The User Guide of TaphonomeAnalyst 2.0

Sampling process Nested plots sampling Evaluation of sampling effort & Theoretical maximum biodiversity estimation Geochemical data Samples lists Number Order Family 2 3 5 er of specimens / So Species correlation analysis Visualization of relative Visualization of geochemical data abundance of species Assembling dissimilarity -Correlation network construction Proportion of taphonomic grade environmental distance test 20 40 60 80 >90 Environmental Dista Mantel Test between species **Buried environment analysis** Comparison of networks abundance and ecological environmental variables **Ecological factor analysis** Abundance analysis **Network analysis**

Code availability: The code of TaphonomeAnalyst 2.0 can be downloaded from https://github.com/wma1995/TaphonomeAnalyst2

Development environments: Python 3.8.8

Article: TaphonomeAnalyst 2.0: integrative analysis software of taphocoenosis co-currence and geochemical data

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Introduction

In recent years, there has been a significant increase in the number of studies aimed at elucidating the structures and dynamics of ancient communities through taphonomic co-occurrence networks (Guo Ma and Tang, 2023; Muscente, 2019; Xu, 2022). As taphonomic co-occurrence data can reflect symbiotic relationships among various groups to some extent, researchers are able to plot symbiotic networks by aggregating large amounts taphonomic co-occurrences. However, many of these studies have focused on large-scale marine biotas, compared to smaller-scale lacustrine biotas that receive less attention (Muscente et al., 2019; Xu et al., 2022). Marine research typically operates at large scales, allowing researchers to deduce symbiotic (in the general and not mutualistic sense of the term) relationships from presence/absence data alone (Muscente et al., 2019; Xu et al., 2022). In contrast, lacustrine studies are conducted on a relatively small scale, where the transportation of fossil remains is more complex and the sedimentary environment more variable. Obtaining co-occurrence data for lacustrine research necessitates gathering of abundance data, which in turn requires the field excavation and lab identification of a large number of specimens, thereby rendering lacustrine co-occurrence research difficult to implement over the long term.

Nevertheless, research on fossil lacustrine co-occurrence networks has also seen meaningful progress. Our team has demonstrated that, even under less-than-ideal conditions such as time averaging and varied transportation, a specific taphocoenosis still retains a wealth of community-level information (Guo, Ma and Tang, 2023). We successfully mapped the Daohugou faunal network from the Middle Jurassic of China and divided it into aquatic, edaphic, mudflat, and silvan modules (Guo, Ma and Tang, 2023). This exercise not only provided statistically significant support for traditional networks based on morphological function and taxonomic uniformitarianism, but also paves the way for further quantitative studies in fossil community ecology.

Our team previously released the original version of TaphonomeAnalyst (Guo, Ma and Tang, 2023), designed for the study of small-scale, terrestrial, fossil assemblages. The TaphonomeAnalyst software package served as a comprehensive tool designed for the downstream community analyses of taphocoenosis data (including abundances and taphonomic preservational grades), primarily focusing on cluster analysis of communities and community network analyses. TaphonomeAnalyst integrated functions for importation, analysis, and visualization of taphocoenosis data. The design idea of the software is based on accumulating a substantial volume of OTU cooccurrence data from fossil sampling plots that enable researchers to delineate species coexistence networks and discern various environmental zones.

Although Taphonome Analyst has core functions such as parsing ancient networks and determining aquatic environments of entombed lacustrine communities, a principal limitation of original version of TaphonomeAnalyst is its inability to explore the linkage between ecological variables and community structure, which substantially affected its research value. To address this constraint, we have developed an advanced iteration, TaphonomeAnalyst 2.0, designed to expand the spectrum of ecological insights that can be derived from taphonomic data. This updated version incorporates several enhancements (Fig. 1; Fig. 2; Table 1):

(1) Integrating operational taxonomic unit OTU) abundance with geochemical data for joint

analysis.

- (2) Adding capacity for deducing synergies between biological differences and multiple geochemical factors.
 - (3) Adding visualized co-occurrence networks from different environmental settings.

Module	Function	1.0	2.0
Assessment of sampling effort and	Sobs	√	√
estimation of theoretical maximum	Chao1	√	√
biodiversity (Module I)	ACE	1	1
Relative abundance of OTU analysis		√	√
(Module II)			
Proportion of taphonomic		√	√
preservational grade of species			
analysis (Module III)		,	,
Taphonomic environment analysis	Includes creation of Venn diagrams	√	√
(Module IV)	that compare the diversity found		
	across sedimentary environments or		
	outcrops.		
Visualization of geochemical data		×	√
(Module V)			
Assembling dissimilarity-		×	√
environmental distance test (Module			
VI)			
Mantel Test between species		×	
abundance and ecological			
environmental variables (Module VII)			
Species correlation semi-matrix		√	
graphics (Module Ⅷ)			
Correlational Network Visualization	SparCC coefficient	×	√
(Module IX)	Pearson's coefficient	1	√
	Spearman's coefficient	√	√
	Kendall's rank coefficient	1	√
Comparison of networks (Module $\mathrm{X})$	Comparison of networks with different	×	
	groups of sampling plots. Visualization		
	of total nodes, total linked nodes, total		
	edges, density, modularity,		
	complexity, degree, and robustness.		

Comparison of functions of the two TaphonomeAnalyst versions.

Operating guide

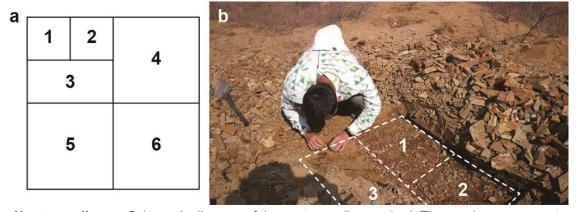
The basic idea of the software

We deem it important to explain the rationale behind naming our software TaphonomeAnalyst and to identify its research focus. Our work has been deeply inspired by the concept of the "microbiome" (Berg et al., 2020; Dhariwal, 2017). Initially, the principal emphasis in microbial ecology research was often placed on microbial communities, which are aggregations of microorganisms that coexist in a shared environment (Berg et al., 2020). Due to the small size of microorganisms and distinctive reproductive configurations, microorganisms can easily be used in research settings by their various life attributes. Consequently, microbial communities are prone to hosting a multitude of transient visitors (Berg et al., 2020). These itinerants typically occur at low abundances and lack ecological functionality. In 1988, Whipps and his colleagues conceptualized the term "microbiome" as a fusion of "micro" and "biome" and designated a "characteristic microbial community" within a "reasonably well-defined habitat which has distinct physio-chemical properties" as its "theatre of activity" (Berg et al., 2020; Whipps et al., 1988). The microbiome is an abstract concept derived from robust statistical analyses of microbial community data at the technical level and the removal of many accidental visitors. For a microbiome, also named an "abstract characteristic microbial community", the species co-occurrences and functions within such an assemblage notably are discernible and can exhibit considerable responsiveness to shifts in environmental conditions. Paralleling the definition of a microbial community, the term "taphocoenosis" encompasses an assemblage that includes a mixture of indigenous organisms living in or near water and transient visitors transported from somewhere else. At this juncture, we can successfully define the taphonome in ecology as characterized by fossil communities in which component function and co-occurrence can be observed and distributed within a certain range of geochemical factors. The taphonome includes a wide variety of species from aquatic to nearshore areas, with the possible exception of the largest predators, whose fossilized remains typically are fragmented and scarce. In ecology, this characteristic community has functional status; in stratigraphy, it has a stable geochemical context within a consistent sedimentary environment.

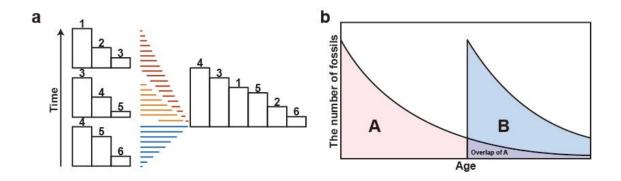
Data input

Palaeoecological research that involves vertical samples that stratally deviate on the scale of millimeters is uncommon and may lack significance. The majority of palaeoecological datasets are derived from talus or float specimens that typically consist of several centimeters of deposition that represent thousands of years. For most non-catastrophic depositional environments, samples from strata several centimeters thick might represent a span of thousands of years. Nevertheless, in paleoecological research, it is difficult to allocate a precise assessment time to the burial of organisms. This is understandable given that most fossil assemblages are subject to time-averaging that result from the mixing of remains from different communities over time (Dhariwal et al., 2017; Wing et al., 1992; Karr and Clapham,

2015; Wright et al., 2003). As a result, fossils occurring within the same stratum might have died and been buried at various points in time. (Fig. 3 a,b) The ecological significance of a taphocoenosis influenced by time (and space) averaging remains a topic of debate (Dhariwal. et al., 2017; Karr and Clapham, 2015; Wing et al., 1992; Wright et al., 2003). However, the prevailing view suggests that a taphocoenosis can either reflect a community under average environmental conditions or constitute a taphonomically altered sum of a community resulting from a particular habitat over some interval of time (Dhariwal et al., 2017; Wing et al., 1992; Karr and Clapham, 2015; Wright et al., 2003). Olszewski (2003) calculated that even if two layers overlap 50% of the time, that the differences between them would still be distinguishable. The taphonome also refers to the characteristic assemblage of organisms that range from aquatic bodies to nearshore areas. Based on this hypothesis, as long as the sedimentary environment of the sample layer is consistent and conformable, it can be suitable for taphonomic studies. This consistency implies that the characteristic bio-abundance and geochemical data are stable, allowing for meaningful analyses.



