Palaeogeography, Palaeoclimatology, Palaeoecology 414 (2014) 133–145

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

Coexistence of brachiopod and bivalves in the Late Paleozoic of Western Argentina

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ARTICLE INFO

Article history:
Received 3 June 2014
Received in revised form 19 August 2014
Accepted 26 August 2014
Available online 3 September 2014

Keywords:
Coexistence
Competition
Brachiopods
Bivalves
Late Paleozoic
Argentina

ABSTRACT

The relationship between brachiopods and bivalves has been widely discussed in previous studies. Based on analyses at different temporal and spatial scales, several authors have argued either for the indifference or the interaction between the two clades. In this contribution we evaluate brachiopod and bivalve coexistence at two different spatial scales in a siliciclastic shelf developed during the Late Paleozoic in Western Argentina. At regional scale, bivalves were more diverse than brachiopods, although both had a similar total number and comparable distribution of occurrences. At local scale, however, multivariate analyses indicate that brachiopods and bivalves were segregated. Null models reinforce this pattern confirming the non-random co-occurrence pattern, and that the coexistence of brachiopods and bivalves was significantly low. In addition, multivariate analyses indicate that the biotic gradient neither followed the bathymetrical, nor a geographical or temporal gradient. The possibility that such segregation would have been caused by taphonomic (storm) reworking, was also disregarded considering multivariate analyses together with taphonomic evidence. The lack of environmental segregation between brachiopods and bivalves, coupled to analyses taking into account ecological guilds, indicates that possible factors controlling the segregation, such as turbidity, substrate or productivity were not relevant. As a whole, these results suggest a possible competitive interaction between brachiopods and bivalves at local scales. Interestingly, brachiopod–bivalve coexistence at regional scale did not foster local coexistence, indicating that the processes acting at these two scales are, at least partially, decoupled. Finally, the regional coexistence pattern suggests that the major transition between brachiopod and bivalve dominated communities was most probably related to processes acting at regional to biogeographic scales rather than to competition.

1. Introduction

The relationship between brachiopods and bivalves has been a matter of discussion for many years. While brachiopods were once the dominant clade in marine benthic communities during most of the Paleozoic (Thayer, 1979, 1985, 1986; Bambach, 1993; Peters, 2008), bivalves dominate such communities since the Mesozoic (Thayer, 1979; Valentine and Jablonski, 1983; Sepkoski, 1984). Because their Phanerozoic diversity trajectories appear to have opposite trends and both clades have similar life habits, some authors claimed that such pattern could have been the consequence of competitive interactions (Sepkoski, 1984, 1996). However, based also on global diversities and metabolic estimates, many authors concluded that brachiopods and bivalves were indifferent to each other (Gould and Calloway, 1980; Babin et al., 1992; Payne et al., 2014).

On the other hand, detailed paleoecological analyses have indicated that brachiopods and bivalves were not that indifferent. Several studies have shown that these groups tend to be segregated, often defining different biofacies or community types (Fürsich et al., 2001; Olszewski and Patzkowsky, 2001; Bonuso and Bottjer, 2006). These studies highlighted that brachiopods were more abundant in carbonate environments, while bivalves in siliciclastic settings (e.g., Tomašových, 2006b). Indeed, such differential environmental preference has been shown to explain large scale diversity trajectories of both clades (Peters, 2008). The preference for either environment, however, can be explained by different hypotheses because both settings differ in multiple characteristics such as productivity, turbidity and substrate stability (Peters, 2008; Nichols, 2009). In addition, all studies have been carried out in low latitude regions (e.g., Bonuso and Bottjer, 2006) and little is known from high latitude regions where carbonate environments do not commonly occur. Therefore, the analyses of brachiopod–bivalve co-occurrences in high latitudinal regions during intervals where both

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http://dx.doi.org/10.1016/j.palaeo.2014.08.022

clades were numerically and taxonomically abundant might shed light on the underlying factors controlling their distributions.

In this contribution we study the coexistence of brachiopods and bivalves at two different spatial scales (regional and local) from west-central Argentina during the Late Paleozoic (Upper Carboniferous–Early Permian), particularly in the youngest terms of Pennsylvanian–Cisuralian transgression, where the glacial sediments are absent due to the glaciers' retreat. The presence of a siliciclastic shelf at high to intermediate latitudes, coupled to the good knowledge of its fauna, provides an ideal place to analyze brachiopod–bivalve coexistence in the southwestern Gondwana margin.

