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Biological Trait Analysis (BTA): New method of analyzing foraminiferal data

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ABSTRACT

Biological Trait Analysis (BTA) is proven to be a useful technique in understanding environmental disturbance in foraminiferal paleoecology. BTA integrates three statistical techniques namely; fuzzy correspondence analysis (FCA), non-metric multi-dimensional scaling (nmMDS) and Similarity Percentage analysis (SIMPER). Variations in foraminiferal fauna and trait compositions were analysed using the technique and it provided a clearer understanding of ecological perturbations in foraminiferal ecology and the ecosystem functions they provided in the community when compared to existing techniques. This innovative technique was applied on foraminiferal population data in the Central Pacific Ocean, South Atlantic Ocean and the vestigial Tethys ocean during the extreme climatic warming event of the Paleocene - Eocene Thermal maximum (PETM). The outcome of our investigation showed a clear separation of foraminiferal traits and fauna compositions from different depths across three intervals of the warming namely; Pre-CIE, CIE and Recovery section. Samples from each group tend to cluster together with the warmest interval, the CIE showing highest level of separation. These separations are interpreted to correlate with extreme environmental conditions. BTA also has the capability of integrating and bringing out important variables from a large data sets and organizing them in a well-structured and more understandable manner.

Keywords: Foraminifera, Ocean, PETM, Traits, paleoecology

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INTRODUCTION

The Biological Trait Analysis (BTA) encompasses all the statistical method use by modern ecologists to study species distribution of macrobenthos, the biological characteristics they exhibit and the relationship behavioural characteristics (trait) to the functioning of their ecosystem (e.g. Bremner et al., 2005; 2006, Charvet et al., 2000; Paganelli et al., 2012; Caswell and Frid, 2017). BTA was initially designed for the study of anthropogenic impact on micro/macro organisms streams, rivers and other terrestrial water biological community but, currently it has been modified for optimal application across variety of ecosystems

including the marine (Caswell and Frid, 2013). Previous applications of biological trait analysis in modern ecosystem (see Charvet et al., 2000; Statzner et al., 2001; Hausner et al., 2003, Bremner et al., 2005; Bremner 2008; Shojaei et al., 2015 and Costello et al., 2015) have shown that the method is capable of distinguishing regional changes across geographical boundaries, provided that the relevant traits of organisms under study were carefully selected and studied in large scales. This publication shows how biological trait analysis (BTA) has been modified and adopted to study the fossil foraminifera traits and fauna composition across the Paleocene - Eocene Thermal Maximum (PETM) with a view to understand if disturbances in the ecology could be detected using the method. Biological Trait Analysis involves the integration of multivariate ordination method in examining the changes biological trait of the organism of study. Fuzzy Correspondence Analysis (FCA), non-metric multi-dimensional scaling (nmMDS) and Similarity percentage analysis (SIMPER) are the key multivariate ordination techniques used in BTA for palaeoecological studies. Fuzzy correspondence analysis (FCA) is multivariate statistical method that uses a parametric linear ordination and Eigen analysis to investigate complex quantitative data set with differences between samples in terms of foraminifers' traits and faunal composition exhibited by species in the foraminiferal assemblages as well as weighted by their abundance. It provides a more distinctive understanding of relationships between categories by ranking the parameters. Non-metric multi-dimensional scaling is a powerful multivariate statistical tool that allows for robust visualization relation between high-dimensional data sets particularly when ordinal or non-linear relationships are involved. It produces an ordination based on a distance or dissimilarity matrix and uses visual representation to reveal subtle patterns and structures in the data. Similarity Percentage Analysis (SIMPER) is a technique used for breaking down and understanding the percentage contribution of individual taxa/trait or other variables to the similarity and dissimilarity in the whole data. It highlights the factors driving ecological and the highest to the lowest contribution (see table 3). Foraminiferal traits selected for this research are key ones known to provide important ecosystem functions. For instance, foraminifera test function as a shield for protecting the organism when alive. It also controls physical, chemical and biological stress in foraminiferal ecology (Armstrong and Brasier 2005). There is a strong relationship between the test shape foraminifera life habit/adaptation and ecological preference. Example, spiral test is closely linked to epifaunal habitat (Corliss, 1998), some of the taxa have trochospiral test with plano-convex shells and large pores (e.g. *Gavelinella ammonoides*). Taxa correlated to shallow infauna community tend to be elongate in shape with uniserial to triserial chamber arrangement and occasionally planispiral coiling,