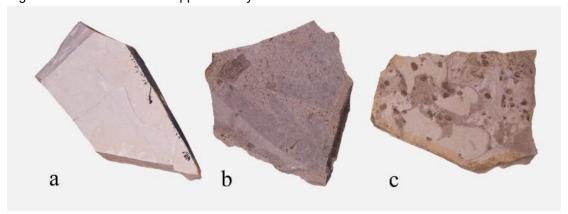
Nest sampling. a, Schematic diagram of the nest sampling method. The numbers represent the steps of plots excavation. **b**, a fieldwork of Nest sampling.



Impact of time-averaging on the relative abundance of species. a Time-averaging under a variable sedimentary environment (cited in Fürsich and Aberhan, 1990). The bars depict the numerical abundances of species 1 through 6. The fossil assemblages in the three different environments are mixed together after fossils have formed. Observations indicate that although the three assemblages become intermingled following time averaging, they exhibit negative quantitative correlations with one another. Statistical methods can be used to separate the three combinations. **b**, Overlap in time between two assemblage distributions

(Thomas Olszewski, 1999).

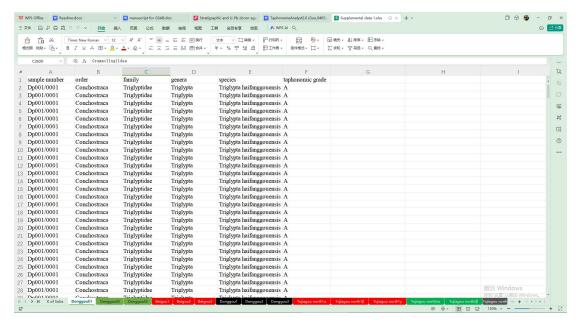
TaphonomeAnalyst 2.0 draws its data from fossil tables and the geochemical abundances in sampled layers. The fossil plots were excavated using the nest sampling methods. All animal fossils were collected and identified. We suggest using operational taxonomic units (OTUs) at all taxonomic levels, instead of Linnean binomial names. An OTU typically represents a species-level taxon that is recognized and morphologically characterized but may not be formally described with a Linnean binomial. Such terminology streamlines ecological research by allowing analysis prior to the formal taxonomic description of the taxon in question. Using OTUs is a more annotated and convenient approach; for instance, Orthophlebiidae gen. sp1. Some taxa, such as holometabolous insects involve immatures and adults of the same species that often have large differences in values of indices characterizing their habitats and morphological functions in the community. Users should mark immatures with "(I)" after the scientific name to differentiate the immatures from the adults. The format of the sample register form is detailed in Supplementary Material 2.



Fossil samples. All fossil samples should be collected from the same stratigraphic layer without significant changes in the depositional environment within, to ensure stable geochemical data, such as specimens a—c above.

The recommended output format is PDF, which is more suitable for editing vector elements.

```
parent_parser = argparse.ArgumentParser(add_help=False)
parent_parser.add_argument('--input', type=str, required=True, help='Absolute or relative path file.(e.g. "./data.xlsx")')
parent_parser.add_argument('--format', type=str, default='png', choices=['png', 'svg', 'pdf'], help='Output format.(default: %(default)s)')
parser = argparse.ArgumentParser(description='A comprehensive visual software for study taphonome.')
parser.add_argument('-v', '--version', action='version', version='TaphonomeAnalyst 2.0')
subparsers = parser.add_subparsers(help='commands')
```



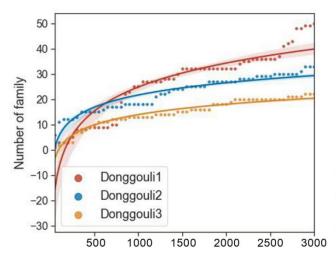
OTU identification form. Each Sheet represents a sampled plot. Sample number refers to the unique identification number assigned to a fossil specimen. When multiple animal individuals are present on a flagstone, each individual specimen should be documented separately by entering their details on each line. When identifying specimens, those that cannot be identified should be recorded as "unknown" in the corresponding biological classification category.

Assessment of sampling effort and estimation of theoretical maximum biodiversity (Module $\, { m I} \,)$

This module has the capability to employ logarithmic curves for assessing sampling efforts and estimating the theoretical maximum biodiversity. It encompasses use of the Sobs, Chao1, and ACE (abundance coverage estimator) indices (Chao and Yang, 1993; Chao, 1984, 1992, 1993). In the field of lacustrine taphocoenosis research, it is often observed that the abundance of dominant aquatic species far exceeds that of terrestrial species, sometimes by several orders of magnitude. This disparity arises because terrestrial organisms had a much lower probability of fossilization when transported to a water body (Chao and Yang, 1993; Chao, 1984, 1992, 1993). Therefore, we recommend that users use Chao1 or ACE methods whenever possible to evaluate the sample coverage, as these methods are more sensitive to rare species.

 S_{obs} is the direct observational diversity, is suited to evaluate the coverage of sampling in strata where aquatic species do not have a significant advantage. During the sampling process, some Daohugou samples could contain over 2000 T. haifanggouensi individuals among 3000 total individuals. In contrast, many terrestrial OTUs only have a few individuals. The Sobs curve may tend to flatten out when the number of samples is few, but sample location may still have significant role in potential diversity. Chao1 is sensitive to OTUs of only one individual, making it more suitable for plots where aquatic species dominate. The abundance coverage estimator considers a wider range of rare species and makes corrections for the coefficient of variation and sample coverage, which is more reasonable. Nonetheless, due to the difference between the buried community and the present-day community, the

definition of the abundance of rare species needs to be considered.



A presents a visualization of Sampling Coverage curves. Users have the discretion to determine how many samples should be taken for a change in each step of diversity.

The Chao 1 estimator is:

Chao1=
$$S_{obs} + \frac{F_1 (F_1-1)}{2(F_2+1)}$$

 S_{obs} : the direct observational diversity; F_1 : the number of OTUs whose abundance is one; and F_2 : the number of OTUs whose abundance is two.

The ACE estimator is:

$$S_{ace} = S_{abund} + \frac{S_{rare}}{C_{ace}} + \frac{F_1}{C_{ace}} \gamma_{ace}^2$$

 S_{abund} : the count of abundant OTUs that typically includes those exceeding a rarity threshold-often set at 10 individuals. However, in our experience with fieldwork, a threshold of 10 individuals may be excessive. Our software allows the user to set the rare species threshold when all samples are pooled. S_{rare} : the number of rare OTUs (with less than or equal to rare threshold individuals) when all samples are pooled; C_{ace} : the sample abundance coverage estimator; F_1 : the number of OTUs whose abundance is one. γ_{ace}^2 : the estimated coefficient of variation for rare OTUs, which is

$$\gamma_{\text{ace}}^2 = max \left[\frac{S_{rare}}{C_{ace}} \frac{\sum_{i=1}^{10} i(i-1)F_I}{(N_{rare})(N_{rare-1})} - 1, 0 \right]$$

Users have the flexibility to set the taxonomic level used for plotting sampling curves, with the default set at the family rank. Alternative options include order, family, genus, and species ranks.

Sobs

 $sample curve_parser = subparsers.add_parser(name='sample curve', parents=[parent_parser], \\ help='Sampling coverage curve. (Module I) tresplot]') \\ sample curve_parser.add_argument('--level', type=str, default='family', choices=['order', 'family', 'genera', 'species'], help='Taxonomic level.(default: %(default)s)') \\$

```
samplecurve_parser.add_argument('--groups', type=str2dictlist, required=True, help='Grouping plots (Sheet names) with customized names.\t[e.g. "plotA:plotA1/plotA2,plotB:plotB1/plotB2"]') samplecurve_parser.add_argument('--output', type=str, default='./samplecurve', help='Absolute path or relative path and filename.(default: %(default)s)') samplecurve_parser.set_defaults(func=samplecurve)
```

Command line:

python TaphonomeAnalyst2.py samplecurve --input ./Supplementary material2.xlsx --level 'family' --groups

'plot1:plot1-1/plot1-2/plot1-3,plot2:plot2-1/plot2-2/plot2-3,plot3:plot3-1/plot3-2/plot3-3'

Chao1

```
chao_parser = subparsers.add_parser(name='chao', parents=[parent_parser], help='Chao1 potential diversity curve. (Module I )\t[regplot]') chao_parser.add_argument('--level', type=str, default='family', choices=['order', 'family', 'genera', 'species'], help='Taxonomic level.(default: %(default)s)') chao_parser.add_argument('--groups', typedissenvtest = str2dictlist, required=True, help='Grouping plots (Sheet names) with customized names.\t[e.g. "plotA:plotA1/plotA2,plotB:plotB1/plotB2"]') chao_parser.add_argument('--output', type=str, default='./chao', help='Absolute path or relative path and filename.(default: %(default)s)') chao_parser.set_defaults(func=chao)
```

Command line:

python TaphonomeAnalyst2.py chao --input ./Supplementary material2.xlsx --level 'family' --groups 'plot1:plot1-1/plot1-2/plot1-3,plot2:plot2-1/plot2-2/plot2-3,plot3:plot3-1/plot3-2/plot3-3'