2. Geological setting

The Late Paleozoic marine ingression of Western Argentina was developed on retroarc and arc-related basins (Astini et al., 2005), located at intermediate to high latitudes (~40° South, Geuna et al., 2010). The region has been classically divided in different depocenters, although similarities in the tectono-sedimentary evolution indicate a shared evolution of the whole region (López Gamundí et al., 1994; Astini et al., 2005). The latest Carboniferous–earliest Permian interval in the studied area is associated to a Paleo-Pacific transgressive event that represents the transition from the glacial to postglacial condition, characterized by the establishment of lakes and fjord embayments with the posterior climatic amelioration (López Gamundí, 1989; Limarino et al., 2002).

The combined effect of glacioeustatic sea-level rise and subsidence along basin margins allowed the creation of space to accommodate a transgressive systems' tract (TST), that can be recognized all along the studied area (Limarino et al., 2002). The basins record a siliciclastic shelf with a broad array of sedimentary environments, ranging from offshore to shallow-marine storm-dominated and tide-dominated deposits, and estuaries and deltaic systems. The predominant marine facies basinward are interbedded with fluvial deposits to the east (Desjardins et al., 2009, 2010; Limarino et al., 2013 and references cited therein).

The chronostratigraphic issues are well resolved in this region (Lech, 2002; Gulbranson et al., 2010; Barredo et al., 2011; Césari et al., 2011) and paleontological data widely known (Césari et al., 2007 and references therein cited). Invertebrate faunas have been studied in several lithostratigraphic units in two main areas: Río Blanco–Western Paganzo basins in the north and Calingasta–Uspallata in the south (Fig. 1). The marine fauna is composed of brachiopods (rhynchonelliformeans and linguliformeans), bivalves, gastropods and ostracods. Brachiopods and bivalves considered in this analysis are well known by many contributions that have dealt with systematic (Manceñido et al., 1977; González, 1997; Taboada, 1998, 2006; Cisterna and Simanauskas, 2000; Sterren, 2000, 2004; Archbold and Simanauskas, 2001; Cisterna et al., 2002; Archbold et al., 2005; Cisterna and Sterren, 2007; Cisterna, 2011); In addition, information concerning the biostratigraphic (Cisterna et al., 2006; Cisterna, 2010) and taphonomic (Sterren, 2000, 2008) aspects are well known.

The marine invertebrates associated with this transgression belong to the *Tivertonia jachalensis*–*Streptorhynchus inaequiornatus* zone, originally considered Moscovian–Kasimovian (Sabattini et al., 1990) and Asselian by other authors (Cisterna et al., 2002; Archbold et al., 2004). However, the recent radiometric ages support a Late Carboniferous age for this zone (Gulbranson et al., 2010; Césari et al., 2011). To the south of the Calingasta–Uspallata Basin, the fauna integrates the *Costatumulus amosi* zone (Taboada, 1998), considered Early Permian by Cisterna (2010) and Late Sakmarian–Early Artinskian by Taboada (2010).

3. Data

3.1. Sampling and dataset

More than fifty samples coming from six different formations in two related basins were obtained for these analyses (Fig. 1, Supplementary information). Most of this dataset has been published elsewhere for taphonomic, biostratigraphic or systematic analysis. In previous contributions, many samples were lumped as single assemblages, however we here used the original samples.

Although all body fossils were collected, only brachiopods and bivalves are analyzed. Fossils were identified to the lowest taxonomic level possible but the analysis is performed at generic level. While relative abundances record important information for paleoecological studies (Ludvigsen et al., 1986), presence–absence datasets register similar information for multivariate paleoecological analyses (Olszewski and Patzkowsky, 2001; Balseiro et al., 2011). The final dataset consists of 55 samples and 247 occurrences of 26 brachiopod and 35 bivalve genera.

