

Species-abundance models for brachiopods across the Ordovician–Silurian boundary of South China

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Abstract. Species-abundance models have been an important method for investigating community structure in modern biology in the past decades. Different species-abundance models can reflect different ecological meanings. The method is relatively new to palaeoecology. We take the latest Ordovician–earliest Silurian *Cathaysiorthis* brachiopod fauna of South China as an example, program the calculation in the R language, introduce the application of the species-abundance models and discuss the relationship between the abundance model and the ecological bathymetry of a certain brachiopod fauna. Finally, we testify the validity of the method and suggest that the species-abundance models should be treated as one of the supporting evidences in investigating the brachiopod palaeoecology.

Key words: species-abundance models, palaeoecology, brachiopod, *Cathaysiorthis* fauna.

INTRODUCTION

Measuring the abundance of a species is a very important initial step in investigating the ecology of populations and communities (Begon et al. 2005). Since a community contains many species with a different proportion of the total specimen number, all species can be arranged on a spectrum of abundance which can be called ‘ranked species abundance’. The spectrum of relative abundance of the species is a key to understand the ecological traits of the community. The species-abundance models have been one of the crucial tools for investigating community structure in modern biology in the past decades, by which ecologists can describe species abundance distribution (Tokeshi 1993).

How do species-abundance relationships reflect the ecological traits of a community? If a community (or a collection) consists of species with similar resource requirements (indicating a similar niche), the process of niche apportionments for all species can be divided by certain rules (Tokeshi 1990). The key is that the division rules vary in different species-abundance models, so these models contain certain ecological meanings.

The species-abundance models are widely used in modern biology, however, very few related cases have been reported in palaeoecological studies (e.g. Driscoll & Swanson 1973). Since the method is relatively new to palaeontology and is promising in ecological study, here we discuss the application of species-abundance

models to the palaeoecological study using collections of the latest Ordovician–earliest Silurian *Cathaysiorthis* brachiopod fauna from South China (Rong & Zhan 2006; Huang 2008; Rong et al. 2008, 2013; Huang et al. 2010). After testing five widely used models, we evaluate abundance distribution across four different collections of the *Cathaysiorthis* fauna. By employing Akaike information criterion (AIC) values to test goodness-of-fit for these models, we try to investigate the relationship between the abundance model and the ecological bathymetry of a certain brachiopod fauna.

DATA AND METHOD

Data

The *Cathaysiorthis* fauna is a brachiopod-dominated shelly fauna from the uppermost Ordovician–lowermost Silurian of SE China, succeeding the cool-water *Hirnantia* Fauna (Rong et al. 2013). All the collections of this fauna contain four key samples that represent different palaeoecological associations of the fauna: (1) AFL30: 0.25 m thick, basal Shiyang Formation (lower Rhuddanian); (2) AFL68: 0.9 m thick, basal Shiyang Formation (lowest Rhuddanian: *Akidograptus ascensus* Biozone); (3) AFL161: 1.5 m thick, basal Anji Formation (lower Rhuddanian); (4) AFL303: 0.5 m thick, top Yuqian Formation (upper Hirnantian). It should be mentioned that, although the collection AFL303 is of

late Hirnantian age, the brachiopods from it are closely related to the other three samples. They are all assigned to the *Cathaysiorthis* fauna and represent brachiopods of the early survival interval after the end-Ordovician mass extinction (Rong et al. 2013).

These four samples yield nearly 5000 brachiopod specimens identifiable to more than 30 species. We analyse here the abundance data (see Rong et al. 2013, Table 1 for details) of these four collections and fit five different models.

Method

Species-abundance models have been studied for a long time. Since Motomura (1932) developed the geometric series model to describe the structure of an aquatic community, ecologists have built many models to fit species-abundance data derived from communities or collections. Species-abundance models can mainly be classified into empirical types and theoretical types. Empirical models are inferred only from statistical hypothesis, which places them under the category of ‘statistical models’. Empirical models include negative binomial distribution, log-series distribution, geometric distribution, lognormal distribution and so on. Empirical models can fit the abundance data of communities very well. However, due to statistical derivation of data, they can reveal very limited information about the ecological structure of communities (Tokeshi 1990; Wilson 1991). By realizing that ‘statistical models’ always have ambiguous ecological meaning, MacArthur (1957) developed the broken-stick model and the overlapping niche model on the basis of niche theory, which can be assigned to the theoretical types. Many more theoretical models have been developed since that time, such as preemption (geometric series), particulate niche, random assortment, random fraction, Zipf and Mandelbrot models.