Ace: In the field of microbial ecology, the default abundance threshold for rare species is set below ten. However, this value may be overestimated. It is recommended that users make adjustments accordingly and provide explanations in their studies.

```
ace_parser = subparsers.add_parser(name='ace', parents=[parent_parser], help='ACE potential diversity curve. (Module I )\t[regplot]') ace_parser.add_argument('--level', type=str, default='family', choices=['order', 'family', 'genera', 'species'], help='Taxonomic level.(default: %(default)s)') ace_parser.add_argument('--groups', type=str2dictlist, required=True, help='Grouping plots (Sheet names) with customized names.\t[e.g. "plotA:plotA1/plotA2,plotB:plotB1/plotB2"]') ace_parser.add_argument('--output', type=str, default='./ace', help='Absolute path or relative path and filename.(default: %(default)s)') ace_parser.add_argument('--rare', type=int, default=10, help='ACE rare threshold.(default: %(default)s)') ace_parser.set_defaults (func=ace)
```

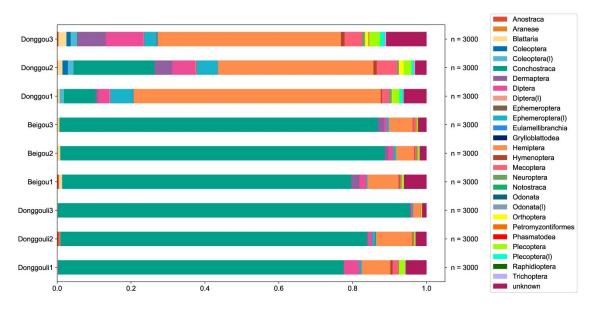
Command line:

python TaphonomeAnalyst2.py ace --input ./Supplementary material2.xlsx --level 'family' --groups 'plot1:plot1-1/plot1-2/plot1-3,plot2:plot2-1/plot2-2/plot2-3,plot3:plot3-1/plot3-2/plot3-3'

--rare 10

Relative abundance of OTU analysis (Module II)

This module facilitates the generation of bar graphs that illustrate species abundances. Given that the abundance of fossils does not reliably indicate the actual diversity of the original community, the relative abundance suggested by an OTU should be regarded as an imperfect measure (McNamara et al., 2012; Smith and Moe-Hoffman, 2007; Wang et al., 2019). The representation of species within a taphocoenosis, or fossil assemblage, is influenced by factors such as taxonomic unit investigated and physical size (Smith and Moe-Hoffman, 2007; McNamara et al., 2012). To some degree, these abundances can offer insights into the varying source distances and trophic levels of the species present in the fossil community.



Compositional proportion of the Yanliao Fauna by taxa from the sampled plots. The taxon rank is the order.

Users have the flexibility to set the taxonomic level.

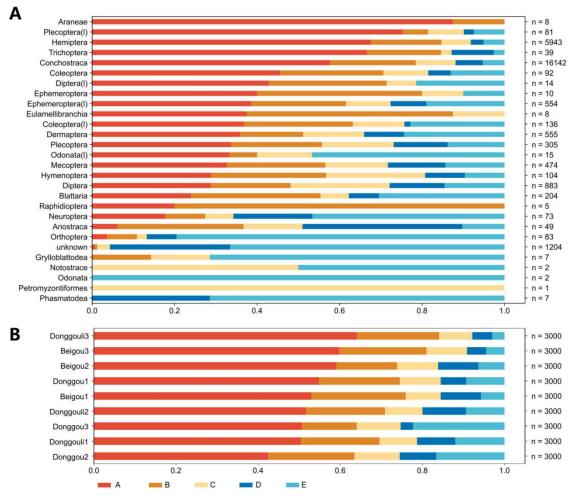
```
abundplots_parser = subparsers.add_parser(name='abundplots', parents=[parent_parser], help='Abundance-sampling plots. (Module II )\t[barh]')
abundplots_parser.add_argument('--level', type=str, default='order', choices=['order', 'family', 'genera', 'species'], help='Taxonomic level.(default: %(default)s)')
abundplots_parser.add_argument('--output', type=str, default='./abundplots', help='Absolute path or relative path and filename.(default: %(default)s)')
abundplots_parser.set_defaults(func=abundplots)
```

Command line:

python TaphonomeAnalyst2.py abundplots --input ./Supplementary material2.xlsx --level 'order'

Proportion of taphonomic preservational grade of species analysis (Module III)

The taphonomic grade module evaluates the preservational quality of fossils, as reflected by their structural integrity and joint articulations (Guo, Ma and Tang, 2023). The taphonomic grade is categorized into five levels, ranging from A to E, where A represents the best preservation and E indicates the poorest (Guo, Ma and Tang, 2023). This module offers taphonomic grade bar graphs for various taxa. The taphonomic grade module assesses the preservational quality of the fossils based on their structural integrity, such as the extent of intact articulations of joints visible in the fossil. The taphonomic grade also can be used to interpret the distance between the original habitat and its eventual deposition into lake sediment. Although influenced by factors such as the robustness of body parts, particularly appendages, and body size, this method is extensively employed in taphonomic analyses. Users have the option to choose the level of classification for taxa.



Proportion of taphonomic grades. Taphonomy Analyst 2.0 offers the capability to selectively output the preservation levels of different OTUs (Operational Taxonomic Units) or the varying degrees of preservation across different sample plots. **A**, Proportion of taphonomic grades (A–E) by taxa. **B**, Proportion of taphonomic grades (A–E) by the sampling plot.

Proportion of taphonomic grades (A–E) of the taxa. Users need to set the taxonomic level themselves.

```
TGotus_parser = subparsers.add_parser(name='TGotus', parents=[parent_parser],
help='Taphonomic grades-taxa. (Module III)\t[barh]')
TGotus_parser.add_argument('--level', type=str, default='order', choices=['order', 'family',
'genera', 'species'], help='Taxonomic level.(default: %(default)s)')
TGotus_parser.add_argument('--output', type=str, default='./TGotus', help='Absolute path or
relative path and filename.(default: %(default)s)')
TGotus_parser.set_defaults(func=TGotus)
```

Command line:

python TaphonomeAnalyst2.py TGotus --input ./Supplementary material2.xlsx --level 'order'

Proportion of taphonomic grades (A–E) by sampling plot. Users need to set the taxonomic level themselves.

```
TGplots_parser = subparsers.add_parser(name='TGplots', parents=[parent_parser], help='Taphonomic grades-sampling plots (in customized order). (Module III)\t[barh]')
TGplots_parser.add_argument('--groups', type=str2list, default=None, help='Environment groups.(Recommend to group the plots by different aquatic and terrestrial environments)\t[e.g. "plotA1/plotB2,plotB1/plotA2,plotC1/plotC2"]')
TGplots_parser.add_argument('--output', type=str, default='./TGplots', help='Absolute path or relative path and filename.(default: %(default)s)')
TGplots_parser.set_defaults(func=TGplots)
```

Command line:

Default sort

python TaphonomeAnalyst2.py TGplots --input ./Supplementary material2.xlsx

Custom sort

python TaphonomeAnalyst2.py TGplots --input ./Supplementary material2.xlsx --groups 'plot3-3/plot3-1/plot3-2,plot1-1/plot2-2/plot2-1/plot2-3/plot1-2/plot1-3'

Grade	Clam shrimps	Other arthropods	Vertebrates
A B	Shell edge > 90% pre served. growth bands are fully clear. Shell edge > 70% pre served. growth bands	> 90% preserved. Body arti-cula ted, wing veins visible and alm ost complete. 80–90% preserved. Body almost complete, including head, thora	Body and limbs are c omplete and articulat ed. 70–80% torso and lim bs are complete. Parti
	are almost clear.	x, abdomen and thoracic appen dages, details such as antennae or cerci lost.	al joint displacement.
С	Shell edge > 60% pre served. growth band a re partially clear.	60–80% preserved. Body defor med, at least one of six legs lost.	60–70% torso preser ved.
D	Shell edge >50% pres erved.	30–60% preserved. Wings disart iculated, remains of head, thorax and abdomen preserved	Torso with missing tail or head.
E	Shell fragments	< 30% preserved. High disarticul ated body, isolated structures su ch as single legs, abdomen and/ or wings preserved.	Scattered bones.



Definition of taphonomic grades. The taphonomic grade categorizes the preservational quality of fossils into five levels, ranging from A to E. Level A signifies the highest quality of preservation, whereas level E denotes the poorest quality of preservation

Taphonomic environment analysis (Module IV)

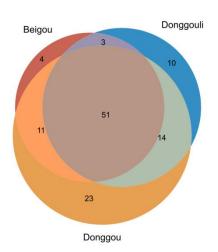
The primary aim of this module is to contrast and display the variations in species abundance across different sampling plots, and subsequently categorizing these samples into distinct groups. Since aquatic organisms typically undergo minimal transport during fossilization, their populations remain relatively stable, offering a robust reflection of the environmental conditions at the time of fossil deposition. The hierarchical clustering is calculated after a filter threshold is set at an individual count greater than 5. Hierarchical clustering is performed using the average linkage method and Bray-Curtis distance metric, which are commonly employed in biodiversity studies. We suggest that users conduct a joint analysis by integrating environmental clustering, species distribution, and geochemical heatmap collages. By integrating geochemical heat maps, users can clearly discern the distribution of aquatic OTU abundances across different clusters, as well as associated differences in environmental factors. Additionally, the module generates Venn diagrams that illustrate the differences in diversity within different taphonomic environments.