We modified the dataset two different ways. First, an exhaustive dataset was created by removing all monospecific samples. The exhaustive dataset contains 42 samples and 60 genera. Second, a restrictive

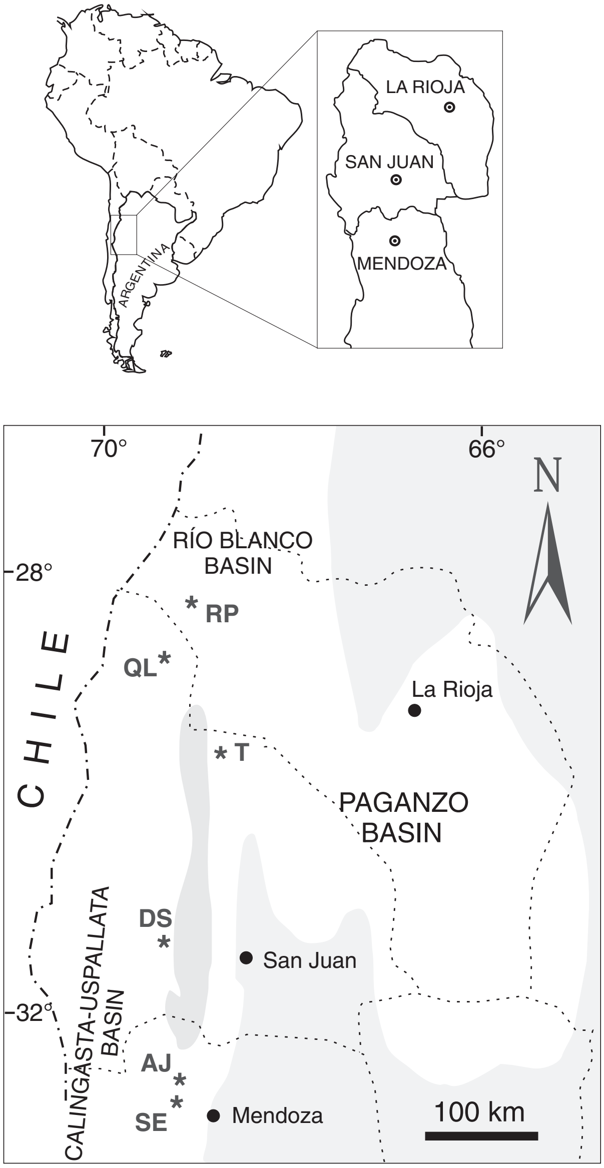

Fig. 1. Map of South America indicating the location of the studied region, and detailed map showing paleogeography of the basins and sampled formations (and localities). RP: Río del Peñon Formation (Anticlinal del Río Blanco), QL: Quebrada Larga Formation (Quebrada Larga), T: Tupe Formation (Quebrada de la Herradura and Quebrada de la Delfina), DS: Del Salto Formation (Quebrada del Salto), AJ: Agua del Jagüel Formation (Quebrada de Agua de Jagüel), SE: Santa Elena Formation (Quebrada de Santa Elena).

dataset was created by removing all monospecific samples and genera present in only one sample. The restrictive datasets contains 42 samples and 37 genera.

3.2. Environmental assignment

The samples were environmentally classified on the basis of the sedimentological analysis available (e.g., Archangelsky et al., 1987, 1996; Desjardins et al., 2009; Henry et al., 2010; Dineen et al., 2013). Following Walker and Plint (1992) we used three main depositional environments: shoreface for environments above fair weather wave base, offshore transition for environments between fair weather and storm wave base and offshore for environments below storm wave base. The same environmental classification was used by Sterren (2008) for taphonomic analyses.

3.3. Geographical and temporal distribution

Although the basins in the region studied were probably related (Astini et al., 2005), the distinction of a northern (Western Paganzo–Río Blanco) and a southern (Calingasta–Uspallata) basin is useful as a simple proxy for the study of geographical differences in the area Therefore, we used it to classify all samples geographically.

We also differentiate samples between two biozones, namely the *Tivertonia jachalensis–Streptorhynchus inaequiornatus* and the *Costatumulus amosi* zones. Some authors have argued that these two zones could be chronologically equivalent, and their differences were caused by their geographic position in the basin (Cisterna, 2010). In any case, distinguishing the two assemblages is a conservative test for possible compositional differences between them (Taboada, 2006).

