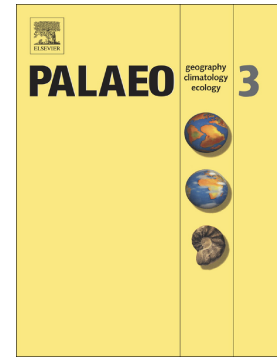


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Biogeographic response to major extinction events: the case of Triassic bivalves

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ABSTRACT

Mass extinctions decimate the biota causing the disappearance of existing palaeobiogeographical patterns, which is not surprising given that palaeobiogeographical units are usually established on the basis of endemic taxa and these are the most affected in global crisis events. This paper deals with the evolution of the biogeographic pattern shown by bivalve genera in response to the end-Permian extinction event. From a network analysis (based on Simpson's and Bray-Curtis' similarity indices) and an Occurrence Ratio Profile, the Early Triassic is recognized as a time of general biogeographic homogeneity. The Middle Triassic shows a clear differentiation, with the evolution of many new genera and an increase in endemism, which reaches a maximum by the Carnian. During the Norian-Rhaetian the main biogeographic biochoremas appear well differentiated. Unlike other invertebrates, like brachiopods, bivalves show generally high similarity values between biogeographic units, and in this particular case study, Early Triassic biogeographic units appear more related to each other than to the corresponding Middle or Late Triassic units.

1. Introduction

Post-extinction recovery-patterns are the result of a complex interaction of processes, like the differential survival of lineages, the expansion of opportunists, the innovation and diversification of new lineages, and the reappearance of Lazarus taxa (Erwin, 1998). The end-Permian mass extinction, the most extensive of the Phanerozoic, led to a severe reduction in both taxonomic richness and ecological complexity of marine communities, eventually culminating in a dramatic ecological restructuring of communities (Schubert and Bottjer, 1995; Dineen et al., 2014; Foster and Twitchett, 2014; Huang et al., 2023). Some estimations suggest that about 95% of animal species were eliminated (Raup, 1979; Erwin, 1993), though those values might be overestimated (McKinney, 1995) and more recent studies suggest an extinction of about 80% of marine animals (Benton and Twitchett, 2003; Stanley, 2016).

Early survival assemblages include opportunistic associations of paper clams (which thrives in low-oxygen settings) and the brachiopod *Lingularia*, together with widespread production of stromatolites (Erwin, 1998; Rodland and Bottjer, 2001; Petsios and Bottjer, 2016). Some of the first groups to recover were ammonoids (Brayard et al., 2009) and bivalves (Tu et al., 2016), and Lazarus taxa only reappeared with the full recovery of marine communities (Erwin, 1998). The end-Permian extinction is much severe than any of the other events, showing a relatively long recovery phase (Erwin, 1998; Chen and Benton, 2012), although not in the same way everywhere (Hofmann et al., 2014) and with some examples of diverse and trophically multileveled marine ecosystem (Brayard et al., 2017; Dai et al., 2023). This complex biotic recovery pattern was possibly due to stressful environmental conditions still

prevailing during the Early Triassic (Woods, 2005; Foster et al., 2018). Alternatively, it has also been proposed that the low rates of diversification are correlated with low levels of competition, with the interspecific competition as a main driver of recovery-phase diversification (Hautmann et al., 2015).

Mass extinctions also have a profound effect on biogeographic patterns (Kocsis et al., 2018) and geographic distribution of taxa may bear multiple implications on survival and recovery stages (Harries et al., 1996; Erwin, 1998; Jablonski, 1998). During global crisis events endemism tends to decrease (Bretsky, 1973) and as a consequence, biogeographic patterns tend to disappear. Recently, Yan et al. (2023) have demonstrated a significant bivalve cosmopolitanism event following the end-Permian mass extinction, in agreement with the pattern found when various marine invertebrate groups are considered together (Kocsis et al., 2013).

Though the palaeobiogeographic patterns of Triassic bivalves have been variably treated in previous literature (e.g., Westermann, 1973; Hallam, 1981; Yin, 1981; Hautmann, 2001; Damborenea, 2002; Niu et al., 2011; Damborenea et al., 2013), these case studies usually focus on particular ages or epochs, or are treated from a regional perspective.

In recent years network-analysis has become a widely used technique in palaeontology research. The study of palaeobiogeographic patterns evolution (Vilhena and Antonelli, 2015; Kiel, 2016, 2017; Button et al., 2017; Kocsis et al., 2018; Zhao-Hui et al., 2022), quantification of ecological impacts of mass extinctions (Muscente et al., 2018) or the study of ecological recovery from mass extinctions (Huang et al., 2016) are being carried out with this technique. With this approach it is possible to fully appreciate the dynamics of biogeographical evolution.

The Triassic is an excellent period of geological time to study this topic because

it is bounded by two of the largest mass extinctions in the history of life:

Permian/Triassic and Triassic/Jurassic events. In addition, during the Late Triassic (Maldonado et al., 2018; Pérez-López and Pérez-Valera, 2021), Pangaea begins to break up and this will lead to changes in the distribution of organisms. Bivalve molluscs, furthermore, have a great potential for palaeobiogeographical analyses due to their high fossilization potential, high abundance in different sedimentary environments, high diversity and wide larval dispersal (Damborenea et al., 2013).

The aims of this paper are (1) to analyze the effect of the end-Permian extinction event and the post-extinction recovery on palaeobiogeographic patterns, and (2) to delimit major biochoremas during the Triassic and their continuity through time. To achieve these goals, network analysis techniques will be utilized to better understand the complex relationships between organisms and their distribution in space and time during this pivotal time in Earth's history.

2. Material and methods

2.1. Material

Occurrences of Triassic bivalve genera were compiled from various published sources (literature cited in Ros-Franch et al., 2014) and the authors' data, and plotted age by age from the Induan to the Rhaetian (see Tables S1–S5). We use data at genus level and we revised all the literature to give an accurate distribution. We recognized 13 Operational Biogeographic Units (OBU), based on geographic criteria (included on Table S6), but also relying on a conventional qualitative method centered around endemism. This approach is complemented by considering other factors, like diversity, to delineate biogeographic units, as were established for the Late Triassic by previous

authors (Damborenea et al. 2013). We have deliberately refrained from assigning hierarchical names like Realm or Province to these units under discussion. Instead, we opt to identify them as 'biochoremas' (a group of similar biotopes, the largest division of animal and plant environments, Cecca and Westermann, 2003; i.e., a biogeographic unit regardless of its rank, Damborenea, 2017), occasionally indicating their relative rankings without formal categorization. Not all the OBUs are represented in all stages, and sometimes, though present, they had very low diversity, so they were not used in the subsequent analyses.

Geochronologic units used through the analysis are epochs for the first part of the period (Early Triassic and Middle Triassic) and ages for the Late Triassic (Carnian, Norian and Rhaetian). This uneven treatment is necessary in order to get time bins of similar duration (Early Triassic ~5 Myr, Middle Triassic ~10 Myr, Carnian ~10 Myr, Norian ~18 or 22 Myr and Rhaetian ~2 or 4 Myr). The short duration of the Early Triassic (and maybe the Rhaetian) may result in relatively higher endemism values than other time bins (newly evolved genera have less time for dispersal) and may reduce similarity values among the nodes. On the other hand, the long duration of the Norian may result in the opposite effect, with lower endemism values than other time bins and higher similarity values among OBUs. We prefer not to subdivide the long ages due to the nature of the data compilation (biostratigraphic information available lacks the accuracy required in many cases), but also due to the uncertainties yet standing on the Triassic time scale (Ogg et al., 2020). An interpretation based on geochronologic units, considering these biases, is preferred in order to get more robust results.