An average assign is:

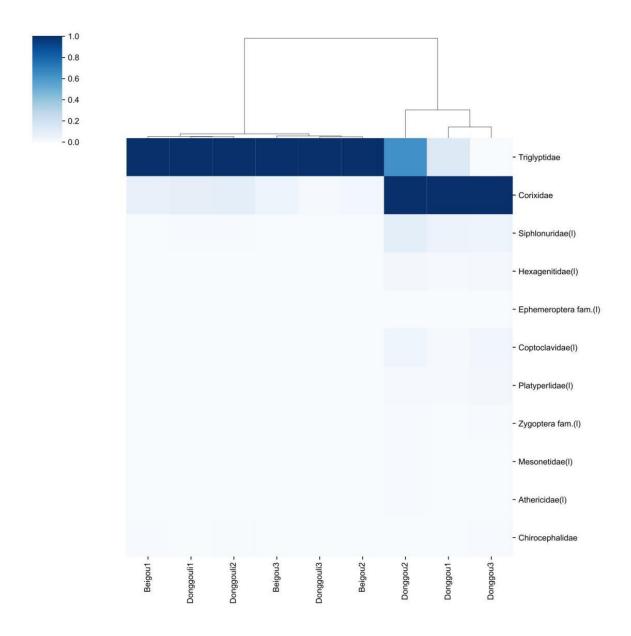
$$d_{(u,v)} = \sum_{ij} \frac{d(u[i],v[j])}{(|u|*|v|)}$$

And the Bray-Curtis distance is:

$$d_{(u,v)} = \frac{\sum_{i} |u_i - v_i|}{\sum_{i} |u_i + v_i|}.$$



This module also provides Venn maps that compare biodiversity in different sedimentary environments and outcrops.



Diversity and abundance comparisons of different plots and sedimentary environments.

Hierarchical clustering is shown of nine sampling plots of sedimentary environments. The plots were clustered based on aquatic taxonomic abundance (n > 5) using the average assigns clustering method and Bray-Curtis distance metric. The clustering results show that the sedimentary environments can be divided into three types. The color of the heat map indicates the normalized abundance of biological distribution.

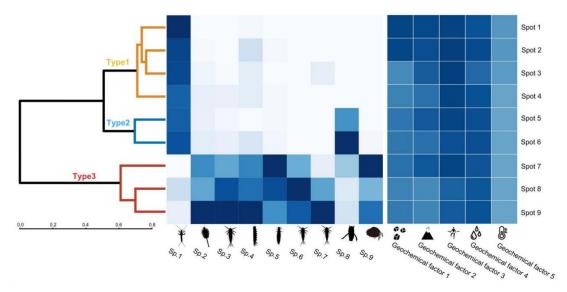
Visualization of geochemical data (Module V)

The environmental variables that shaped ancient ecosystems are not directly measurable and often necessitate the extrapolation of geochemical data for accurate interpretation. The ratios of elements and oxides have been widely used in ancient environmental studies to gain insights into salinity, temperature, water depth, humidity, intensity of volcanic activities, and other factors (Bai et al., 2020; Chen, Wan, 1999; Chen et al., 1999; Feng et al., 2003; Hou et al.,

2018; Hou et al., 2023; Fu et al., 2018; Harnois,1988; Nesbitt, Young, 1982; McLennan, 1993; Stanistreet et al., 2020; Swain et al., 2022; Wang et al., 2023; Yang et al., 2022; Zhou and Sun, 2023). Beyond serving as final resting grounds for fossilized remains, ancient water bodies act as primary archives for geochemical information, frequently encapsulating environmental contexts crucial to the majority of terrestrial organisms inhabiting aquatic habitats to littoral zones. This module provides a geochemical heat map of different sampling plots. This figure can be automatically combined with the sedimentary environment cluster tree and the distribution heat map of aquatic organisms. It can simultaneously reflect the distribution of biological and geochemical factors in different environmental groups.

sample number	Geochemical factor1	Geochemical factor	2 Geochemical faGeochemical factor4	Geochemical factor5
plot1-1	0.050277585	2.085012087	6.381 8.215891304	12.25805475
plot1-2	0.044962642	1.88177864	6. 57 8. 253242777	7.625969722
plot1-3	0.120648387	6.602077869	6. 248 8. 267124956	8. 960424791
plot2-1	0.309145015	8.565605513	12.865 21.71957373	8.620356037
plot2-2	0.091410129	3.985073903	7. 279 7. 309533891	19.81483572
plot2-3	0.06083691	5.582370985	7. 774 8. 112493614	1.450443191
plot3-1	0.131808667	3.084634553	10. 252 10. 18660248	12.08372541
plot3-2	0.066304692	4. 216297844	6. 252 7. 634473194	13.09164963
plot3-3	0.10304122	2.507430481	15. 457 14. 42240219	2.46604432

Style of geochemical tables. See Supplementary material3 for details



Integrative visualization based on OTUs abundance and geochemical data. This module can be automatically combined with the sedimentary environment cluster tree and the distribution heat map of aquatic organisms. It can simultaneously reflect the distribution of biological and geochemical factors in different environmental groups.

Module ${\rm IV}$ and ${\rm V}$ were integrated together. If geochemical data is not available, only the clustering tree and abundance heatmap will be generated. A list of aquatic OTUs is required for this step. The taxonomic level of aquatic OTUs must correspond your research.

```
clusterenv_parser = subparsers.add_parser(name='clusterenv', parents=[parent_parser], help='Hierarchical clustering-sedimentary environment. (Module IV and V)\t[clustermap]') clusterenv_parser.add_argument('--level', type=str, required=True, choices=['order', 'family', 'genera', 'species'], help='Taxonomic level.(For both statistical and aquatic OTUs.)') clusterenv_parser.add_argument('--aquatic', type=str2list, default=None, help='Aquatic OTUs.(default: all OTUs)\t[e.g. "OTU1,OTU2,OTU3"]') clusterenv_parser.add_argument('--geochem', type=str, required=False, help='Absolute or relative path geochemical file.(e.g. "./geochem.xlsx")') clusterenv_parser.add_argument('--output', type=str, default='./clusterenv', help='Absolute path or relative path and filename.(default: %(default)s)') clusterenv_parser.set_defaults(func=clusterenv)
```

Command line:

python TaphonomeAnalyst2.py clusterenv --input ./Supplementary material2.xlsx --aquatic 'Daohugounectes primitinus(I),Triglypta haifanggouensis,Triglypta haifanggouensis,Yanliaocorixa chinensis,Karataviella popovi,Samarura gigantea(I),Anisoptera fam. gen. sp1.(I),Platyperla platypoda(I),Ferganoconcha sibirica,Qiyia jurassica(I),Mesomyzon sp1.,Triops sp1.,Chirocephalidae gen. sp1.,Eurythoracalis mirabilis(I),Shantous lacustris(I),Foliomimus latus(I),Furvoneta viriosus(I),Furvoneta raucus(I),Mesobaetis sibirica(I),Clavineta eximia(I)' --geochem './Supplementary material3.xlsx' --level 'species'

Command line:

python TaphonomeAnalyst2.py mantel --input ./Supplementary material2.xlsx --rhome 'C:\Program Files\R\R-4.3.2' --geochem './Supplementary material3.xlsx' --aquatic 'Daohugounectes primitinus(I),Triglypta haifanggouensis,Triglypta haifanggouensis,Yanliaocorixa chinensis,Karataviella popovi,Samarura gigantea(I),Anisoptera fam. gen. sp1.(I),Platyperla platypoda(I),Ferganoconcha sibirica,Qiyia jurassica(I),Mesomyzon sp1.,Triops sp1.,Chirocephalidae gen. sp1.,Eurythoracalis mirabilis(I),Shantous lacustris(I),Foliomimus latus(I),Furvoneta viriosus(I),Furvoneta raucus(I),Mesobaetis sibirica(I),Clavineta eximia(I)' --level_aquatic 'species' --level_terrestrial 'family' --corr 'pearson'

Venn diagrams that show differences in biodiversity across various sedimentary environments or outcrops. Users need to define the taxonomic levels and plots groupings.

```
divvenn_parser = subparsers.add_parser(name='divvenn', parents=[parent_parser], help='Venn diagram-sampling locations or environments. (Module IV)\t[venn]') divvenn_parser.add_argument('--level', type=str, default='family', choices=['order', 'family', 'genera', 'species'], help='Taxonomic level.(default: %(default)s)') divvenn_parser.add_argument('--groups', type=str2list, required=True, help='Custom')
```