3.4. Taphonomy

Each sample comes from single bed, represented either as a fossil concentration or as fossils dispersed in the matrix. Sterren (2008) developed a taphonomical classification scheme for Upper Paleozoic fossil concentrations from Western Argentina. Based on different taphonomic attributes, Sterren (2008) recognized fourteen types of fossil concentrations. Ten out of the fourteen were present in the whole dataset (Supplementary information), while only eight types are represented in the exhaustive dataset, namely CF1, CF4A, CF4B, CF4C, CF5A, CF5B, CF6, and CF9B. To test for taphonomic biases, we classified each sample according to this scheme. Following Tomašových (2006b) we differentiated between reworked and non-reworked concentrations. According to the analysis performed by Sterren (2008), concentrations CF1, CF4A, CF4B, CF4C, and CF5B evidenced reworking, while concentrations CF9B, CF6, and CF5A did not.

3.5. Guilds

All genera were ecologically classified in different guilds. The definition of guilds might or might not take into account taxonomic classification (Simberloff and Dayan, 1991). Due to the scope of our analysis we preferred not to use taxonomic classification as a variable. We defined two major guilds based on substrate usage, an epifaunal guild and an infaunal guild. Following (Thayer, 1979, 1983) we classified all semi-infaunal taxa as epifaunal.

Some authors (e.g., Tomašových, 2006a) have used gill type to differentiate guilds in bivalves. However, in our dataset all infaunal bivalves are eulamellibranch bivalves while all epifaunal are filibranchs, hence the current guild definition includes the differences in gill types.

3.6. Mineralogical composition

We coded the major mineralogical composition of each genus in the dataset. Three possible compositions were used, namely 1) low Mg calcite, 2) aragonite, and 3) phosphatic. The data was obtained from the Paleobiology Database (Aberhan et al., 2004; Clapham, 2011).

4. Analytical methods

For the study of paleoecological patterns we used multivariate analysis. First, we employed a two way cluster analysis (Patzkowsky and Holland, 2012), using Bray–Curtis distance and Ward's clustering method. The Bray–Curtis distance is the most common distance for ecological analysis (Legendre and Legendre, 1998). The Ward's clustering method minimizes the within-group sum of squares (Borcard et al., 2011). It needs to be remarked that although the Ward's method is based on an Euclidean model, it produces meaningful results even with non-Euclidean distances such as Bray–Curtis (Borcard et al., 2011). For the two-way cluster analysis we used the heatmap() function in R (R Development Core Team, 2010) and the vegdist() function in the vegan package for R (Oksanen et al., 2010).

Second, we used multivariate ordination to assess the relationship between samples and taxa. Contrary to cluster analysis, ordinations do not tend to create groups and show gradients in a better way (Legendre and Legendre, 1998). Nonmetric Multidimensional Scaling (NMDS) was used for the ordination analysis. NMDS creates an *n* dimension sample map that preserves the ordering relationships among objects, but not the actual distances between them (Legendre and Legendre, 1998). A stress function is used to measure the goodness of fit of the results. The NMDS has the great advantage of not making a priori assumptions of the data (Shi, 1993) and recovers better underlying gradients than other techniques (Kenkel and Orloci, 1986). A two dimension NMDS was performed using the metaMDS() function available in the vegan package for R (Oksanen et al., 2010). The selected distance metric was the Bray–Curtis and 100 random starts were used to search for stable solutions.

To test for statistical significance of taxonomic composition among samples we used nonparametric MANOVA (Anderson, 2001). Nonparametric MANOVA, also known as permutational MANOVA or PERMANOVA, is based on the partition of sum of squares of a given distance matrix, and contrary to parametric MANOVA it has the advantage of allowing the use of different distances such as Bray–Curtis and not being sensitive to correlation between variables (Anderson, 2001). Moreover, although it is sensitive to dispersion effects, nonparametric MANOVA performs better than ANOSIM (Warton et al., 2012). We carried out the nonparametric MANOVA using adonis() function in the vegan package for R (Oksanen et al., 2010) using 5000 permutations for the estimation of p-values.

We also tested for homogeneity of multivariate dispersion as a priori test for nonparametric MANOVA. Multivariate dispersion was measured as the distances to the centroid in a space defined by a principal coordinate analysis using Bray–Curtis distance (Anderson, 2006) This procedure was performed using the betadisper() function in the vegan package for R (Oksanen et al., 2010). We used the Bray–Curtis distance for all multivariate analysis (i.e., NMDS, npMANOVA and multivariate dispersion).