The database was compiled at global scale. The genus distribution data compilation was systematically and stratigraphically updated as far as possible and dubious records were excluded. The most serious problems related to such global

databases are the incompleteness of the fossil record and the taxonomic distortions introduced by different authors working in different areas at different times. The first problem has no immediate solution, while the second can be somewhat reduced by critical evaluation of the data. In order to obtain a sound foundation for biogeographic considerations, only genera adequately described and figured were included; uncritical listing of taxa from sources lacking illustrations was avoided.

2.2. Methods

2.2.1. Endemicity/cosmopolitanism

To evaluate the variations in endemicity throughout the Triassic, an Occurrence Ratio Profile (ORP) was performed (see Brayard et al., 2006 for technical implementation). For each genus on each age the proportion of OBUs in which it is present was calculated. Values close to 0 will indicate an endemic distribution for the genus, while a value of 1 will indicate a cosmopolitan genus. Then the frequency distribution (as percentage) was plotted in a five-class histogram with an 0.2 binsize, together with their 95% confidence intervals. Confidence intervals were calculated with the histogram function of PAST 4.0 (Hammer et al., 2001).

Though the original method (Brayard et al., 2006) was based on a ten-class histogram, the low number of OBUs prevents doing so in this case. Besides, since the OBUs cover a wide geographic range, a high level of endemicity is to be expected (particularly during the Late Triassic, Damborenea et al., 2013) and the results here obtained can not be directly compared to others based on localities (Brayard et al., 2006; Vörös and Escarguel, 2020). Nonetheless, the results will be useful for comparison between the time bins here defined and some variations in the general values between different intervals are to be expected.

2.2.2. Network analyses

Network analysis was used to trace the evolution of biogeographic units through time. The OBUs represent the nodes (regions with less than five genera were excluded from these analyses), while the links are the values of similarity between them, resulting in a weighted network. The availability of the data is limited for some areas, like North Tethys, and the northern North Pacific. To deal with such different sampling, Simpson's coefficient of similarity (Simpson, 1943) was preferred, since it may be suitable when sampling is considered to be incomplete (Hammer and Harper, 2006). Bray-Curtis' index (Bray and Curtis, 1957), which for presence-absence data is equivalent to Dice's coefficient (Dice, 1945), was also used for comparative purposes, but also to check for the robustness of the results. In both cases, values range between 0 and 1, with higher values indicating a higher proportion of shared genera between the nodes.

The data from the entire Triassic period were analyzed as a single complex network in order to evaluate the relative importance of time and geography in delimiting the major biogeographic units (Kiel, 2017). A threshold method was employed to analyze the relationships between biogeographic units. The threshold is the minimum weight for the links used to construct the network. At high values the network is broken up into components with strong links between their nodes; as the threshold value decreases, the components will add nodes and/or merge with other components, but with weaker links (see Kiel 2017, for details).

In order to detect groups within the network for the entire Triassic, a community detection approach was used once the threshold value was reached. Community detection requires the partition of a network into communities of densely connected nodes, with the nodes belonging to different communities only sparsely connected

(Blondel et al., 2008). The quality of the partition is measured by the modularity of the partition, a value that ranges from -1 to 1 which measures the density of links inside communities as compared to links between communities (Blondel et al., 2008). Both the thresholding approach and the community detection were performed on Gephi 0.10.1 (Bastian et al., 2009).

3. Results

3.1. Occurrence Ratio Profile

The results of the analysis are shown in the histogram of Fig. 1. The proportion of genera with a restricted distribution (lower values of the index) tend to increase from the Early Triassic to the Carnian, showing a sudden drop during the Norian and the Rhaetian. The Early Triassic shows the highest proportion of widely distributed genera (high values of the index).

3.2. Network analyses

At high similarity values, with a threshold value of 0.9 using Simpson's coefficient, connections between nodes occur mostly within time bins, with the main exception of the Norian-Rhaetian North Pacific and Boreal regions (Fig. S1). At threshold values of 0.8 (Fig. S2), the Early Triassic regions show high similarity and no connections with the remaining of the network. The Middle and Late Triassic regions show a pattern dominated by geographic rather than temporal relationships, with the Tethys biochorema on one side and the circum-Pacific on the other; few connections between both of them can be found. With threshold values of 0.7 (Fig. S3) the Early Triassic relates to the main network, and a continuity of the Maorian region from the

Carnian to the Norian can be recognized (extending to the Rhaetian at a threshold of 0.65, Fig. S4); no OBU from the Middle Triassic appears related to the circum-Pacific biochorema. The percolation point can be considered reached at 0.62, with only six OBUs and the Norian-Rhaetian Boreal region unrelated to the network (Fig. 2). At this point, the Maorian region starts to relate to the circum-Pacific. The Boreal region appears disconnected from other regions, showing continuity only from the Norian to the Rhaetian (Fig. 2). At a threshold value of 0.55 only the Early Triassic Boreal and Middle Triassic Maorian regions are disconnected from the network; the network is fully connected at the threshold value of 0.3. The community detection analysis was performed on the network with the 0.62 threshold value, resulting in six main communities plus the six unconnected OBUs (shown on Fig. 2) and a modularity index of 0.528.

Though there was a community configuration with a slightly higher modularity index (0.540) the results are quite similar (Fig. S5), with two main differences: the Maori region is included within a circum-Pacific biochorema, while the Rhaetian northern North Pacific, North West Tethys and the Norian-Rhaetian West Pacific conform a northern mid-latitude group.

General similarity values with Bray Curtis' index are lower than with Simpson's coefficient. With a threshold value of 0.6 many connections between Norian and Rhaetian corresponding OBUs begin to develop (Fig. S6). At a threshold of 0.45 (Fig. S7) the Early Triassic OBUs are highly connected, while the Late Triassic circum-Pacific and Tethys biochoremas start to differentiate; some mid-Triassic OBUs merge with the Tethys network. At a threshold value of 0.32 (Fig. 3) the percolation point is reached, with almost all regions merging in a single network (with the exception of both mid-Triassic polar nodes and the Carnian South Tethys; Late Triassic Australian nodes

show connections among them, but the group does not merge with the network). At this stage, both Late Triassic polar regions appear related to the circum-Pacific biochorema. The community detection analysis resulted in six groups (three main regions and three small groups) plus three disconnected OBUs (Fig. 3), with a modularity index of 0.471. The network is fully connected at the threshold value of 0.2.

The results for the community detection approaches show some similarities for both coefficients. The clearest result is the strong differentiation of the Early Triassic OBUs from all others. The Middle Triassic appears also well connected, but always related to (at least part of) the Late Triassic Tethys; the Pacific OBU appear as peripheric to this mid-Triassic Tethyan biochorema. With Simpson's coefficient, the Late Triassic Tethys (particularly the Norian-Rhaetian) appears differentiated from the Middle Triassic one. In both cases the differentiation of the Late Triassic circum-Pacific biochorema is remarkable, with Boreal and/or Maorian regions closer to it than to the Tethyan realm.