In recent years, most ecologists have preferred theoretical models rather than empirical types to investigate the community structure. The broken stick, preemption, Zipf and Mandelbrot models have been most widely used. These four theoretical models were

also assigned to niche apportionment models, which are biological models used to explain relative species abundance distributions. As an empirical type, the lognormal distribution model is similar to the central limit theorem (one of the fundamental theorems of probability; May 1975) and thus attained its ecological meaning called ‘Hierarchical niche breakage’ (Sugihara 1980), which was adopted for comparison with the theoretical models.

To test the fitness of the models, the AIC is adopted here. Based on information entropy, which offers a relative estimate of the information lost when a given model is used to represent the process that generates the data, the AIC is a measure of the relative quality of a statistical model, for a given set of data (Akaike 1974). As such, the AIC provides a mean for model selection.

RESULTS

Using R project (version 3.0.3) within R-studio, calculations for abundance models and AIC values are programmed and performed. Three of the five models performed well in fitting into the species abundance patterns for the four collections (Table 1). The AIC values indicated that the Zipf model is best fitted for AFL30, Mandelbrot for AFL68 and preemption for AFL161 and AFL303. Fitting curves are shown in Fig. 1.

All of the Zipf, Mandelbrot and preemption models emphasize that the existence of a species depends on the environment and its precursor ascendent species. This may explain why the three models can fit both communities of forest and modern oceanic benthic faunas (Frontier 1985). Since all brachiopods feed with lophophores, the feeding strategies of different species are similar. The spectrum of brachiopod abundance is formed by the competition among brachiopods in different niches. Boucot (1975) discussed the relationship between the abundance of brachiopods and water depth when he initiated the concept of Benthic Assemblage (BA). Although abundance distribution is dependent on many

Table 1. Abundance, diversity, and AIC of the five models for the four collections; numbers in bold represent the model best fitted for the species-abundance relationship

Collection	Abundance (number of specimens)	Species diversity	AIC values				
			Broken- stick	Pre- emption	Zipf	Mandel- brot	Log- normal
AFL30	508	7	542.76	151.64	55.64	57.64	101.04
AFL68	2133	22	1049.83	163.13	506.59	157.80	284.11
AFL161	2064	31	1159.95	169.05	689.96	173.04	414.93
AFL303	195	24	117.40	89.81	135.61	93.50	115.07