Nodosariidae or Buliminidae are good examples. Taxa associated with deep in fauna foraminiferal community usually have ovate to triserial test shape. They are characterised by species with imperforate test such as *Oolina globos*, *Tapanina selmensis* etc. The composition of foraminiferal test could also indicate variation in the ambient environmental chemistry and composition. Foraminifera chamber arrangement as well as the shape of the chamber have been linked to factors like ecological stress, for instance if a species changes its coiling from sinistral to dextral or evolute to involute and vice versa are indication of change in water temperature and bathymetry (Boltovskoy et al., 1991). Traits like ornamentation in foraminifera have some significance in their feeding strategy, adaptation to changes in environmental condition and relationship with other organisms living in the same community. It is also a great adaptation for escaping from predators. The form of apertures, the presence of accessory structures and their primary position vary with change in environmental condition. For instance *Haynesina germanica* have well developed ornamentation, apertural accessories and tubercle at optimum water temperature and chemical conditions, but these features are poorly developed in species found in extreme environmental conditions (Dubicka et al. 2015). The perforations of foraminiferal tests are critical functional feature of the organism. Foraminiferal pores are used for nutrient intake, osmoregulation, gas exchange, excretion and ecosymbiosis species with large perforations occur in a well oxygenated environment and those with microperforation are common in oxygen deprived environment (Jorissen et al., 2007). In some species foraminifera secretes an organic adhesive which helps the organism to attach to hard substrate in the environment.

MATERIALS AND METHODS

Foraminiferal specimen preparation followed the conventional preparation procedures (Nwojiji et al., 2023). The focus on this section is on Biological Trait Analysis workflow. Thirteen foraminiferal traits have been identified to be useful for this study namely; test shape, test composition, chamber arrangement, chamber shape, ornamentation, nature of aperture (form, accessory, structure & position), test perforation, life habit, feeding habit and mobility (see table 1). The thirteen foraminiferal traits were subdivided in sub-traits referred to as categories (table 1). These categories were further classified into subcategories and known as modalities. For example, the trait ‘test shape’ is classified into five modalities namely; spiral, elongate, globose, tubular, subquadrate, etc. These categorization does not completely exhaust all the trait categories but it does select the important modalities that are;

crucial in the species of interest. The selected traits are believed to be related to the main ecological functions rendered by foraminifera in their ecosystem.

Table 1: Foraminiferal traits and resultant modalities used in this study

Traits	Modalities
A. Test Shape	A1. Spiral, A2. Elongate, A3. Globose, A4. Subquadrate, A5. Others
B. Test Composition	B1. Hyaline calcite, B2. Hyaline aragonite, B3. Porcellanous, B3. Agglutinated
C. Chamber arrangement	C1. Uniserial, C2. Bi/Tri-serial, C3. Planispiral, C4. Trochospiral, C5. Other
D. Chamber shape	D1. Spherical/Oval, D2. Tubular, D3. Triangular or trapezoidal, D4. Semi-circular, D5. Others
E. Macro ornamentation	E1. Depressed sutures, E2. Raised sutures, E3. Keeled sutures, E4. Others
F. Test micro-ornamentation	F1. No ornament, F2. Reticulate, F3. Hispid, F4. Spinose F5. Striate,
G. Aperture form	G 1. Oval/reniform, G2. Arcuate, G3. Cribrate/Radiate, G4. Slit-like, E5. Others
H. Aperture accessory structures	H1. Lips, H2. Bifid teeth, H3. Umbilical teeth, H4. Neck, H5. None
I. Primary aperture position	I1. Terminal, I2. Basal interiomarginal, I3. Umbilical, I4 Extra-umbilical, I5. Areal
J. Test perforation	J1. Microperforation, J2. Fine perforation, J3. Macro-perforation, J4. No perforation
K. Life habit	K1. Surface dweller, K2. Intermediate dwellers, K3. Deep water dwellers K4. Others
L. Feeding habit	L1. Grazer, L2. Suspension feeder, L3. Deposit feeder, L4. Symbionts, L5. Others
M. Mobility	M1. Sessile, M2. Clinging, M3. Free-living, M4. Others

The technique used to express the affinity of a particular modality to the associated trait of a foraminiferal species is the Fuzzy coding method; it is expressed on a scale of 0.0–1.0. The absence of an affinity for any trait selected above is denoted with 0 whereas 1 is used to code a species that expressed high level of affinity to the trait under consideration (Table 2). This

coding technique can allow for species to be coded with decimal values depending on their level of affinity but all the summation of all the modalities must be equal to 1.

DATA ANALYSIS

Matrix multiplication was applied in the trait modality coding and taxa abundance to get the frequency of each trait modality in the datasets. The trait modality scores was cross multiplied by the abundance count of each species exhibiting those modalities across the samples (see supplementary data; Charvet et al., 1998; Caswell and Frid, 2013). Statistical analyses of both taxonomic abundance and trait distribution were carried out using the PRIMER v. 6 (PRIMER-e, Plymouth, UK). Prior to the quantitative analysis, data were subdivided into three sections to correspond to the stages in PETM events, pre-carbon isotope event (pre-CIE, Carbon Isotope Event (CIE) and recovery intervals. The pre-analysis treatment of the samples required standardization of the species data by transforming the data with $\text{Log}(x+1)$ to reduce the influence of dominant taxa/species on the overall result. The similarities of both species and biological traits between samples were calculated using Bray-Curtis index to create resemblance matrices (Clarke, 1993). The Non-metric multidimensional scaling (nmMDS) ordination technique was used to visualize the similarities/differences in species and trait distribution between the different periods of the PETM. Species/taxa composition and biological trait data were compared using Analysis of Similarity (ANOSIM), and subsequently the similarity percentages (SIMPER) routine to identify which taxa or traits that were responsible for the most differences identified from the ANOSIM across the PETM.