4. Discussion

4.1. Biogeographic evolution and the cosmopolitanism event

The lack of provinciality and the occurrence of widely distributed to cosmopolitan faunas after the Permian/Triassic extinction event is well documented in many groups, such as ammonoids (Brayard et al., 2006, 2007; Dai and Song, 2020), brachiopods (Ke et al., 2016) and terrestrial tetrapods (Button et al., 2017) among others.

This pattern is also well documented on bivalves. Working on four major continental geographic units, Bretsky (1973) found that across most major extinction

events endemic genera tend to proportionally decrease approaching to the extinction, while cosmopolitan ones tend to increase. More recently, Yan et al. (2023), working on a much detailed geographic grid, quantitatively identified a significant bivalve cosmopolitanism event in the Induan (and possibly in the Hettangian too), marked by an increase of Biogeographic Connectedness (BC) and a drop in multiple site β -diversity. Interestingly, the BC graph (high BC values indicate high proportion of cosmopolitan taxa) show a slightly increasing trend previous to both Permian/Triassic and Triassic/Jurassic extinctions (Yan et al., 2023, fig. 2A). This suggest a gross pattern similar to the main results of Bretsky (1973), but the differences in time scale should be considered: while Bretsky (1973) recognized the beginning in the loss of endemics in the transition between the Carboniferous and the Permian, Yan et al. (2023) show the increase in BC from the Middle Permian onwards.

The analyses here performed also show a clear pattern of low endemism and high similarity among Early Triassic OBUs. The ORP (Fig. 1) shows the highest proportion of widely distributed genera (high values of the index) during the Early Triassic. Less than 50% of the genera show values lower than 0.2 for the occurrence ratio (i.e., they appear in less than 20% of the OBUs) and more than 10% show values above 0.6 (Fig. 1). These values were not reached again during the rest of the Triassic.

In the network analysis, the Early Triassic nodes show a high similarity among them, and at the percolation point (with Simpson's coefficient) show a single connection with the remaining of the network (Fig. 2).

Dai and Song (2020) propose three theoretical models for a cosmopolitanism event: 1- a selective extinction against endemic taxa; 2- a non-selective extinction, but with survivals becoming cosmopolitan through dispersal; and 3- newly evolved taxa becoming rapidly cosmopolitan. Bretsky (1973) considered the increase in

cosmopolitanism a consequence of differential extinction of endemic taxa (i.e., model 1), while Yan et al. (2023) concluded that the main factors leading to the cosmopolitanism of bivalves in the Induan were the selective extinction of endemics (model 1), but also the expansion of survivors after the extinction (i.e., model 2).

When our data are discriminated between Palaeozoic survivors and Triassic newcomers (Fig. 4), we see that for wider distributions, Palaeozoic survivors dominate, while the endemic to narrowly distributed genera are mostly newcomers. *Claraia*, *Promyalina*, *Eumorphotis* and *Leptochondria*, all Palaeozoic survivors, show the widest distributions (OR higher than 0.6) and have been referred to as “disaster taxa” during the Early Triassic due to its wide distribution and opportunistic behaviour (Petsios and Bottjer, 2016; Prinoth and Posenato, 2023); none of them shows a wide distribution during the Late Permian. *Claraia* occurs in the South, South East and North East Tethys and Boreal region (Nakazawa et al., 1975; Muromtseva, 1984; Fang, 1993, 2003; Newell and Boyd, 1995; Yang et al., 2001; Kotlyar et al., 2004), being absent from the Western Tethys and the circum-Pacific so far. *Promyalina* was found in the North East and North West Tethys (Farahbegoli et al., 2007; He et al., 2007), while *Leptochondria* is restricted to the North East Tethys and the West Pacific (Nakazawa and Newell, 1968; Hayami, 1975; Hayami and Kase, 1977; He et al., 2007) and *Eumorphotis* was recently recorded in North West Tethys (Prinoth and Posenato, 2023). This suggests a dispersal of the four of them after the extinction, favouring a model 2.

An interesting fact of this cosmopolitanism event is that the wide distribution does not seem to provide a differential surviving chance during the recovery stage. Of the four genera with widest distribution during the Early Triassic, only *Leptochondria* survives into the Middle Triassic, being its last record of Norian age. Narrowly distributed genera (occurrence ratio between 0 and 0.4), in contrast, show surviving

percentages of about 70%.

The ORP (Fig. 1) shows a general increase in endemism until the Carnian, followed by a sudden drop during the Norian-Rhaetian. The biases related to time bins of different length should be considered here. The Early Triassic results are of particular interest: due to its relatively short duration compared to other time bins, it is expected to show higher endemism than the other intervals. Nonetheless, it shows the lowest endemism proportion. This supports, once again, the reality of the cosmopolitanism event. The low endemism for the Norian, on the other hand, may be related to its longer duration. Yan et al. (2023) found that BC values were lowest during the Norian, pointing to high provinciality; the increasing trend began during the Rhaetian. In our results, the Rhaetian shows a very similar ORP to that of the Norian (Fig. 1), suggesting certain biogeographic stability through these two ages. Another important fact to consider is that, although the proportion of genera with lowest Occurrence Ratios (0-0.2) significantly decrease, there is not a significant increase in cosmopolitan genera (0.8-1.0). That's because there is a peak in the percentage of intermediate values, particularly on the values between 0.2 and 0.4 (about a 30% of genera for both ages). These results suggest that there is a trend to a more regional distribution of genera during the Norian-Rhaetian, probably related to the strengthening of the main biogeographic barriers (see below).

4.2. Evolution of the major biogeographic patterns

The main consequence of the cosmopolitanism event is the lack of a clear biogeographic pattern during the Early Triassic (Figs. 2 and 3). Nonetheless, it must be considered that the scarcity of data may impose some limitations to this kind of analysis (Hallam, 1981), particularly for the Early and Middle Triassic of the Southern

Hemisphere (Damborenea et al., 2013). Simpson's coefficient is a good similarity estimator when sampling is incomplete, but with small samples a few shared genera may result in poorly-supported high similarity values. OBUs with less than 5 genera were excluded from the analysis, but yet some of them can be considered as poorly sampled. Table 1 shows the similarities higher than the threshold value at the percolation point for some of the nodes with few genera recorded (excluding those from the Early Triassic which in general have low diversity).

The western Pacific node for the Rhaetian has a record of seven genera resulting in high similarities with four nodes and probably causing the detection of a mid-latitude community (Fig. S5). The intermediate position these nodes occupy in the network at the percolation point, showing connections with the other three main groups (the Middle Triassic–Carnian Tethys, the Late Triassic Tethys and circum-Pacific), may also contribute to the detection of that community.

Conversely, the northern Tethys Carnian node (with only five genera) has low Bray-Curtis' similarity values with only two nodes and one is with the corresponding Norian node, causing the differentiation of a small community (Fig. 3); the Simpson's coefficient values, showing higher similarities with many other nodes (many of them Tethyan) is probably a better representation of those scarce data.