 $\label{lem:comment} Groups. (Recommend to group the plots by environments or locations) $$ t[e.g. "plotA1/plotB2,plotB1/plotA2,plotC1/plotC2"]') $$ divvenn_parser.add_argument('--output', type=str, default='./divvenn', help='Absolute path or the plots by environments or locations). $$ t[e.g. "plotA1/plotB2,plotB1/plotA2,plotC1/plotC2"]' $$ divvenn_parser.add_argument('--output', type=str, default='./divvenn', help='Absolute path or locations). $$ t[e.g. "plotA1/plotB2,plotB1/plotA2,plotC1/plotC2"]' $$ divvenn_parser.add_argument('--output', type=str, default='./divvenn', help='Absolute path or locations). $$ t[e.g. "plotA1/plotB2,plotB1/plotA2,plotC1/plotC2"]' $$ t[e.g. "plotA1/plotB2,plotB1/plotA2,plotC1/plotC2"]' $$ t[e.g. "plotA1/plotB2,plotB1/plotA2,plotC1/plotC2"]' $$ t[e.g. "plotA1/plotB2,plotB1/plotA2,plotC1/plotC2"]' $$ t[e.g. "plotB1/plotA2,plotC1/plotC2"]' $$ t[e.g. "plotB1/plotA2,plotB1/plotA2,plotC1/plotC2"]' $$ t[e.g. "plotB1/plotA2,plotC1/plotC2"]' $$ t[e.g. "plotB1/plotA2,plotB1/plotA2,plotC1/plotC2"]' $$ t[e.g. "plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotC1/plotC2"]' $$ t[e.g. "plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1/plotA2,plotB1$

relative path and filename.(default: %(default)s)')

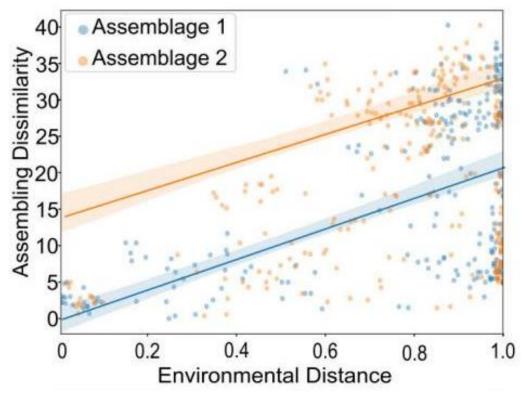
divvenn parser.set defaults(func=divvenn)

Command line:

python TaphonomeAnalyst2.py divvenn --input ./Supplementary material2.xlsx --groups 'plot3-3/plot3-1/plot3-2,plot1-1/plot2-2/plot2-1/plot2-3/plot1-2/plot1-3' --level 'family'

Assembling dissimilarity – environmental distance test (Module VI)

Assemblage similarities were quantified using the Bray-Curtis distance metric derived from various sampling plots, whereas environmental distance was determined by employing an Euclidean distance matrix based on measured geochemical variables. This module quantifies the responses of aquatic and terrestrial community components to changes in environmental factors. In this statistical graph, the greater the slope of pronounced differentiation among the biological abundance, the more pronounced is the differentiation among the biological assemblages in response to changes in environmental factors.



Assembling dissimilarity - environmental distance test. The slope of the line indicates the degree of abrupt environmental changes corresponding to the assemblage.

A list of aquatic OTUs is required for this step. The list aquatic OTUs taxonomic level must correspond your research.

dissenvtest_parser = subparsers.add_parser(name='dissenvtest', parents=[parent_parser],

```
help='Assembling dissimilarity- environmental distance test. (Module VI)\t[regplot]') dissenvtest_parser.add_argument('--geochem', type=str, required=True, help='Absolute or relative path geochemical file.(e.g. "./geochem.xlsx")') dissenvtest_parser.add_argument('--aquatic', type=str2list, required=True, help='Aquatic OTUs.\t[e.g. "OTU1,OTU2,OTU3"]') dissenvtest_parser.add_argument('--level_aquatic', type=str, required=True, choices=['order', 'family', 'genera', 'species'], help="Taxonomic level for aquatic OTUs.") dissenvtest_parser.add_argument('--level_terrestrial', type=str, required=True, choices=['order', 'family', 'genera', 'species'], help="Taxonomic level for terrestrial OTUs.") dissenvtest_parser.add_argument('--output', type=str, default='./dissenvtest', help='Absolute path or relative path and filename.(default: %(default)s)') dissenvtest_parser.set_defaults(func=dissenvtest)
```

Command line:

python TaphonomeAnalyst2.py dissenvtest --input ./Supplementary material2.xlsx --aquatic 'Daohugounectes primitinus(I),Triglypta haifanggouensis,Triglypta haifanggouensis,Yanliaocorixa chinensis,Karataviella popovi,Samarura gigantea(I),Anisoptera fam. gen. sp1.(I),Platyperla platypoda(I),Ferganoconcha sibirica,Qiyia jurassica(I),Mesomyzon sp1.,Triops sp1.,Chirocephalidae gen. sp1.,Eurythoracalis mirabilis(I),Shantous lacustris(I),Foliomimus latus(I),Furvoneta viriosus(I),Furvoneta raucus(I),Mesobaetis sibirica(I),Clavineta eximia(I)' --level_aquatic 'species' --level_terrestrial 'family' --geochem './Supplementary material3.xlsx'

Mantel Test between species abundance and ecological environmental variables (Module VII)

In 1967, Nathan Mantel revolutionized statistical analysis by proposing the Mantel Test. This method advanced beyond the constraints of traditional correlation coefficients, which then were only equipped to analyze pairwise relationships among variables within a single data matrix. The Mantel Test broke new ground by facilitating the assessment of correlations between two distinct matrices.

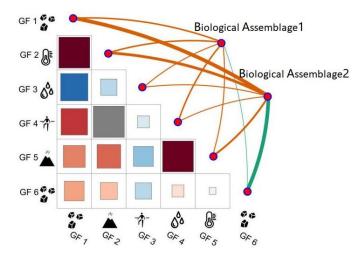
Since its inception, the Mantel Test has been integral to understanding the rapid evolution and application across diverse scientific domains, notably in microbial community ecology. In the realm of paleoecology, the Mantel Test serves as an invaluable tool for probing the connections between geochemical factors and fluctuations in biological abundance. To quantify similarities in species assemblages, the Bray-Curtis dissimilarity metric is commonly employed and is derived from comparative data gathered from various sampling plots. Concurrently, the environmental distances are defined using a Euclidean distance matrix predicated on quantified geochemical variables.

The Bray-Curtis distance is:

$$d_{(u,v)} = \frac{\sum_{i} |u_i - v_i|}{\sum_{i} |u_i + v_i|}$$

And the Euclidean distance is:

$$d = \sqrt{\sum_{i=1}^{n} (x_i - y_i)^2}$$



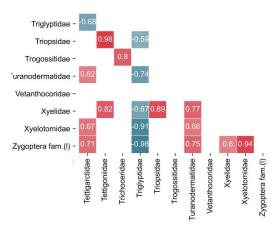
Mantel test between environmental factors and palaeocommunity composition. The strength of the correlation is represented by the partial Mantel's r statistic, with line width indicating the magnitude of the correlation and line color denoting statistical significance. Pairwise comparisons of environmental factors were also conducted, with a color gradient representing the strength of the Pearson correlation.

Here, it is necessary to set the taxonomic level used for quantifying assemblage differences. A list of aquatic OTUs is required for this step. The list of aquatic OTUs taxonomic level must correspond to your research.

```
mantel parser = subparsers.add parser(name='mantel', parents=[parent parser],
help='Mantel Test between species abundance and ecological environmental variables.
(Module VII)\t[multiplot]')
mantel_parser.add_argument('--rhome', type=str, required=True, help='Absolute path of
R HOME.(e.g. "C:\Program Files\R\R-4.3.2")')
mantel parser.add argument('--geochem', type=str, required=True, help='Absolute or relative
path geochemical file.(e.g. "./geochem.xlsx")')
mantel parser.add argument('--aquatic', type=str2list, required=True, help='Aquatic
OTUs.\t[e.g. "OTU1,OTU2,OTU3"]')
mantel parser.add argument('--level aquatic', type=str, required=True, choices=['order',
'family', 'genera', 'species'], help="Taxonomic level for aquatic OTUs.")
mantel parser.add argument('--level terrestrial', type=str, required=True, choices=['order',
'family', 'genera', 'species'], help="Taxonomic level for terrestrial OTUs.")
mantel_parser.add_argument('--corr', type=str, default='pearson', choices=['pearson',
'spearman', 'kendall'], help='Correlation algorithm for geochem.(default: %(default)s)')
mantel_parser.add_argument('--output', type=str, default='./mantel', help='Absolute path or
relative path and filename.(default: %(default)s)')
mantel parser.set defaults(func=mantel)
```

Species correlation semi-matrix graphics (Module Ⅷ)

The module for species correlation analysis aims to uncover possible interactions among fossil species, which are indicative of symbiotic relationships. TaphonomeAnalyst 2.0 offers a variety of techniques to compute correlations and to generate semi-matrix graphics, including Pearson's, Spearman's, Kendall' s rank, and SparCC correlation coefficients.



Semi-matrix of taphonomy correlations among organisms (a part of an entire figure).

Red indicates a positive correlation, blue a negative correlation. Missing cells are due to filtering of data with insufficient significance levels. Users can adjust the intensity of data filtering as needed.