RESULTS AND DISCUSSION

This new technique of using the BTA to analyse foraminifera in paleo-record was applied in fossil foraminifera from the Central pacific Ocean, South Atlantic Ocean and the Tethys sea during the extreme environmental period of PETM. Our results showed that the BTA could be used to decipher and interpret ecological community disturbance in the in the ocean using foraminifera. The evidence of ecological disturbance was shown in nNMDS ordination plots presented below (Figure 1- 9). The clustering of the analysed samples in ordination chart showed that the Pre-CIE, CIE and Recovery of the PETM sections clustered separately, while the sample at the peak of the PETM (CIE) that experienced the most environmental perturbation tend to always be the most scattered. ANOSIM values from the three studied

locations indicated that the three PETM groups significantly differed from each other with global $R = 0.581 - 0.693$ and $p < 0.01$ (Nwojiji et al., 2023)

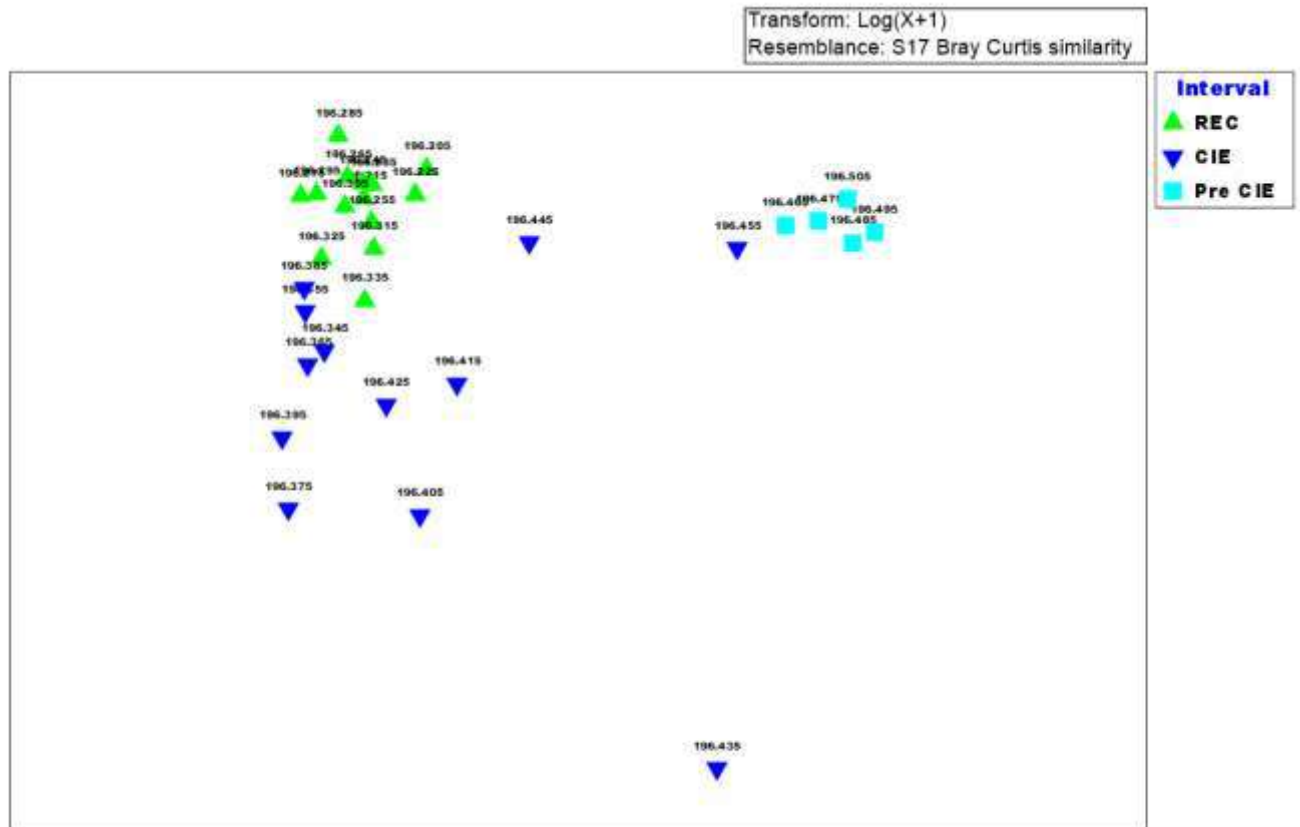


Figure 1: Sample ordination of foraminiferal species count (transformed with log x+1) using Bray-Curtis similarity from ODP Site 1209B in the Pacific Ocean. The samples are grouped into three intervals depicting the PETM sections. Sample 196.435 represents core of the PETM and the period of Benthic foraminiferal extinction event (BEE).