The analysis here implemented, treating the occurrence data of bivalve genera throughout the entire Triassic as a single complex network, allows for a better understanding of the evolution of the main biogeographic biochoremas, including their temporal and spatial relationships.

Though bivalve recovery started soon after the extinction, it was during the Anisian (Middle Triassic) that the main diversification took place according to the analysis of the database (Ros and Echevarría, 2011) and other datasets (e.g., McRoberts,

2001; Tu et al., 2016; Friesenbichler et al., 2021). From a biogeographic point of view, this high origination during the Middle Triassic (the number of genera doubled during the Anisian), combined with the relatively high extinction of the Early Triassic (35% percent of the genera did not reach the Middle Triassic), results in the strong temporal differentiation between the Early Triassic OBUs and the remaining ones (Figs. 2 and 3).

During the Middle Triassic, the main Triassic biochoremas started to develop. As would be expected, endemism raised quickly (Fig. 1). Like during the Early Triassic, there is an almost undifferentiated network, but with the polar nodes unconnected (Figs. 2 and 3). This suggests a latitudinal differentiation with a relatively homogeneous tropical belt showing low similarity with the polar regions. At the percolation point, almost all the connections with Late Triassic OBUs are with Tethyan nodes (for Simpson's coefficient all of them, Fig. 2), suggesting that this biochorema can be recognized since the Middle Triassic. On the other hand, it must be considered that most Pacific nodes have little or no records for the Early and Middle Triassic, difficulting the comparison.

During the Carnian, the trend of increasing endemism continued (Fig. 1). This was most likely fuelled by the strong turnover and high evolutionary rates among bivalve genera, particularly epifaunal ones (Ros and Echevarría, 2011). New genera were appearing fast, and sometimes went extinct before the end of the age, hence having little chance to migrate to new basins. Considering the length of the age (about 10 Myr, only surpassed by the Norian) the high endemism becomes more relevant, since long ages are expected to have low endemism. This high turnover and endemism may be the reason why the Tethys appears somewhat divided during this age with Simpson's coefficient, showing some OBUs more related to the Middle Triassic ones, and some others to the Norian or even the Rhaetian ones (Fig. 2). The network produced with the

Bray-Curtis' coefficient shows a homogeneous Tethys from the Middle Triassic to the Rhaetian.

During the Carnian, two major biochoremas (circum-Pacific and Tethys) begin to differentiate. By Norian-Rhaetian they are fully separated (Figs. 2 and 3); both stages show strong connections, and at threshold values of 0.9 for Simpson's coefficient (Fig. S1) they show the only edges between two time bins. The conformation of these two major biochoremas can explain the sudden drop of endemic genera (Fig. 1) as discussed in the previous section. The high connectivity among the Norian Pacific American nodes may be the result of the longer duration of that age in comparison to the Carnian and the Rhaetian.

4.2.1. Tethys

Suess (1893) recognized the existence of an inland ocean between westernmost Mediterranean region of today to eastern Asia, citing the presence of comparable fossils in Europe and Africa and named this body of water "Tethys". Since then, on the basis of differences between the biota—mainly ammonoids, bivalves, brachiopods, conodonts, and nautiloids, a biochorema associated to that ocean (and its predecessor, the Palaeo-Tethys) has been classically distinguished, particularly from the Boreal region, and recognized as early as the Early Triassic (Dagys, 1976; Klets, 2008; Brosse et al., 2013). In our analysis, the Tethys region appears related to tropical latitudes since the Middle Triassic. Genera like *Umbrostrea*, *Myophoria*, *Elegantinia*, *Coelopsis* and *Pseudocorbula* are endemic to this biochorema since that time, having a widespread record until the Rhaetian. By Late Triassic many other endemic genera are incorporated, like *Persia*, *Krumbeckiella*, *Prosogyrotrigonia*, *Prolaria*, *Thracia* and *Cercomya* among others.

The Late Triassic Australian region seems to appear related to the Tethys biochorema, thanks to the presence of *Myophoria*, *Prosogyrotrigonia* and *Coelopsis*. Though identified as an independent unit using the Bray-Curtis' coefficient (Fig. 3), unrelated to the general network, this is most likely due to the low number of genera (Table 1). On the other hand, the Norian-Rhaetian Australia appears related to the Middle Triassic-Carnian Tethys, and also shows a strong similarity to a Pacific node (Fig. 2, Table 1), suggesting a possible transitional nature for this region.

4.2.2. Circum-Pacific

The circum-Pacific biochorema has been recognized by several authors (e.g., Hallam, 1981; Damborenea et al., 2013). The present analysis shows its development since the Carnian to the Rhaetian, with the widespread genera *Liostrea*, *Gryphaea*, *Maoritrigonia*, *Minetrigonia*, *Myophoria* and *Perugonia* as representatives of the biochorema; all of them, with the exception of the last two, relate this region with one or both polar regions.

The network analysis provides a track to the origin of the circum-Pacific. The community detection approach recognized the biochorema mostly due to the similarity of all its nodes to the Norian OBUs (highly connected among them), showing little connection during the Carnian. The Carnian and Rhaetian North Andean nodes, for example, are included in the major group due to their relationships with the Norian nodes, being disconnected from their contemporary Pacific OBUs. That doesn't invalidate the patterns here recognized, on the contrary, add an important temporal dimension of biogeographic units: the similarity between non-contemporary nodes may reveal dispersal pathways. This suggests that after the increased origination of new genera during the Carnian, like *Perugonia* or *Liostrea*, these started to migrate during

the Norian, generating a more continuous biogeographic pattern. The circum-Pacific coast, and particularly the American Pacific margin, appears then characterized by an active and fluent dispersal of bivalves, generating a biogeographic identity even though at a single time slice some OBUs may show a relatively high level of endemism. That active biogeographic nature of the American Pacific margin was also recognized for different groups of Early Jurassic bivalves (e.g., Damborenea and Manceñido, 1979; Echevarría et al., 2021, 2022).

The West Pacific node provides a good example of the advantages of network analysis applied on biogeographic studies. Niu et al. (2011) found that in the Carnian the Eastern part of South China together with Japan began to differentiate from their North Eastern Tethyan province, merging to the circum-Pacific region by Norian-Rhaetian times. The West Pacific node of our analysis (including Japan) is related to the Tethyan realm during the Middle Triassic and the Carnian (Fig. 2), and though it shows a high similarity with the Norian node, it merges with the circum-Pacific biochorema during the Norian-Rhaetian according to the community detection algorithm, corroborating this observation. It must be considered, nonetheless, that the Rhaetian node has low diversity (Table 1).

Also, the Late Triassic Maorian region is included in the circum-Pacific biochorema, but that is not totally unexpected, since it shows connections with some of its nodes, and the affinity of the New Zealand bivalves with other Pacific faunas has been long recognized (Hallam, 1981; Silberling, 1985; Stevens, 2012; Damborenea et al., 2013).

4.2.3. Polar regions

The strong differentiation that the two high latitude OBUs show with the

remaining ones is remarkable (Figs. 2 and 3). The Boreal region appears disconnected from the others at the percolation point (Fig. 2); only the Norian and Rhaetian Boreal nodes are connected with each other. The Early Triassic isolation of the Boreal node (Fig. 2) may suggest some latitudinal differentiation, though with Bray-Curtis' coefficient the node merge to the general network (Fig. 3). Interestingly, the region shows a trend of increasing similarity between nodes of successive time bins (Table 2), pointing to decreasing turnover.