Here the user is required to enter the taxonomic rank, correlation type and intensity, and P-value.

```
corrotus_parser = subparsers.add_parser(name='corrotus', parents=[parent_parser], help='Heatmap-OTUs correlation analysis. (Module VIII)\t[heatmap]')
corrotus_parser.add_argument('--level', type=str, default='family', choices=['order', 'family', 'genera', 'species'], help='Taxonomic level.(default: %(default)s)')
corrotus_parser.add_argument('--corr', type=str, default='pearson', choices=['pearson', 'spearman', 'kendall', 'sparcc'], help='Correlation algorithm.(default: %(default)s)')
corrotus_parser.add_argument('--p_value', type=float, default=0.1, help='Maximum threshold of p-value.(default: %(default)s)')
corrotus_parser.add_argument('--output', type=str, default='./corrotus', help='Absolute path or relative path and filename.(default: %(default)s)')
corrotus_parser.set_defaults(func=corrotus)
```

Command line:

python TaphonomeAnalyst2.py corrotus --input ./Supplementary material2.xlsx --level 'family' --corr 'pearson' --p_value 0.1

Correlational Network Visualization (Module IX)

IX.1 Overview

If you encounter any issues, please feel free to reach out to Wang Ma(马旺) (wma19952022@163.com).

A network characterized by nodes and links, is a composition of both elements. In such a network, the nodes symbolize taxa found within sampling plots, while the edges represent the taphonomic co-occurrences among these taxa. Animals inhabiting the same microenvironment also demonstrate co-occurrence during the process of fossilization. Therefore, the phenomenon of taphonomic co-occurrence partly can be explained by the extent of habitat overlap between two taxa. In constructing the network, two crucial considerations must be addressed: the methodology for correlation calculation and division of network modules.

IX.2 Correlation

Module links include various correlation methods, such as Pearson 's correlation, Spearman's rank correlation, Kendall's rank correlation, and SparCC (Sparse Correlations for Compositional data) coefficients for network visualization. It also enables users to define their own filters, including correlation strength and P-values.

The most widely employed method in microbial research is SparCC correlation coefficient, which is a computational method designed to identify correlations between specifications within a community by analyzing sequential data. SparCC does not use variance as a direct measure of correlation, but instead adopts a more complex method to estimate the correlation between species with sparse data. SparCC improves the estimation of correlation between microbial abundances by log-transforming the observed abundance data and using the variance of log ratios to correct for biases. The method also employs a bootstrap procedure to calculate P-values, allowing for assessment of the statistical significance of the correlations. However, its performance is constrained when computing interaction networks for high dimensional datasets. Typically, microbial network studies require a minimum of 3000 samples within the total dataset, with a OTUs diversity not exceeding 800.

SparCC is based on the log-ratio transformation:

$$y_{ij}\text{=}log\frac{x_i}{x_i}\text{=}log_{x_i}\text{-}log_{x_j}$$

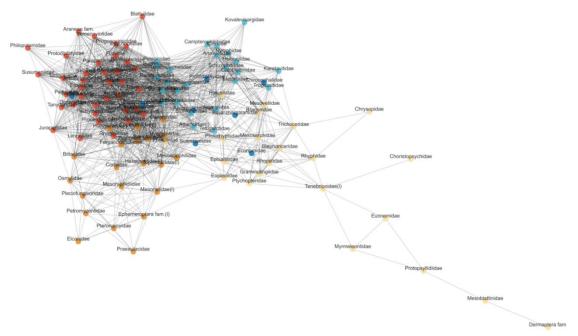
 x_i : the fraction of OTU i. x_i : the fraction of OTU j.

Aitchison proposed using the quantity where the variance is taken across all samples to describe the dependencies in a compositional dataset.

$$t_{ij} = Var[\frac{x_i}{x_i}] = Var[y_{ij}]$$

When OUT i and j are absolutely correlated and their ratio is constant, consequently t_{ij} =0 $t_{ii}=w_i^2+w_i^2-2\rho_{ii}w_iw_i$

 w_i^2 , w_j^2 : The variances of the log-transformed basis abundances OUT i and j. ρ_{ij} : the correlation between them OUT i and j.



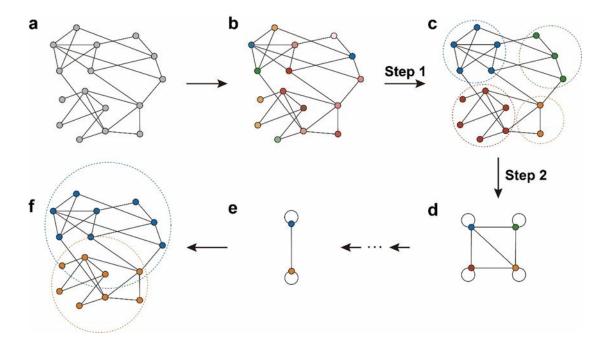
Network visualization. Points of the same color represent the same module, indicating that these organisms likely inhabit the same environment. The output image is in PDF format, allowing users to adjust the font size in a PDF editor to meet publishing requirements.

IX.3 Louvain algorithm

The Louvain algorithm identifies communities based on the concept of modularity. When there is a high density of connections within a module and a low density of connections between modules, the network exhibits high modularity as a result of this partitioning. The iteration process ceases automatically when there is no additional increase in modularity. Modularity $Q\subseteq [-0.5,1)$, and it can also be used to evaluate the effectiveness of network module division. The larger the value, the better the module division effect. When the modularity is between 0.3 and 0.7, it indicates that the clustering effect is very good. The formula for modularity is:

$$Q = \frac{1}{2m} \sum_{\nu\omega} \left[A_{\nu\omega} - \frac{k_{\nu}k_{\omega}}{2m} \right] \delta(c_{\nu}, c_{\omega})$$

m: indicates the total number of connections of all nodes. υ and ω : two nodes in the network. $A_{\upsilon\omega}$ =0, if υ and ω are not linked. $A_{\upsilon\omega}$ =1, if υ and ω are linked. k_{υ} = degree of the node υ . k_{ω} = degree of the node ω . $\delta(c_{\upsilon},c_{\omega})$ =0, if υ and ω are not linked. $\delta(c_{\upsilon},c_{\omega})$ =1, if υ and ω are not linked.



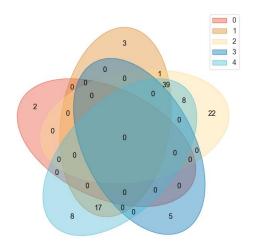
The operation procedure of Louvain algorithm.a, The network is constructed based on correlation matrix. b, c, Step one: Each node in the network is assigned to its individual module. The Louvain algorithm examines the increase in modularity if neighboring nodes of node u are assigned to the same module. If no increase in modularity results when neighboring nodes joined, then node- neighboring nodes remains in their original module. This procedure is repeatedly carried out until no further enhancement in modularity can be achieved by altering the community assignments of any nodes, at which point the first phase is concluded. c, d, Step two: After algorithm divides the modules in the first round, each module is merged into a large self-looping node. and its weight is the sum of the link weights of all nodes in the original module. The newly merged nodes 's weight is the sum of the link weights of all nodes in the original module. d, e, The subsequent calculation method is the same as step one. f, The final output of the resulting graph.

The Louvain algorithm consists of two steps. In step one each node in the network is assigned to its individual module. Then the Louvain algorithm examines the increase in modularity if neighboring nodes of node υ are assigned to the same module. If there is no increase in modularity when neighboring nodes are joined (i.e., the gain in modularity is zero or negative), then node-neighboring nodes remain in their original module. This procedure is repeatedly carried out until no further enhancement in modularity can be achieved by altering the community assignments of any nodes, at which point the first phase ends. Step two: After the algorithm divides the modules in the first round, each module is merged into a large self-looping node. and its weight is the sum of the link weights of all nodes in the original module. The newly merged nodes 's weight is the sum of the link weights of all nodes in the original module. The subsequent calculation method is the same as the step one. The increase in community modularity can be computed using following formula:

If you encounter any issues, please feel free to reach out to Wang Ma(马旺) (wma19952022@163.com).

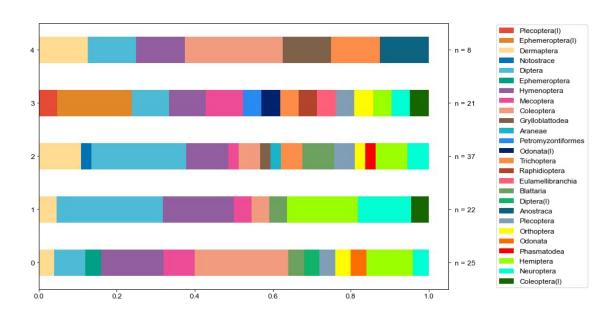
$$\Delta Q = \left[\frac{\sum in + k_{\upsilon,in}}{2m} - \left(\frac{\sum tot + k_{\upsilon}}{2m} \right)^2 \right] - \left[\frac{\sum in}{2m} - \left(\frac{\sum tot}{2m} \right)^2 - \left(\frac{k_{\upsilon}}{2m} \right)^2 \right]$$

 \sum in: the sum of the weights of all links in same module. \sum tot: the sum of the weights of all links that are external to the module. k_i : the sum of weights of node υ . $k_{i,in}$:the sum of weights between node υ to the module where node υ are tried moved.



Veen map of biodiversity between different output modules is output with the network.

The diversity and intersections of different modules in the network can be viewed.



A histogram of the biodiversity for each module is output with the network.

Users need to input the taxonomic level, types and strength conditions of correlations, and p-value conditions.