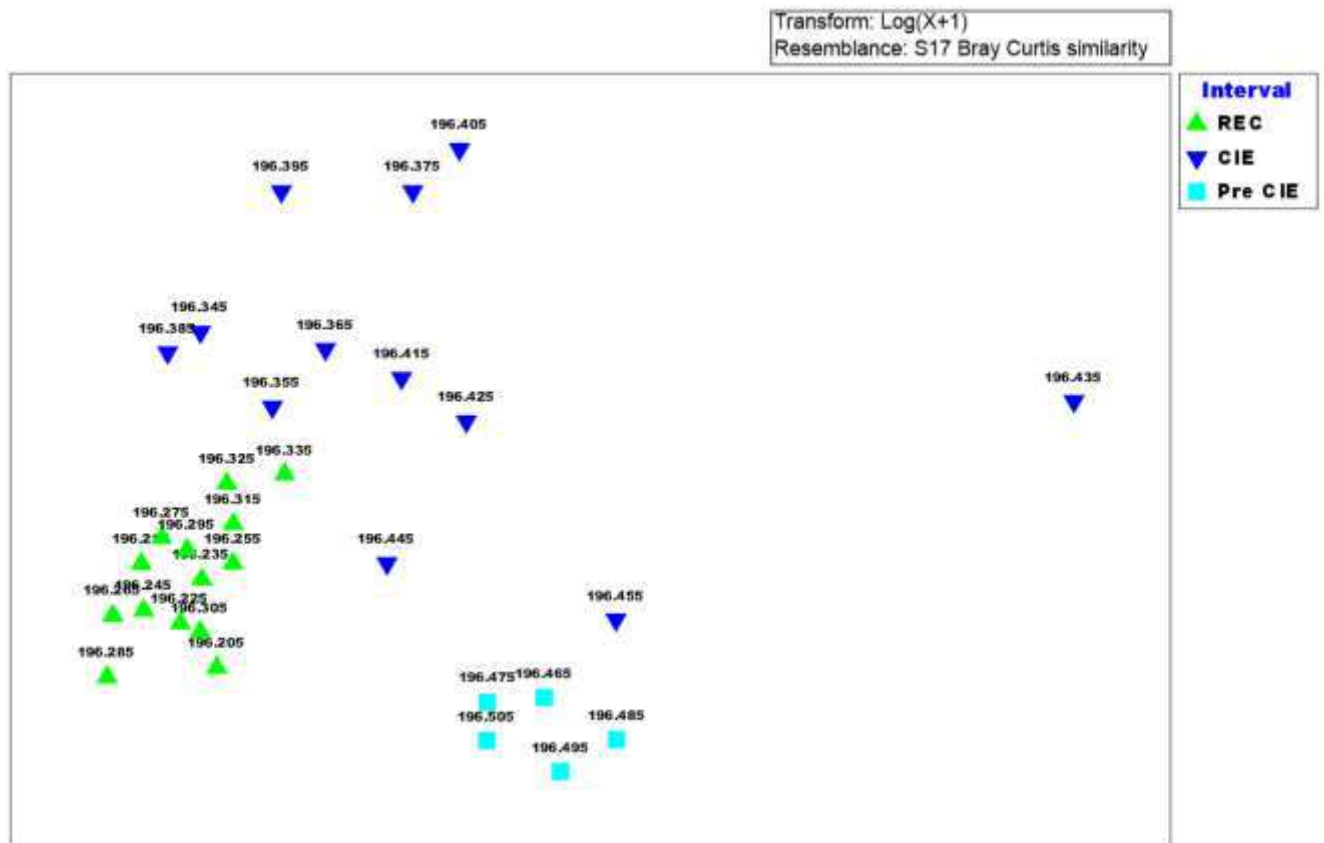


Figure 2: Sample ordination of foraminiferal trait frequency (transformed with log x+1) using Bray-Curtis similarity from ODP Site 1209B in the Pacific Ocean. The samples are grouped into three intervals depicting the PETM sections. The outlier 196.435mbsf indicates the horizon of BEE.