Damborenea et al. (2013) recognized a Maorian endemic centre in the Middle Triassic. Similarity values between its nodes on different time bins show no shared genera between the Middle Triassic and the Carnian but a strong relationship between Late Triassic nodes (Table 2), suggesting that the biochorema was clearly defined by the Carnian. This region shows a similar pattern to the Boreal one (Fig. 2), though it shows some similarity values over the threshold of 0.62. Most interestingly, it is related to the circum-Pacific during the Late Triassic (Fig. 2), being even included in the same community with the alternative grouping (Fig. S5) or with Bray-Curtis' index (Fig. 3). This suggests a migration of some genera between both biochoremas. The genus *Maoritrigonia*, for example, has its first record in the Carnian of New Zealand, migrating in the Norian-Rhaetian to the American Pacific margin. More widespread genera, like *Pinna*, *Limatula* and *Tutcheria*, also appeared in the Carnian record of New Zealand (though for the first two that's not their earliest worldwide record), being found in the East Pacific since the Norian.

Conversely, the genus *Phaenodesmia* appeared in the Middle Triassic of Tethys, having a North Andean Carnian record and reaching the Maori region by Norian times.

Though Maorian and Boreal nodes do not appear connected in the analysis with Simpson's coefficient (Fig. 2), they are contemporarily connected with the Bray-Curtis'

index (Fig. 3). They do share some genera, with highest similarity values by the Late Triassic (Simpson's coefficients of 0.111 for the Middle Triassic, 0.375 for the Carnian, 0.318 for the Norian and 0.353 for the Rhaetian). These values may be related to a pattern of increasing bipolarity, though it must be remembered that the shared genera do not necessarily qualify as bipolar, since they can be widely distributed genera found also in low latitudes. When the complete distribution of the genera involved is considered, only two records can be defined as bipolar: one (out of six shared genera) for the Carnian (*Triaphorus*) and one (out of nine shared genera, for the Norian and the Rhaetian (*Ochotomya*), although several other shared genera have distributions in mid-high latitudes (e.g. *Aparimella*, *Asoella*, *Maoritrigonia*, *Minetrigonia*)

4.3. Comparison with other invertebrate groups

Among the many groups of benthic invertebrates, brachiopods provide the best case for comparison with bivalve biogeographic patterns. Ke et al. (2016) recognized a general palaeobiogeographical pattern evolution for Triassic brachiopods very similar to the one recognized here for bivalves. By the earliest Triassic, they recognized brachiopod communities composed mainly of small, cosmopolitan or widely-distributed thin-shelled taxa. Provincialism reappeared during the Olenekian nonetheless, earlier than in bivalves.

By the Anisian, the Gondwanan realm (represented by the Austrazean province, equivalent to the Maori region for bivalves) can be well distinguished from the Tethyan realm, but the Boreal realm is not well differentiated from the Tethyan one; global palaeobiogeography appeared to have fully recovered during the Ladinian (Ke et al., 2016). Among bivalves, a general differentiation between tropical and polar regions can be recognized by Middle Triassic (Figs. 2 and 3).

The three widely-recognized realms for brachiopods (Boreal, Tethyan and Gondwanan) were maintained during the Late Triassic (Ke et al., 2016). Interestingly, global provincialism was most developed during the Carnian age, the moment when the bivalves also reach their maximum level of endemism. At this point, the Sino-Mongolian-Japanese province for brachiopods, related to the Tethys during the Middle Triassic, merged to the Boreal realm (Ke et al., 2016); something similar to what happened to the similar West Pacific OBU for bivalves, though during Norian times. During the Norian, provincialism is lost within brachiopods realms (Ke et al., 2016), coinciding with the decrease of endemism and increase of widely distributed (though not cosmopolitan) bivalves; at this time, the Grandian brachiopod province, related to the Boreal realm, advanced southwards along the American Pacific coast (Ke et al., 2016), paralleling the development of the circum-Pacific biochorema for bivalves.

Ke et al. (2016) concluded that palaeolatitude-related thermal gradient might have been the primary controlling factor for the spatial distribution of brachiopods, influenced also by the presence of the supercontinent Pangea as a profound palaeobiogeographical barrier. Also, strong oceanic currents from the North Pole along the western margin of Pangea played a critical role, favouring the biogeographic differentiation of the American Pacific margin during the Late Triassic, and strengthening its palaeobiogeographical affinities with the Boreal realm.

Working on the same brachiopod genera database by Ke et al. (2016), Kiel (2017) applied a network analysis and concluded that this method is a useful tool to investigate biogeography through geologic time. In order to compare with his results, the Bray-Curtis' similarity index was also applied to our data (Fig. 3), obtaining similar results to those based on Simpson's coefficient (Fig. 2). The values obtained show, on average, higher similarities than those obtained by Kiel (2017, though they are

expressed as distances). The differences in geographic and time units should be considered in order to make an adequate comparison. On one hand, some of the time bins here employed are longer (e.g., Early Triassic, Middle Triassic), providing more time for newly evolved genera to migrate and result in the higher similarity values observed among regions. On the other hand, the geographic units here used are much larger than those used by Kiel (2017) and they are defined on endemism criteria, hence, it would be expected to show lower similarity values among them. This last fact suggests that bivalve genera truly tend to have wider distributions.

One of the main conclusions of Kiel (2017) was that geographic proximity had a stronger impact on faunal similarity than geologic time on brachiopod palaeobiogeography: geographically close localities show higher similarity values among them, regardless of the time bin, than with other localities from the same time bin. In his threshold approach the palaeobiogeographic units tend to merge into the main realms recognized instead of into time bins (Kiel, 2017). That is not the case for bivalves: one of the first main groups of OBUs to get connected is the one for the Early Triassic, showing high similarity values with either metric (Figs. 2 and 3). This points to a more cosmopolitan (or at least widespread) bivalve fauna for the Early Triassic, but also for a great turnover during the Middle and Late Triassic; as a result, the Early Triassic OBUs are closer to each other than to their equivalents in the Middle or Late Triassic. It should be noted, nonetheless, that during the Induan no biogeographic pattern could be recognized for brachiopods, and it is in the Olenekian that biogeographic provinces start to be recognized (Ke et al., 2016; Kiel, 2017).

One possible explanation for these differences is the different larval development in both groups: while in filter-feeding bivalves, particularly those from tropical and temperate shelf zones, larvae tend to be planktotrophic, lasting up to five

weeks, in most rhynchonelliformean brachiopods larvae have a short free-swimming period of a few hours or at most a few days, (Steele-Petrović, 1979).