We used nonparametric Kruskal–Wallis test for statistical comparisons between medians using the kruskal.test() function in R, and the Kolmogorov–Smirnoff test to compare distributions using the ks.test().

We used null models to test whether co-occurrence patterns between bivalves and brachiopods were different from expected by chance. Co-occurrence null models randomize the occurrence matrix and compare if empirical co-occurrences match the random ones. There are different methods based on the constrains used for the randomization of the matrix (Gotelli and Graves, 1996). We used the fix–fix method which keeps the row and column sums. This means that in each random matrix each sample has the same richness as the original matrix, and each taxon has the same number of occurrences. We used two difference indexes to estimate the co-occurrence, the C-score and the number of checkboards (Gotelli and Graves, 1996). The number of checkboards measures the total amount of species that never co-occur in the matrix. This index, however, is sensitive to sampling problems (Gotelli, 2000). On the other hand, the C-score is based on the average co-occurrence of all species pairs, and it has been shown to be the most stable and robust index (Gotelli, 2000). Null model analyses were performed in R with the commsimulator() function in the vegan package (Oksanen et al., 2010) using the quasiswap method (Miklós and Podani, 2004) with 5000 permutations. We further calculated standardize effect size (SES) in order to see how different is the empirical co-occurrence index from the random distribution. SES is calculated as

$$SES = (I_{obs} - I_{sim})/Sd_{sim}$$

where I_{obs} is the observed index, I_{sim} is the mean of all simulated indexes and Sd_{sim} is the standard deviation of all simulated indexes.

Standard co-occurrence null models indicate if the whole matrix co-occurrence pattern is random. To know which are the actual pairs that are co-occurring more or less frequently than random, is more complicated to analyze because individual pairs are not independent (Gotelli and Ulrich, 2010). Recently, Gotelli and Ulrich (2010) developed a method to test this. It consists of recognizing the significant pairs using confidence limits based on the random distributions (standard CL method) and further restricting these significant pairs using an empirical Bayes approach. This empirical Bayes has two methods of restricting the significant pairs depending on how they are chosen. The Mean Bayes approach is less restrictive, while the CL Bayes approach is the most conservative one (See detailed description of the method in Gotelli and Ulrich, 2010). The analysis of significant pairs was carried out in Pairs (Ulrich, 2008), using the C-score and 5000 permutations.

5. Results

5.1. Cluster analysis

The two-way cluster analysis of the restrictive dataset indicates two clearly defined sample groups that largely coincide with two major clusters of taxa (Fig. 2). The first sample group coincides with a cluster mainly composed by brachiopods with a few bivalves (Fig. 2). Indeed all brachiopods in the dataset group together in this cluster, and bivalves that are present are either rare or not identified to the genus level. The most frequent taxa in this cluster are *Septosyringothyris*, *Tivertonia*, and *Costatumulus*. The second sample group is characterize by bivalve dominated samples and coincides with the cluster containing exclusively bivalves (Fig. 2). The most common genus is *Modiolus* followed by *Schizodus*.

The cluster analysis of the exhaustive dataset reveals a similar pattern, but also some differences. On the one hand, the sample groups are basically the same with those observed in the restrictive analysis (Fig. 2), with a bivalve dominated group and a brachiopod dominated one. On the other hand, however, genera do not cluster in two clear groups but in three major groups. One large cluster contains all brachiopods plus some bivalves. Most of these bivalves are rare, being present in few samples. Another cluster groups are almost exclusively bivalves which tend to be present in many samples with the exception of a rare brachiopod (*Rhynchopora*), while a third cluster is formed by bivalves present only in one particular sample (DS Nivel D).

Regardless of slight differences, both results highlight the presence of two major groups which will be called brachiopod and bivalve sample groups. All samples dominated by brachiopods compose the brachiopod sample group, while all samples dominated by bivalves compose the bivalve sample group.