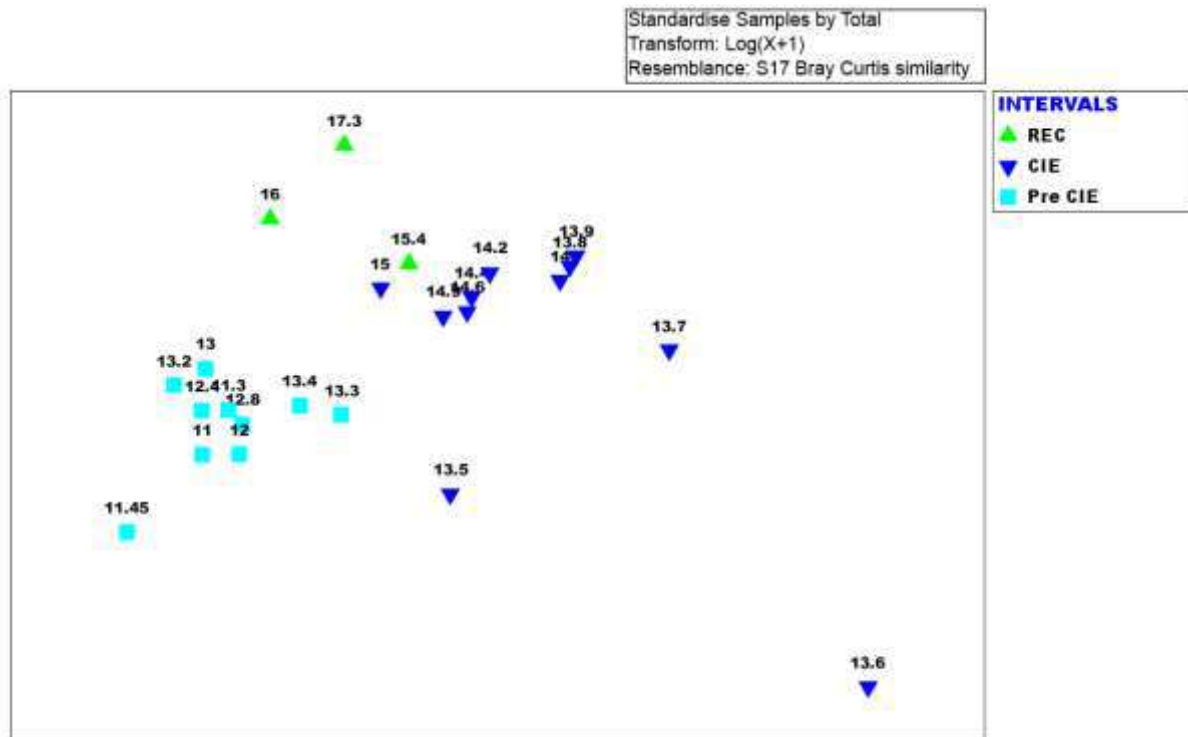
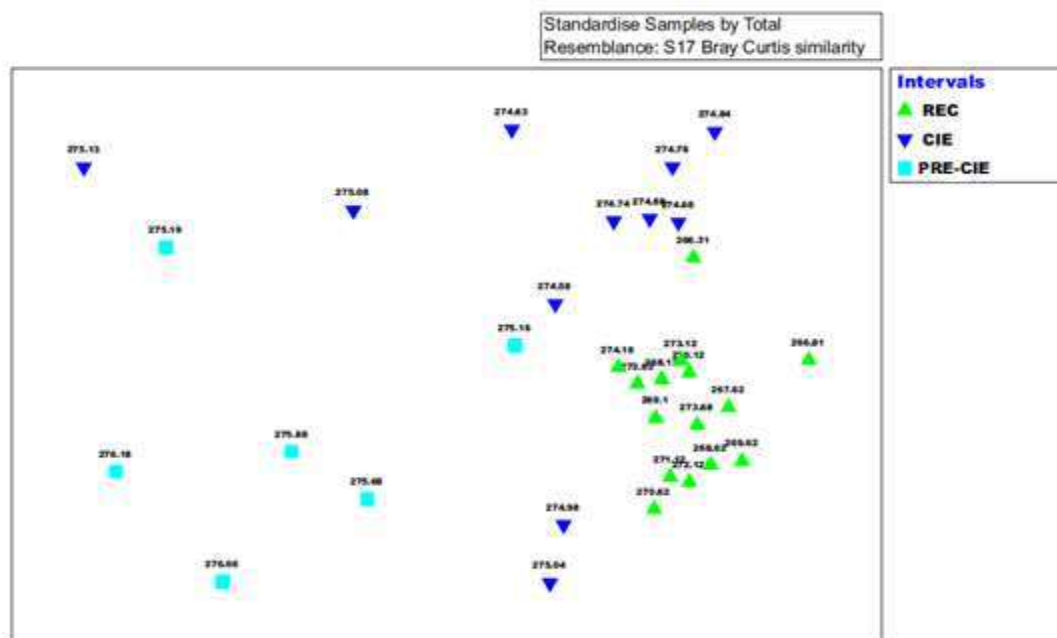


Figure 3: Sample ordination of foraminiferal species composition of Bray-Curtis similarity in nMDS plot from the Alamedilla outcrop, Spain (Tethys sea). The samples was standardised by total resemblance.