Another interesting pattern found by Kiel (2017) for Triassic brachiopods is the relatively low degree of connectedness in the Tethys compared to the Pacific Ocean, pointing to high heterogeneity in brachiopod faunal composition probably due to the higher evolutionary rates in the tropic (and also reinforced by larvae with low dispersal capability). When all the Bray-Curtis' coefficients are analyzed in bivalve faunal composition, we found a similar pattern, though with clear variations through time. For Early and Middle Triassic Tethys the degree of connectivity is relatively high, strongly lowering during the Carnian and rising again during the Norian and the Rhaetian (Table 3). OBUs for the circum-Pacific are too few during the Early and Middle Triassic, but we found a high degree of connectedness for the Biochorema during the Carnian and the Norian, and in both cases higher than those for Tethys (Table 3); only during the Rhaetian, the values for the circum-Pacific appear lower than those for Tethys. When the same analysis is done on Simpson's similarities, the results differ a little bit. The high similarity within the Tethys during the Early Triassic increased during the Middle Triassic, and strongly dropped during the Carnian (Table 3), remaining low during the Norian; by Rhaetian times they increased again. Simpson's similarity values within the circum-Pacific are similar to those within Tethys during the Carnian, strongly increasing during the Norian and dropping again during the Rhaetian. This pattern can be seen in the network at the percolation point (Fig. 2), with a lot of edges linking the Pacific nodes during the Norian, but much fewer during the Rhaetian. Little information is available on gastropod major Triassic biogeographic patterns. Like bivalves, they have a relatively high number of genera surviving from the Permian into the Early Triassic (Erwin and Hua-Zhang, 1996; Nützel, 2005). The biogeographic

pattern of the end-Permian event shows that the successive extinction peaks affected mostly endemic genera (56% of extinct genera in the Wordian), affecting progressively a higher proportion of widespread genera (Erwin and Hua-Zhang, 1996) and driving 20% of families into extinction (Nützel, 2005). A similar pattern was recognized on bivalves (Bretsky, 1973) resulting in the cosmopolitan, homogeneous biogeographic pattern for the Early Triassic (Yan et al., 2023). From the earlier appearance in China than in other major regions, Tong and Erwin (2001) suggested that the eastern Tethys may have served as a refuge during the end-Permian mass extinction. By Middle Triassic, marine assemblages recovered among gastropods, showing a similar taxonomic composition to those from the Middle Permian (Erwin and Hua-Zhang, 1996). A high similarity between Chinese and European gastropod assemblages was recognized by Tong and Erwin (2001), as well as a weak relationship with American taxa, pointing to a major differentiation between Tethys and the Pacific margin. Once again, the latitudinal extension of Pangea together with the wide development of the Panthalassa ocean were invoked as the main barriers responsible for gastropod biogeographic distribution (Tong and Erwin, 2001). The group will show a major taxonomic turnover after the end-Triassic extinction event (Ferrari and Hautmann, 2022).

A different biogeographic pattern was found for malacostracan crustaceans. While during most of Palaeozoic some of the main groups were restricted in their distribution, the conformation of Pangea allowed them to reach a cosmopolitan distribution during the Permian-Triassic (Schram, 1977; Taylor, 1999). During the Triassic (and subsequent periods) there was a radiation of new forms, leading many of the Palaeozoic survivors either to extinction or to survival in gondwanan refugia (Schram, 1977). It must be noted, nonetheless, that this pattern was found on high-order

taxonomic groups.

Among pelagic invertebrates, ammonoids recovered fast from the Permian-Triassic extinction event (Brayard et al., 2006). Their Triassic biogeographic history is marked by the iterative development and loss of sea surface temperature gradients, causing a latitudinal gradient of generic richness together with an increase of endemism in the first case, and a more homogeneous, cosmopolitan configuration in the second (Brayard et al., 2006, 2007, 2015; Dai and Song, 2020). The lack of gradients could occur in contexts of either high (like in the Griesbachian) or low (like in the late Smithian) temperatures (Brayard et al., 2015; Dai and Song, 2020). As a result, their biogeographic patterns, dependent on highly variable sea surface temperatures, tend to differ from those found here for bivalves, related to more stable sea bottom environments. Already in the Early Triassic some differentiation between eastern Panthalassa (developing northwards) and Tethys (developing southwards) was developed, with a strong transoceanic equatorial connection (Brayard et al., 2007).

Conodonts also show two large domains during most of the Triassic, Panthalassa and Tethys, though they show a high degree of generic correspondence, differing in the frequency and ranges of various genera (Chen et al., 2016). Their provincialism is low in the Anisian with rather uniform faunas. That provincialism increased and strengthened during the early Ladinian to reach a peak around the mid-Ladinian, and remained strong till the lowermost Carnian. By the end of this age, it dropped to an all-Triassic low but rebounded later on the specific level (Chen et al., 2016).

A Late Triassic differentiation between Tethys and eastern Panthalassa was also recognized for calcareous nannoplankton, but in that case is most likely related to differential transport by oceanic currents, since the Panthalassa assemblage appears as an impoverished version of the Tethyan one (Pérez Panera et al., 2023).

5. Conclusions

The Early Triassic shows the expected pattern of lowest endemism and highest proportion of widely-distributed to cosmopolitan genera, pointing to a biogeographic pattern of relative homogeneity after the mass extinction. It is also well differentiated from the other time intervals, indicating a great taxonomic turnover during the recovery from the extinction.

The Middle Triassic shows a clear increase in endemism, which reaches a maximum during the Carnian; this age shows low values of similarity between OBUs, probably related to the high turnover rates, with many singletons evolving in each biochorema but being unable to disperse. The Norian-Rhaetian time interval shows a decrease in endemism and an increase in genera with moderately low values of occurrence ratios, suggesting a good differentiation of the major biochoremas.

The Tethys biochorema seems to begin its development during the Middle Triassic, with many OBUs showing high similarity values; this early region shows a clear relationship with the Carnian Tethys; by Norian-Rhaetian times a turnover of genera separates this biochorema from the previous one.

By Late Triassic times the circum-Pacific biochorema appears well differentiated, showing some affinities with the Maorian region, and sometimes also with the Boreal one.

The Boreal region may have its origin in the Early Triassic but appears better differentiated by Middle Triassic, and shows a more continuous pattern during the Late Triassic.

The Maori region appears differentiated by Middle Triassic, but showing no

relationship with later bivalve fauna. By Late Triassic times is better defined and shows affinities with the circum-Pacific biochorema.

The major bivalves biochoremas recognized for the Triassic, and their evolution, are congruent with those defined for other benthic marine invertebrates, particularly brachiopods, and in some general trends are even comparable with some pelagic organisms. Unlike the results obtained for brachiopods by other authors, the Early Triassic OBUs are closer to each other than to their equivalents in the Middle or Late Triassic.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data is included in the supplementary material.

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FIGURE/TABLE CAPTIONS

Fig. 1. Occurrence Ratio Profile (Brayard et al., 2006) for bivalve genera during the Triassic. The Occurrence Ratio indicates the proportion of regions in which a genus is found. Values close to 0 indicate endemic genera, while values of 1 indicate a cosmopolitan distribution.

Fig. 2. Palaeogeographic maps for the Triassic showing the biogeographic network for bivalves at a threshold of 0.62 (Simpson's coefficient of similarity) and the groups detected (modularity index: 0.526).

Fig. 3. Palaeogeographic maps for the Triassic showing the biogeographic network for bivalves at a threshold of 0.32 (Bray-Curtis' coefficient of similarity) and the groups detected (modularity index: 0.471).

Fig. 4. Comparison of the Occurrence Ratios of Paleozoic survivors vs. Triassic newcomers bivalve genera for the Early Triassic.

Table 1. Similarity coefficients values above the threshold value at the percolation point for some of the nodes with low number of genera.

