depicted for graphical clarity. Refer to Figure 2 for taxa labels.

Supplemental Material Fig. 4. Distribution model of trace fossil taxa across the Phanerozoic. Two rules explain real-world data about trace fossils: a generalist rule, according to which taxa change their ranges at each time window; a specialist-rule, according to which taxa maintain the same large environmental range.

Supplemental Material Fig. 5. Small-world characteristics of the model. Networks produced by setting $t_{\max}=10$, $g=5$, $w_{\max}=0.01$, $r_{\max}=0.001$. a. The average path length L increases slower than the logarithm of the network size n . The scatterplot shows that, once the model approaches 25 nodes, average path length reaches a plateau around $L=1.4$. This may suggest a universal property of ichnological networks. b. Average degree increases linearly with the number of nodes.

Supplemental Material Fig. 6. Internal variability of the model. All networks have been produced by setting $n=32$ and $t_{\max}=10$, and then producing 100 networks for each change in the x-axis variable. The variables $w_{\max}$ and $r_{\max}$ are expressed as a fraction of the total environment width, i.e., the size of the virtual seafloor in which the simulation takes place. a, b. Network metrics for increasing values of $r_{\max}$. Networks produced by setting $g=5$, $w_{\max}=0.05$. c, d. Network metrics for increasing values of $w_{\max}$. Networks produced by setting $g=5$, $r_{\max}=0.005$; e, f. Network metrics for increasing values of g . Networks produced by setting $w_{\max}=0.05$, $r_{\max}=0.005$. An increase in specialist-related variables ($w_{\max}$, $r_{\max}$) results in increasing average clustering coefficient and average degree (a,b), whereas average distances are shorter as the values of $w_{\max}$ and $r_{\max}$ increase (b). These results are explained by the fact that $w_{\max}$ and $r_{\max}$ control the overall width of environmental ranges; the wider the environmental ranges, the higher probabilities of range overlap and taxa co-occurrence. Results also show that the larger is the number of environmental generalists, the higher are the average clustering coefficient and degree (c,d). This phenomenon is explained by the fact that the ranges of generalists are by definition large, and therefore they overlap with the ranges of other taxa, thus increasing the number of links in the resulting networks. This also explains the fact that larger numbers of generalists result in shorter average path lengths (d).

Supplemental Material Fig. 7. Predictive ability of the model. Stars indicate topological measures of the ichnofossil network, whereas box-and-whiskers plots synthesize the topological measures of 1000 model-derived networks. The model-derived networks have been produced with these values: $w_{\max}=0.1$, $r_{\max}=0.01$, $g=1$, $s=31$ ($w_{\max}$ and $r_{\max}$ are expressed as a fraction of total environment width). a. average path length, average clustering coefficient, average density. b. average degree, number of subgroups.