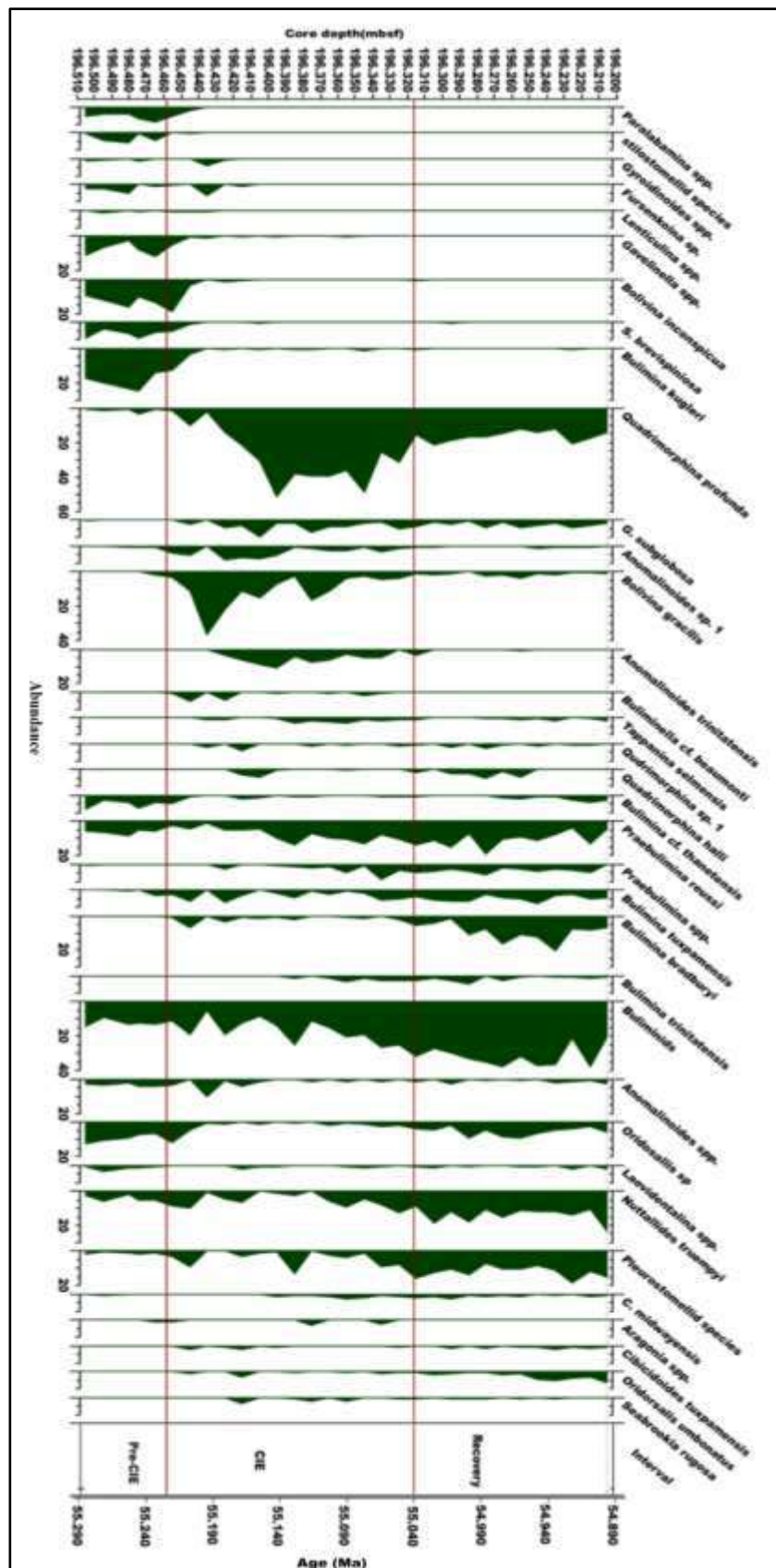


Figure 5: The distribution chart of Benthic foraminifera at ODP Site 1209B (adopted from Nwojiji et al., 2019)

Furthermore, strength of the BTA techniques is its ability to synthesize large volume of data and highlights what is significant in the voluminous data using the similarity percentage. For instance foraminiferal population from site 1209B (figure 9) was subjected to SIMPER and it categorized and highlighted the important species that is responsible for the most changes that occurred in the community (Figure 5, see also Table 2)

Table 2: Mean abundance of benthic foraminiferal species dissimilarity and percentage contribution from ODP Site 1209B across the PETM sections from simper analysis. The presented data was limited to 50% cumulative similarity.