5.2. Ordination analysis

Results of the ordination analysis are similar to those results observed in the cluster analysis. In both restrictive and exhaustive ordinations there is a clear segregation of brachiopod and bivalve genera, and of brachiopod- and bivalve-dominated samples (Fig. 3). In the exhaustive dataset, however, there is a higher superposition of brachiopods and bivalves than in the restrictive dataset. The opposite occurs for sample groups where brachiopod-dominated samples tend to be more segregated from bivalve dominated samples in the exhaustive than

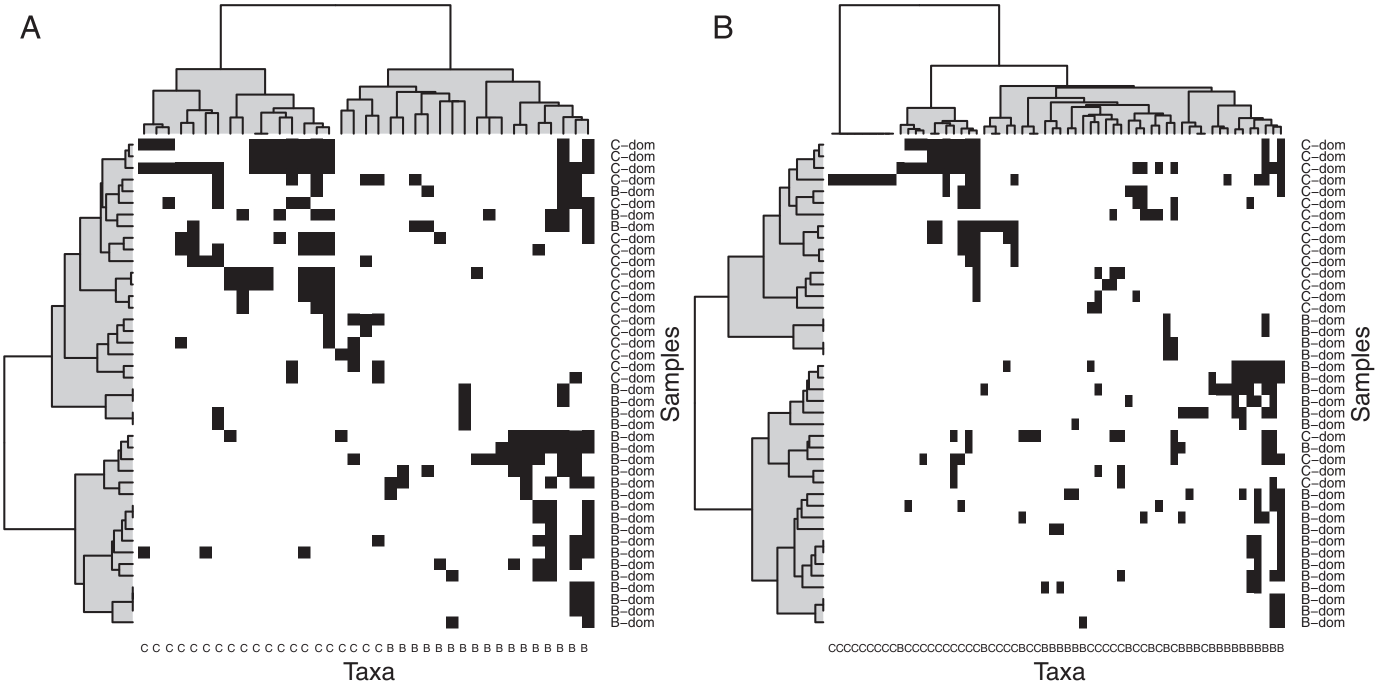

Fig. 2. Two way cluster analyses. A) Restrictive dataset. B) Exhaustive dataset. C: Bivalves, B: Brachiopods, C-dom: samples dominated by bivalves (bivalve sample group), B-dom: samples dominated by brachiopods (brachiopod sample group).