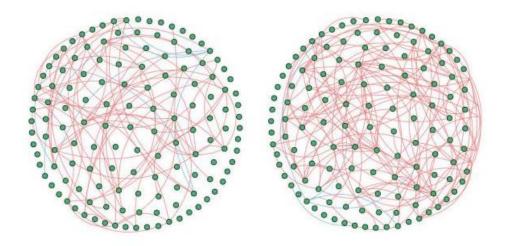
```
cooccurnet_parser = subparsers.add_parser(name='cooccurnet', parents=[parent_parser], help='Co-occurrence networks. (Module IX)\t[network]')
cooccurnet_parser.add_argument('--level', type=str, default='family', choices=['order', 'family', 'genera', 'species'], help='Taxonomic level.(default: %(default)s)')
cooccurnet_parser.add_argument('--corr', type=str, default='pearson', choices=['pearson', 'spearman', 'kendall', 'sparcc'], help='Correlation algorithm.(default: %(default)s)')
cooccurnet_parser.add_argument('--corr_coef', type=float, default=0.7, help='Minimum threshold of correlation coefficient.(default: %(default)s)')
cooccurnet_parser.add_argument('--p_value', type=float, default=0.1, help='Maximum threshold of p-value.(default: %(default)s)')
cooccurnet_parser.add_argument('--output', type=str, default='./cooccurnet', help='Absolute path or relative path and filename.(default: %(default)s)')
cooccurnet_parser.set_defaults(func=cooccurnet)
```

Command line:

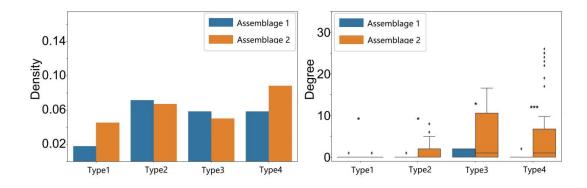
python TaphonomeAnalyst2.py cooccurnet --input ./Supplementary material2.xlsx --level 'family' --corr 'pearson' --corr_coef 0.7 --p_value 0.1

Comparison of networks (Module X)

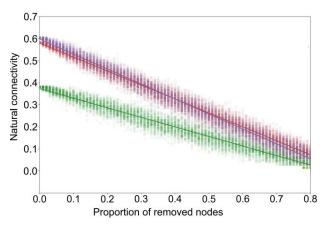
This module offers the capability to compare networks under different groups of sampling plots. The network set for comparison can be easy to read by using a consistent random layout. Additionally, it presents a bar chart that contrasts key network metrics such as total nodes, total linked nodes, total edges, density, modularity, complexity, degree and robustness.



The network set for comparison can be easy to read by using a consistent random layout. In this image, points at the same location within the network represent the same species. The network enables users to discern differences in community correlations by examining the number of linked points and the connection density of links.



The statistical graphs for total nodes, total linked density, modularity, total linked nodes, total edges, density, modularity, and complexity consist of bar charts.



The robustness analysis of the different assemblages. These colors represent two different network in different environments. Robustness is calculated by simulating the "extinction" of organisms within a community. It involves continuously and randomly removing nodes (species) and then observing the decrease in the number of connections within the community (co-ocurrence). Communities with high robustness experience a slower reduction in links when species are removed. Additionally, this function can also output the slope of the linear decline.

- (1) First, input the sample grouping; if not set, the default is the sedimentary environment clustering result.
- (2) Second, a list of aquatic OTUs is required for this step. The list aquatic OTUs and their taxonomic rank must correspond your research.
- (3) Third, users need to input the taxonomic rank, types and strength of conditions of correlations, and p-value conditions.

```
netVC_parser = subparsers.add_parser(name='netVC', parents=[parent_parser],
help='Generate a unified layout network for comparison. (Module
X )\t[network/boxplot/barplot]')
netVC_parser.add_argument('--aquatic', type=str2list, required=True, help='Aquatic
OTUs.\t[e.g. "OTU1,OTU2,OTU3"]')
netVC_parser.add_argument('--level_aquatic', type=str, required=True, choices=['order', 'family', 'genera', 'species'], help="Taxonomic level for aquatic OTUs.")
```

```
netVC_parser.add_argument('--level_terrestrial', type=str, required=True, choices=['order', 'family', 'genera', 'species'], help="Taxonomic level for terrestrial OTUs.")

netVC_parser.add_argument('--groups', type=str2list, required=True, help='Environment groups.(Grouping the plots by different aquatic and terrestrial environments)\t[e.g. "plotA1/plotB2,plotB1/plotA2,plotC1/plotC2"]')

netVC_parser.add_argument('--corr', type=str, default='pearson', choices=['pearson', 'spearman', 'kendall', 'sparcc'], help='Correlation algorithm.(default: %(default)s)')

netVC_parser.add_argument('--corr_coef', type=float, default=0.7, help='Minimum threshold of correlation coefficient.(default: %(default)s)')

netVC_parser.add_argument('--p_value', type=float, default=0.1, help='Maximum threshold of p-value.(default: %(default)s)')

netVC_parser.add_argument('--output', type=str, default='./netVC', help='Absolute path or relative path and filename.(default: %(default)s)')

netVC_parser.set_defaults(func=netVC)
```

Command line:

python TaphonomeAnalyst2.py netVC --input ./Supplementary material2.xlsx --aquatic 'Daohugounectes primitinus(I),Triglypta haifanggouensis,Triglypta haifanggouensis,Yanliaocorixa chinensis,Karataviella popovi,Samarura gigantea(I),Anisoptera fam. gen. sp1.(I),Platyperla platypoda(I),Ferganoconcha sibirica,Qiyia jurassica(I),Mesomyzon sp1.,Triops sp1.,Chirocephalidae gen. sp1.,Eurythoracalis mirabilis(I),Shantous lacustris(I),Foliomimus latus(I),Furvoneta viriosus(I),Furvoneta raucus(I),Mesobaetis sibirica(I),Clavineta eximia(I)' --level_aquatic 'species' --level_terrestrial 'family' --groups 'plot3-3/plot3-1/plot3-2,plot1-1/plot2-2/plot2-1/plot2-3/plot1-2/plot1-3' --corr 'spearman' --corr_coef 0.7 --p_value 0.01

Evaluation indicators	Significance in netology	Significance in ecology
Total nodes	All nodes present in the network, both connected and unconnected.	The diversity present in the sampling plots.
Total linked nodes	All connected nodes present in the network.	The diversity present clear co-ocurrence with other OTUs.
Total edges	All links present in the network.	Taphonomic co-currence. It can also reflect the symbiotic relationships among OTUs to a certain extent.
Density	The density of interconnecting edges between nodes in a network. $d(G) = \frac{2L}{N(N-1)}$ N: Total nodes. L: Total edges.	The complexity of symbiotic relationship.
Complexity	The complexity of the network. $C_i = \frac{d_i}{n}$ $d_i \text{: Degree of node i.}$ $n \text{: Total nodes.}$ $C_i \text{: Complexity of node i.}$	Community complexity.
Degree	The centrality and importance of network. $\deg\left(v\right) = \sum\nolimits_{u \in V,\ u \neq v} A_{uv}$ V: All the nodes in the network. A: A= 1 if there is an edge from node u to node v, otherwise A=0.	The importance of keystone species in communities
Modularity	The strength of a network divided into modules. A network with high modularity has dense connections between nodes within a module, but sparse connections between nodes in different modules.	The degree of differentiation of the community.
Robustness	Response of network links after nodes are randomly removed.	The ability of communities to resist environmental change

Evaluation indicators of the network.

Frequently Asked Questions

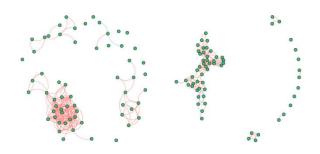
The error of identical OTUs being identified as two separate ones.

This is often caused by incorrect spacing after or in the scientific names of OTUs.

The proportion of taphonomic grades error

The primary reason for the inability to output images is that this module only accepts uppercase letters A through E. Careful proofreading during input is essential, and it is recommended to use Excel's statistical functions to eliminate incorrect data.

The network comparison error



The network comparison visualization may face challenges due to an overabundance of links. This plethora of connections complicates the software's ability to identify matching layouts. We suggest implementing the spearman correlation coefficient or imposing stricter correlation criteria to diminish the link count.

The geochemical heat map error

In geochemical data, the concentration of certain elements may be below the detection limit, which is generally written as BDL in the main text of the paper. However, in the geochemical tables used for calculations, numerical values must be entered. We have referred to some environmental science papers and suggest using half of the detection limit as such a value.

Future developments

TaphonomeAnalyst 2.0 is an ongoing project that will remain in a state of near-term development. The software is designed to keep pace with the ever-evolving field of geochemistry and taphonomy, ensuring that it remains current and relevant as the discipline

advances. To comprehensively grasp biological behaviors and interactions, it is essential to gather, integrate, and analyze multiple types of ecological data. Future advancements in TaphonomeAnalyst will be geared towards a more holistic analyses that encompass various forms of palaeoecological data, including functional morphology, herbivore arthropod and insect damage types, sporopollen taxa, and body size. The objective of TaphonomeAnalyst 3.0 is to facilitate the creation of multilayer ecological networks through the straightforward utilization of a diverse set of fossil community-level data.