Species	Mean abundance			Contribution to dissimilarity (%)
	Pre-CIE	CIE	Recovery	
Quadrимorphina profunda	1.45	27.66	14.58	17.41
Bulimina kugleri	20.27	1.79	0.12	12.47
Bolivina gracilis	0.33	11.87	9.04	8.13
Bolivina inconspicua	12.30	2.08	0.07	7.63
Pleurostomellid spp.	1.14	3.10	11.41	7.52
Buliminids sp.	12.50	14.92	30.79	13.63
Nuttallides sp.	4.27	4.59	13.39	7.61

Foraminiferal traits data for Site 1209B that was more than six pages (see supplementary data A) was synthesized to a single page and it showed that only 19 traits (Figure 7) was highlighted to be responsible for the dissimilarity in traits across the studied section. The traits include spiral and elongate tests; calcite and aragonite tests composition; bi/triserial and planispiral chamber; spherically shaped chambers, depressed sutures, costate ornamentation, fine perforations and bifid teeth. Foraminifera with apertures at the terminal and umbilical positions that lived a sessile lifestyle and shallow – deep in fauna also contributed significantly to the dissimilarities (Figure 6).

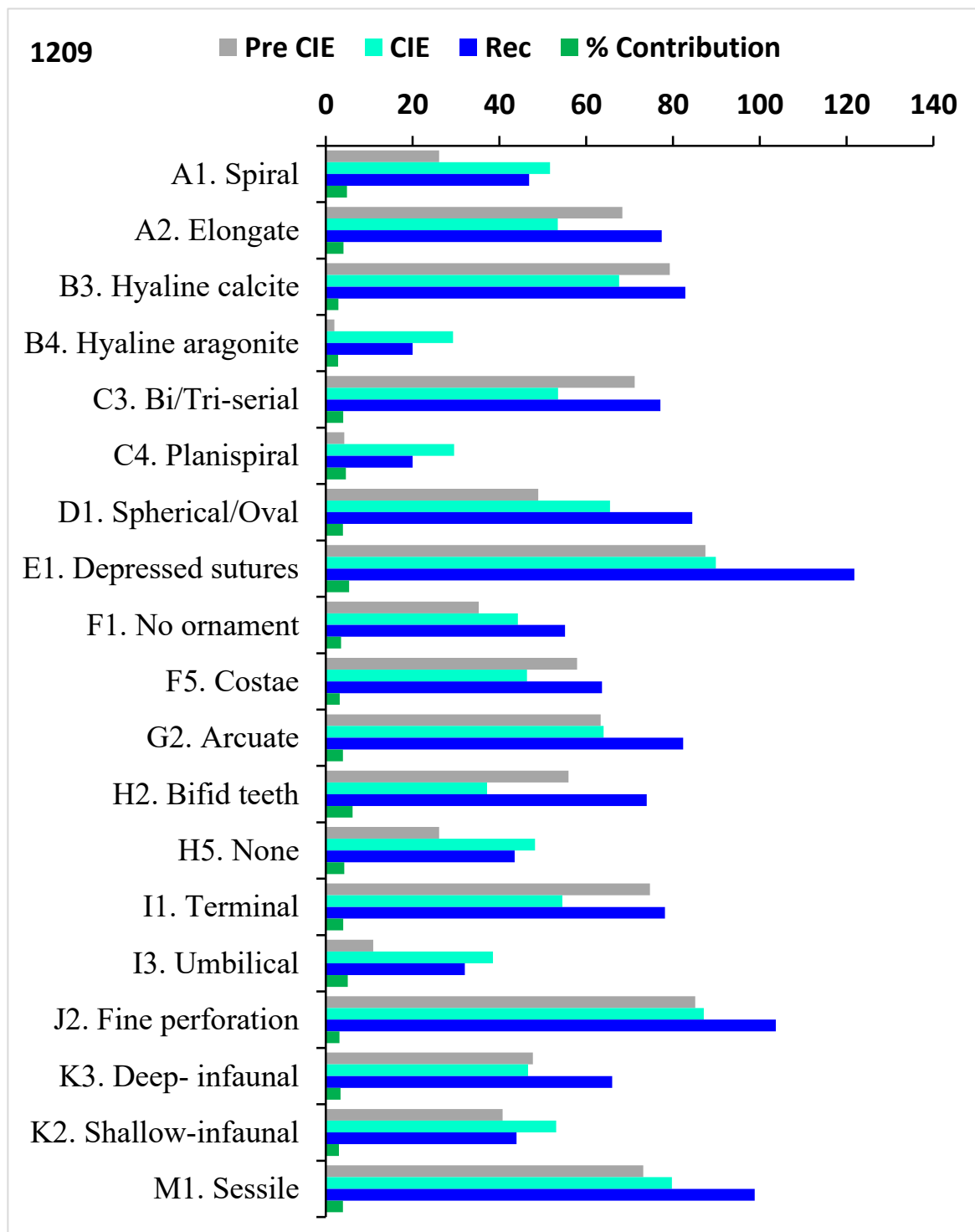


Figure 6: Benthic foraminiferal traits that contributed most to the ecological functioning of the Ocean at ODP Site 1209B during the PETM (Nwojiji et al., 2019)

At Alamedilla in the Tethys Ocean it simplified a data of 117 species and over 6000 specimens of foraminifers' taxa and associated trait to show the traits contributing to significant changes in Figure 7.