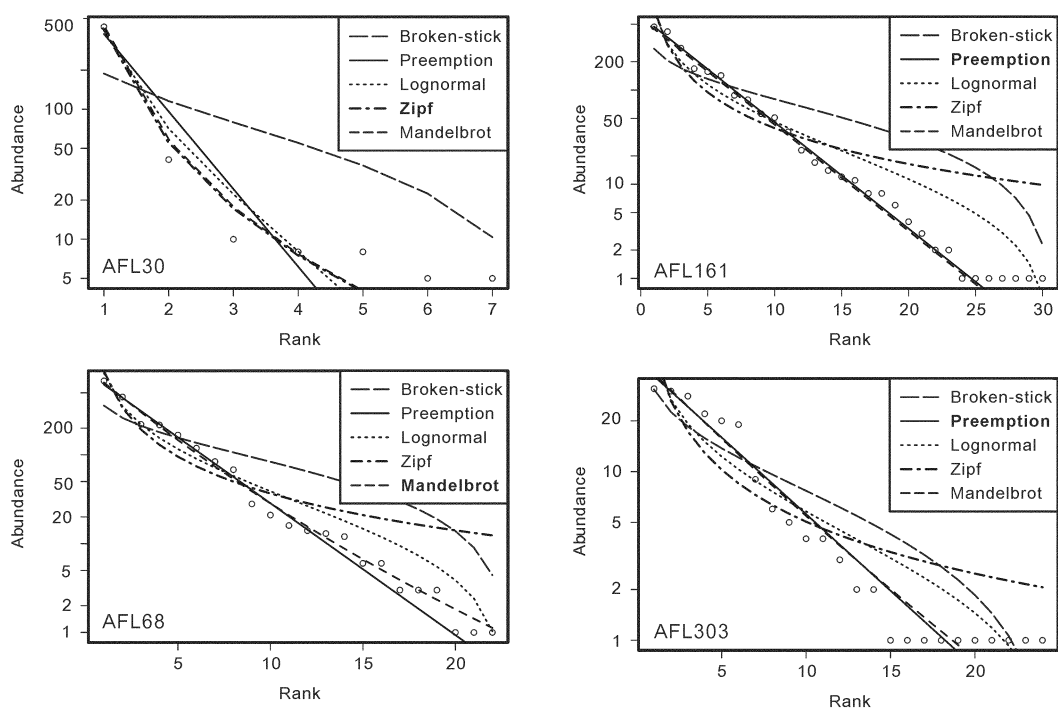


Fig. 1. Species-abundance distribution and fitting curves of five models for four collections of the *Cathaysiorthis* fauna of southeast China. Circles represent ranked abundance data; the best fit for each sample is shown by a bold curve.

factors, it has been proved to be closely correlated with ecological bathymetry (Dodd & Stanton 1990). That the four collections are most fitted in different models suggests that the function of each abundance model may be related to water depth.

Based on the ecological bathymetric indicator of brachiopods and trilobites, together with evidences from sedimentology, AFL30 is assigned to BA2, AFL68 and AFL161 are assigned to BA3 and AFL303 is assigned to BA4–5 (Rong et al. 2013). Except AFL161, the results from AIC suggest that the abundance models can differentiate water depth of habitats for the collections, which is consistent with the bathymetry suggested by previous studies. From shallow to deep water, the best-fitted abundance models change from Zipf, through Mandelbrot to preemption.

It should be noticed that the result for AFL161 may not fit that of the previous study. Rong et al. (2013) proposed a benthic environment of BA3 for AFL161, but the result of abundance model fitting suggests a deeper environment. On further inspection, compared with AFL68, AFL161 should be a deeper assemblage since it has a higher diversity and contains more deep-water indicators (e.g. *Skenidioides* and *Epitomyoina*) than the former. From the fitting model and the evidence above, the water depth of AFL161 is probably between BA3 and BA4, and better to be assigned to outer BA3 (Fig. 2).

The species-abundance models prompted the restudy for the association AFL161. It suggests that we can use the method to test the water depth of a brachiopod association. Moreover, after a few tests we found the methods with other models may be used to detect other ecological differences between brachiopod associations with similar bathymetric conditions, which will be discussed in another paper. However, due to the complexity of ecology of a brachiopod assemblage (e.g. unfavourable or variable living conditions), other evidences (e.g. information from geochemistry, sedimentology) should be adopted to help understand the palaeoecology of brachiopod associations.

CONCLUSION

Building species-abundance models is relatively new to palaeoecological study. After evaluation of abundance models across four different collections, we believe the method can be introduced to palaeoecological studies on brachiopod assemblages. As a numerical method, the species-abundance models should be treated as one of the supporting evidences together with ecological indicators and traits of sediments to investigate the brachiopod palaeoecology.

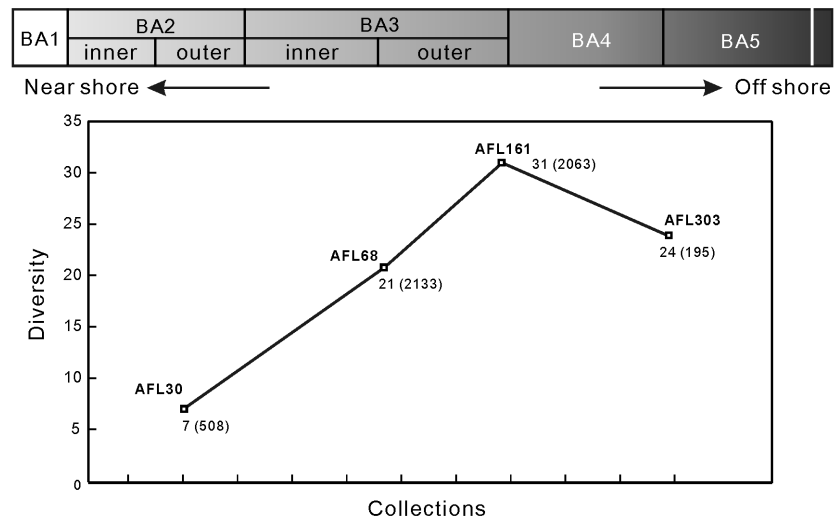


Fig. 2. Assignment of benthic assemblages (BA) of the four collections; the specimen number of the collections is indicated.

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