	Simpson's coefficient		BrayCurtis' coefficient
	Australia Rhaetian (7 g.)		Australia Rhaetian (7 g.)
northwest Tethys	0.857	Australia Norian	0.526

Carnian			
northwest Tethys			
Rhaetian	0.857		
Australia Norian	0.714		
northwest Tethys			
mid-Triassic	0.714		
southern North			
Pacific Norian	0.714		
northwest Tethys			
Norian	0.714		
southeast Tethys			
Rhaetian	0.714		
southeast Tethys			
Norian	0.714		
	Australia Norian (12 g.)		Australia Norian (12 g.)
Australia Rhaetian	0.714	Australia Rhaetian	0.526
northwest Tethys			
Carnian	0.667	Australia Carnian	0.364
	northern Tethys Norian (5 g.)		northern Tethys Norian (5 g.)
northwest Tethys		northern Tethys	
Norian	0.800	Carnian	0.400
southern Tethys			
Norian	0.800		
	northern Tethys Carnian (5 g.)		northern Tethys Carnian (5 g.)
northwest Tethys		northern Tethys	
Carnian	1.000	Norian	0.400
southeast Tethys		western Pacific	
Rhaetian	0.800	Rhaetian	0.333
southern Tethys			
Rhaetian	0.800		
northwest Tethys			
Rhaetian	0.800		
southern Tethys			
Norian	0.800		
northwest Tethys			
Norian	0.800		
southern North			
Pacific Norian	0.800		
western Pacific			
Carnian	0.800		
northwest Tethys			
mid-Triassic	0.800		
northeast Tethys			
mid-Triassic	0.800		

	western Pacific Rhaetian (7 g.)		western Pacific Rhaetian (7 g.)
western Pacific Norian	0.857	western Pacific Norian	0.414
northwest Tethys Rhaetian	0.857	northern Andean Rhaetian	0.364
southern North Pacific Norian	0.714	northern North Pacific Rhaetian	0.353
southern North Pacific Rhaetian	0.714		
northern North Pacific Carnian (8 g.)		northern North Pacific Carnian (8 g.)	
southern North Pacific Norian	0.875	southern North Pacific Carnian	0.600
southern North Pacific Carnian	0.750		
northwest Tethys Carnian	0.625		
Australia Carnian (10 g.)			
		Australia Norian	0.364

Table 2. Similarity coefficient values between successive nodes for both polar regions.

	Simpson's coefficient		BrayCurtis' coefficient	
	Maori	Boreal	Maori	Boreal
Early Triassic/Middle Triassic	-	0.125	--	0.118
Middle Triassic/Carnian	0.000	0.222	0.000	0.154
Carnian/Norian	0.750	0.588	0.632	0.488
Norian/Rhaetian	0.684	0.941	0.634	0.780

Table 3. Mean/median values through time for the Bray-Curtis' and Simpson's similarity coefficients within and between the Tethys and eastern circum-Pacific biochoremas.

	Simpson's similarity			Bray-Curtis' similarity		
	Tethys	Tet/Circu m	Circum- Pacific	Tethys	Tet/Circu m	Circum- Pacific
Early Triassic	0.70/0.6 8	--	--	0.50/0.5 0	--	--
Middle Triassic	0.75/0.7 4	--	--	0.43/0.4 2	--	--
Carnian	0.57/0.5 8	0.37/0.40	0.53/0.50	0.24/0.2 5	0.18/0.16	0.33/0.26
Norian	0.54/0.5 8	0.42/0.40	0.63/0.63	0.30/0.3 1	0.26/0.25	0.47/0.43

	0.64/0.6			0.44/0.4		
Rhaetian	5	0.42/0.41	0.56/0.52	4	0.19/0.17	0.36/0.35

¹Supplemental Material (Tables S1-S6 and Figures S1-S7) is available. Please visit

<https://doi.org/10.1130/XXXX> to access the supplemental material, and contact editing@geosociety.org with any questions.

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Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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Highlights

- Network analysis to study the evolution of palaeobiogeographic patterns on bivalves
- The Early Triassic shows high similarity in bivalve composition among regions
- Endemicity increased during the Middle Triassic and reached a peak in the Carnian
- Tethys realm emerged in the Middle Triassic and consolidated in the Late Triassic
- East Panthalassa emerged in the Carnian and consolidated in the Norian-Rhaetian

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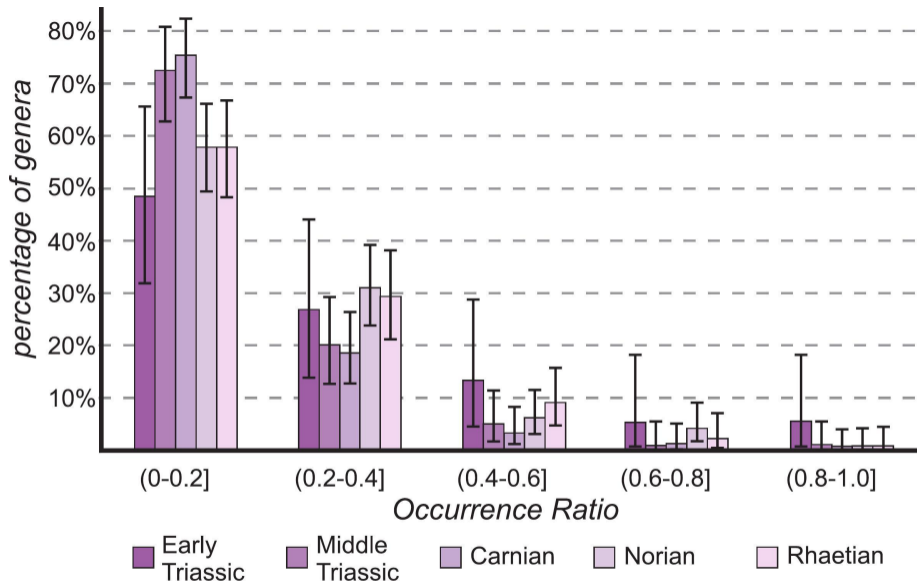