Software Development Environment

The development environment is based on Python 3.8.8 and R 4.3.2, with the following third-party libraries used in Python: matplotlib, numpy, pandas, igraph, networkx, seaborn, scipy, community, skbio, h5py, numba, dask, venn, rpy2. The implementation of the SparCC algorithm originates from the micnet library. In R, the third-party libraries used include dplyr, linkET, and ggplot2.

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References

Allison, P.A., Briggs, D.E.G., 1991. Taphonomy of nonmineralized tissues in Taphonomy. Taphonomy: releasing the data locked in the fossil record. Springer. Press, pp. 25–70.

Bai, H., Kuang, H., Liu, Y., Peng, N., Chen, X., Wang, Y., 2020. Marinoan-aged red beds at Shennongjia, South China: Evidence against global-scale glaciation during the Cryogenian. Palaeogeogr. Palaeoclimatol. Palaeoecol. 559, 109967.

Berg, G., Rybakova, D., Fischer, D., Cernava, T., Vergès, M.C.C., Charles, T., Chen, X., Cocolin, L., Eversole, K., Corral, G.H., Kazou, M., Kinkel, L., Lange, L., Lima, N., Loy, A., Macklin, J.A., Maguin, E., Mauchline, T., McClure, R., Mitter, B., Ryan, M., Sarand, I., Smidt, H., Schelkle, B., Roume, H., Kiran, G.S., Selvin, J., Souza, R.S.C., Overbeek, L.V., Singh, B.K., Wagner, M., Walsh, A., Sessitsch, A., Schloter, M., 2020. Microbiome definition re-visited: old concepts and new challenges. Microbiome 8, 1–22.

https://doi.org/10.1186/s40168-020-00875-0

Blondel, V., Guillaume, J.L., Lambiotte, R., Lefebvre, E., 2008. Fast Unfolding of Communities in Large Networks. J. Stat. Mech.-Theory. E. P10008. https://doi.org/10.1088/1742-5468/2008/10/P10008.

Chao, A., 1984. Non-parametric estimation of the number of classes in a population. Scand. J. Stat. 11, 265–270.

Chao, A., Lee, S.M., 1992. Estimating the number of classes via sample coverage. J. Am. Stat. Assoc. 87 (417), 210–217.

Chao, A., Shen, T. J., 2004. Nonparametric prediction in species sampling. J. Agr. Biol. Envi. St. 9, 253–269.

Chao, A., Yang, M.C. K., 1993. Stopping rules and estimation for recapture debugging with unequal failure rates. Biometrika 80 (1), 193–201.

Chen, J., Wan, G., 1999. Sediment particle size distribution and its environmental significance in Lake Erhai, Yunnan province. Chin. J. Geochem. 18(4), 314–320.

Chen, J., Wan, G., Chen, Z., Huang, R., 1999. Chemical elements in sediments of Lake Erhai and palaeoclimate evoluton. Geochimica 28 (6), 562–570.

Dhariwal, A., Chong, J., Habib, S., King, I.L., Agellon, L.B., Xia, J., 2017. Microbiomeanalyst: a web-based tool for comprehensive statistical, visual and meta-analysis of microbiome data. Nucleic. Acids. Res. 45 (W1), W180–W188.

Feng, L., Chu, X., Zhang, Q., 2003. CIA (chemical index of alteration) and its applications in the Neoproterozoic clastic rocks. Earth Sci. Front. 10(4), 539–544.

Fu, J., Li, S., Xu, L., Niu, X., 2018. Paleo-sedimentary environmental restoration and its significance of Chang 7 Member of Triassic Yanchang Formation in Ordos Basin, NW China. Pet. Explor. Dev. 45(6), 998–1008.

Fürsich, F. T., Aberhan, M., 1990. Significance of time-averaging for palaeocommunity analysis. Lethaia 23, 143-152.

Guo, S., Ma, W., Tang, Y., Chen, L., Wang, Y., Cui, Y., Liang, J., Li, L., Zhuang, J., Gu, J., Li, M., Fang, H., Lin, X., Shih, C.K., Labandeira, C.C., Ren, D., 2023. A new method for examining the co-occurrence network of fossil assemblages. Commun. Biol. 6 (1), 1102. https://doi.org/10.1038/s42003-023-05417-6

Harnois, L., 1988. The C.I.W Index: a new chemical index of weathering. Sediment. Geol. 55 (3), 319–322.

Hou, Q., Jin, Q., Niu, C., Zhang, R., Chen, F., Xu, J., Zhang, F. J., 2018. Distribution characteristics and main controlling factors of main hydrocarbon sourcerocks in Liaodong bay area. Earth Sci. 43 (6), 2160–2171.

Karr, J., Clapham, M., 2015. Taphonomic biases in the insect fossil record: Shifts in articulation over geologic time. Paleobiology 41 (1), 16–32.

McLennan, S.M., 1993. Weathering and global denudation. J. Geol. 101 (2), 295–303.

McNamara, M.E., Briggs, D.E., Orr, P.J., 2012. The controls on the preservation of structural color in fossil insects. Palaios 27 (7), 443–454.

Muscente, A.D., Bykova, N., Boag, T.H., Buatois, L.A., Mángano, M.G., Eleish, A., Prabhu, A., Pan, F., Meyer, M.B., Schiffbauer, J.D., Fox, P., Hazen, R.M., Knoll, A.H., 2019. Ediacaran biozones identified with network analysis provide evidence for pulsed

extinctions of early complex life. Nat. Commun. 10 (1), 911.

Nesbitt, H.W., Young, G.M., 1982. Early Proterozoic climates and plate motions inferred from major element chemistry of lutites. Nature 299, 715–717. Palaeogeogr. Palaeoclimatol. Palaeoecol. 63 (1–3), 73–89.

Newman, M. E. J., 2006, Modularity and community structure in networks. Proc. Natl. Acad. Sci. 103 (23), 8577-8582.

Olszewski, T., 1999. Taking advantage of time-averaging. Paleobiology, 25(2), 226–238.

Smith, D.M., Moe-Hoffman, A.P., 2007. Taphonomy of Diptera in Lacustrine Environments: A Case Study from Florissant Fossil Beds, Colorado. Palaios 22 (6), 623–629.

Staff, G.M., Powell, E.N, 1998. The palaeoecological significance of diversity: the effect of time averaging and differential preservation on macroinvertebrate species richness in death assemblages.

Stanistreet, I.G., Boyle, J.F., Stollhofen, H., Deocampo, D.M., Deino, A., McHenry, L.J., Toth, N., Schick, K., Njau, J.K., 2020. Palaeosalinity and palaeoclimatic geochemical proxies (elements Ti, Mg, Al) vary with Milankovitch cyclicity (1.3 to 2.0 Ma), OGCP cores, Palaeolake Olduvai, Tanzania. Palaeogeogr. Palaeoclimatol. Palaeoecol. 546, 109656.

Swain, A., Maccracken, S.A., Fagan W.F., Labandeira, C.C., 2022. Understanding the ecology of plant-insect interactions in the fossil record through bipartite networks. Paleobiology 48 (2), 239–260.

Wang, S., Hethke, M., Wang, B., Tian, Q., Yang, Z., Jiang, B., 2019. High-resolution taphonomic and palaeoecological analyses of the Jurassic Yanliao Biota of the Daohugou area, northeastern China. Palaeogeogr. Palaeoclimatol. Palaeoecol. 530, 200–216.

Wang, Y., Xu, Z., Hang, L., Xing, T., Hang, W., 2023. Lycoptera Fossil Elemental Imaging and Paleoenvironmental Research via Laser Ionization Time-of-Flight Mass Spectrometry. At. Spectrosc. 44(2), 55–64.

Whipps, J.M., Lewis, K., Cooke, R.C., 1988. Mycoparasitism and plant disease control. Fungi in biological control systems. Manchester University Press, pp. 161–187.

Wing, S.L., Sues, H.D., Potts, R., DiMichele, W.A., Behrensmeyer, A.K., 1992. Evolutionary paleoecology. Terrestrial Ecosystems through Time: Evolutionary Paleoecology of Terrestrial Plants and Animals. The University of Chicago Press, pp. 1–13.

Wright, P., Cherns, L., Hodges, P., 2003. Missing mollusks: Field testing taphonomic loss in the Mesozoic through early large-scale aragonite dissolution. Geology 31 (3), 211–214.

Xu, H., Zhang, Y., Yuan, D., Shen, S., 2022. Quantitative palaeobiogeography of the Kungurian–Roadian brachiopod faunas in the Tethys: Implications of allometric drifting of Cimmerian blocks and opening of the Meso-Tethys Ocean. Palaeogeogr. Palaeoclimatol. Palaeoecol. 601, 111078.

Yang, S., Hu, W., Fan, J., Deng, Y., 2022. New geochemical identification fingerprints of volcanism during the Ordovician-Silurian transition and its implications for biological and environmental evolution, Earth-Sci. Rev. 228, 104016.

Zhou, X., Sun, L., 2023. Factors controlling the formation and evolution of source

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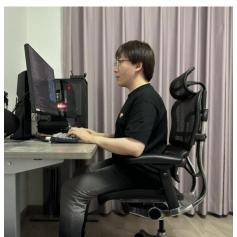
rocks in the Shahezi Formation, Xujiaweizi fault depression, Songliao Basin. Energy Geoscience 4(2), 100140.

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