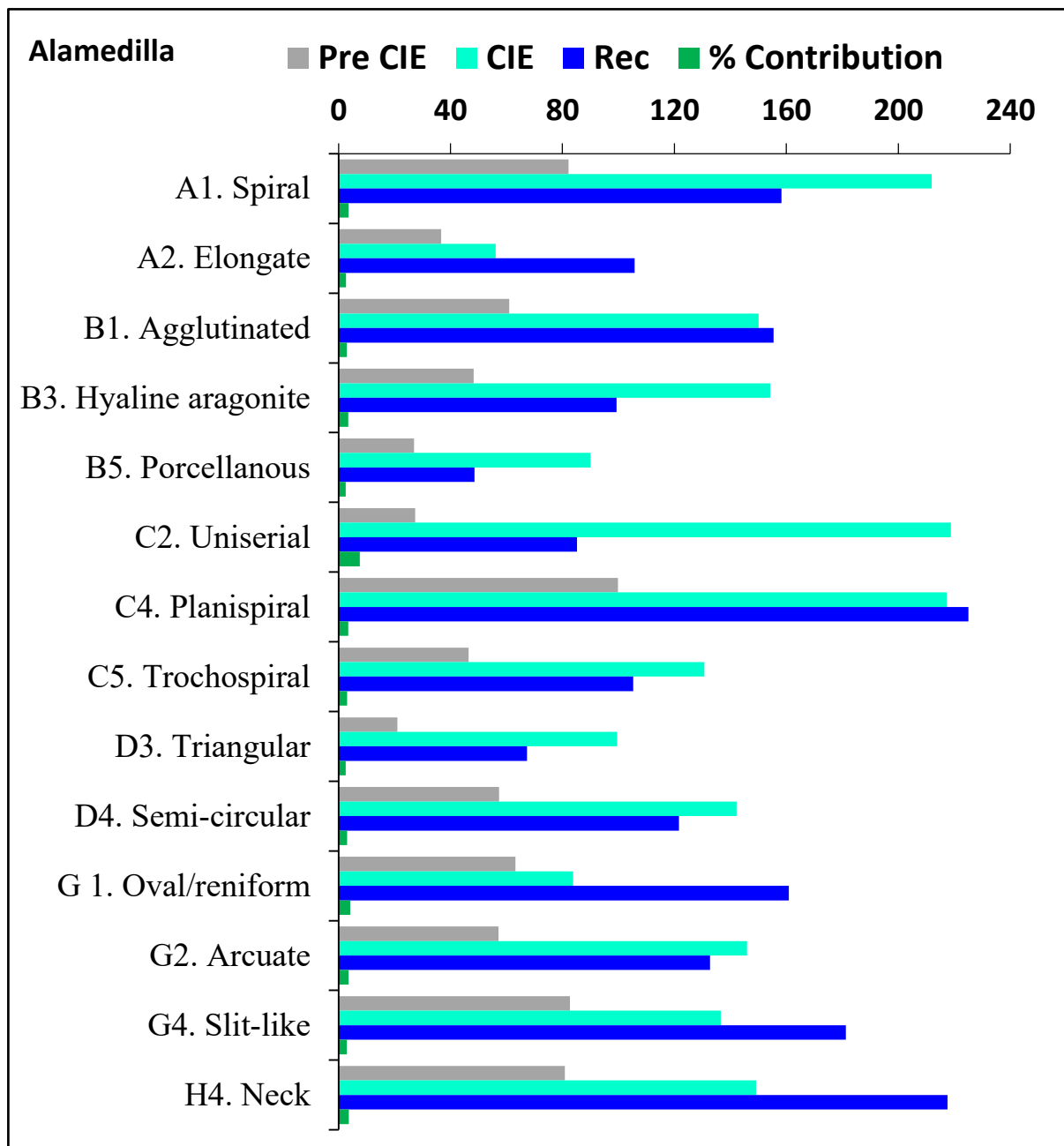


Figure 7: Benthic foraminiferal traits that contributed most to the ecological functioning in the Tethys Sea at Alamedilla section, Spain during the PETM (Nwojiji et al., 2019)

4. CONCLUSIONS

Biological Trait Analysis techniques have brought a new perspective to foraminiferal research by using ordination tool to highlight evidence of ecological disturbance in microfossils ecology. It also produced a more quantitative and integrated picture of palaeoecological change when compared to results from the conventional faunal assemblage analysis. Studies of foraminiferal populations and traits data from the Central Pacific Ocean, South Atlantic Ocean and the Tethys sea during the PETM have shown the BTA is useful in

categorizing, synthesizing and highlighting important variables from large datasets, thereby enhancing accuracy in interpretation and reducing time. ACKNOWLEDGEMENT: We would like to appreciate the International Ocean Discovery Program (IODP) for providing the sediment samples for this work. The data was collected as part of my Ph.D research at the School of Environmental Sciences, University Of Liverpool, UK.

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