Figure 1

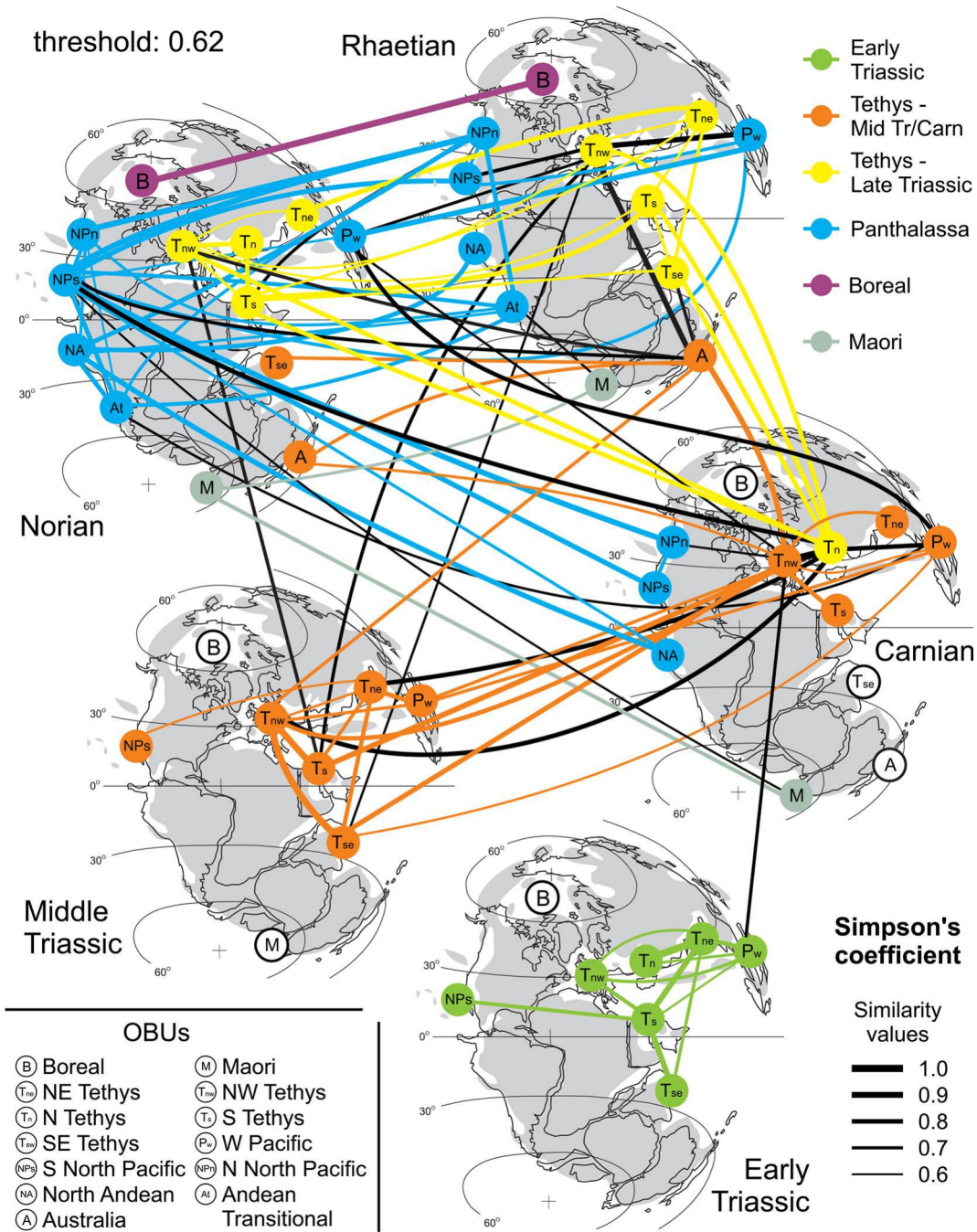


Figure 2

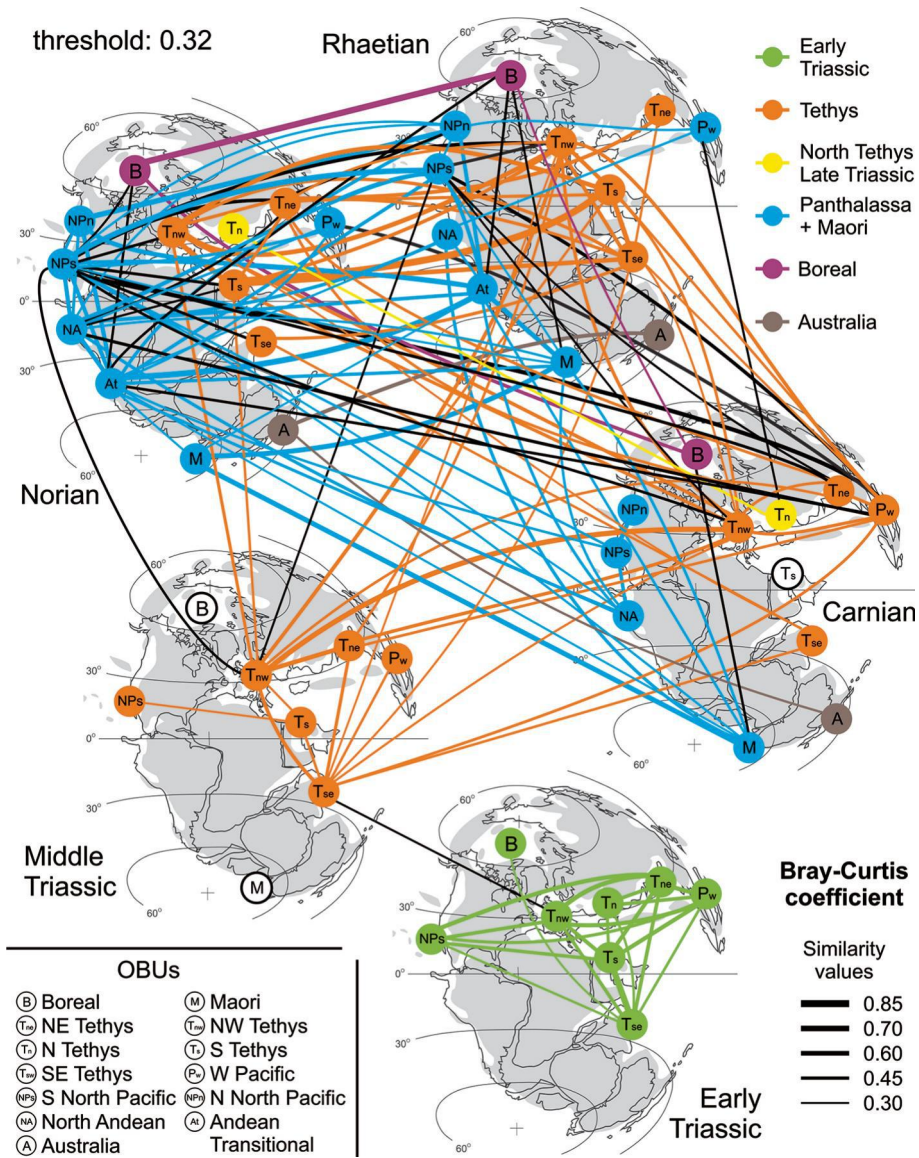


Figure 3

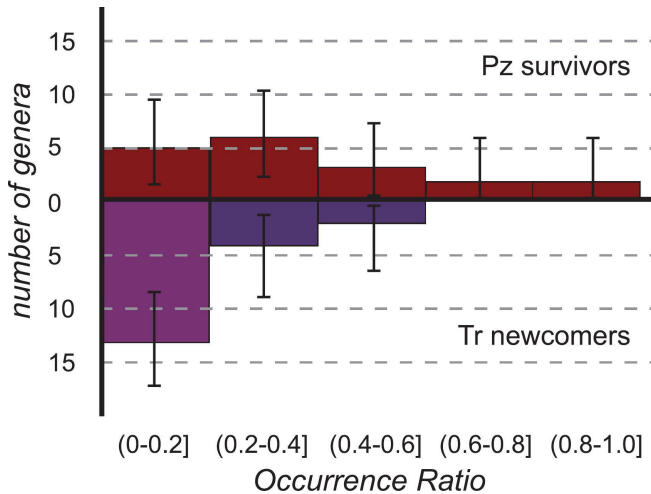


Figure 4