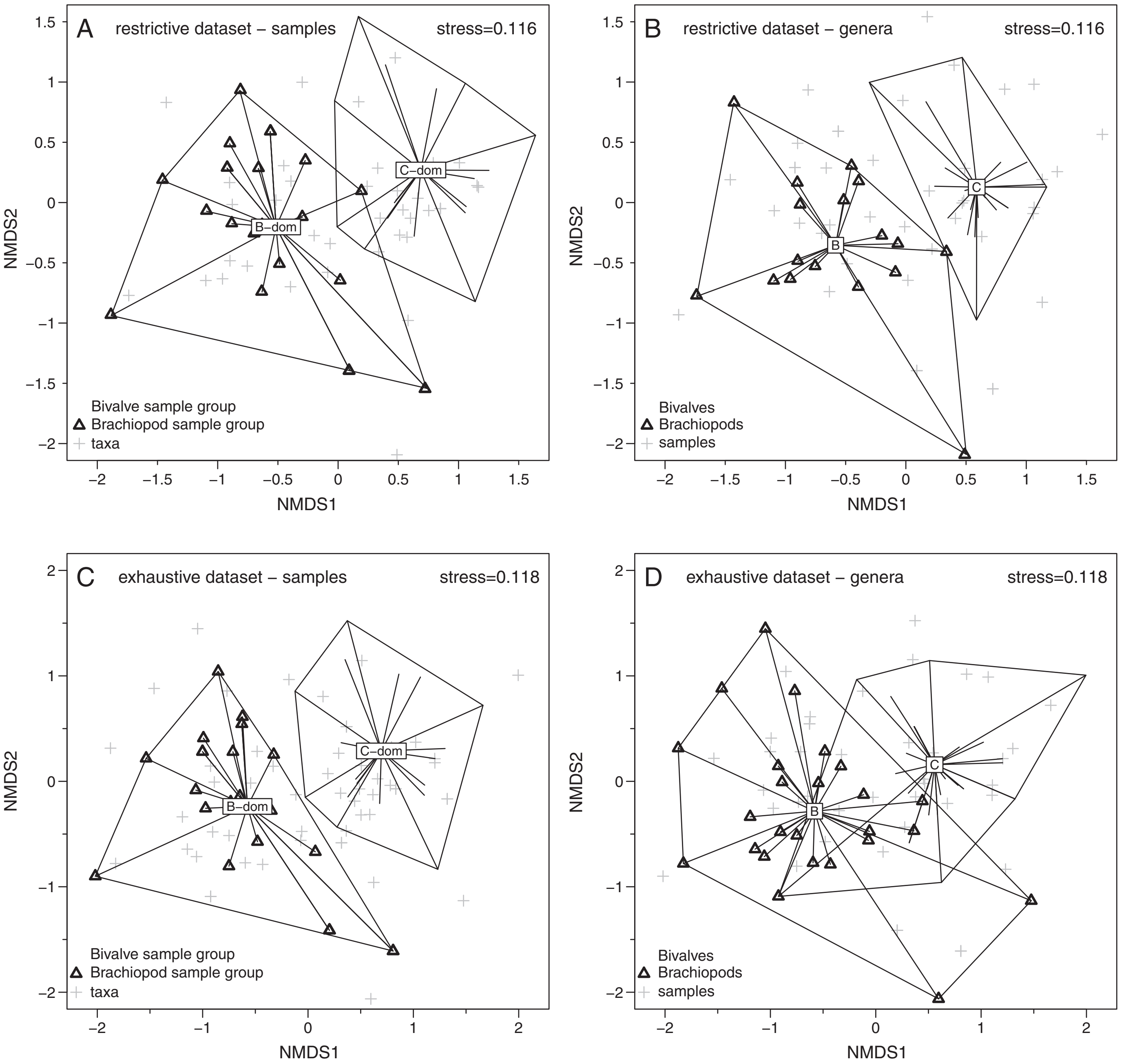

Fig. 3. A–B) NMDS of the restrictive dataset. A) Sample groups, B) taxa. C–D) NMDS of the exhaustive dataset. C) Sample groups, B) taxa. C: Bivalves, B: brachiopods. Note that samples and taxa are plotted in the same multidimensional space.

the restrictive dataset (Fig. 3). For the sake of simplicity, all further results are shown based on the exhaustive dataset exclusively.

The nonparametric MANOVA indicates significant segregation between brachiopods and bivalves genera for both the exhaustive (homogeneity of dispersion $p = 0.3943$; npMANOVA $p < 0.001$) and the restrictive (homogeneity of dispersion $p = 0.2797$; npMANOVA $p < 0.001$), suggesting that brachiopods co-occur more frequently with other brachiopods than with bivalves. In addition, the taxonomic composition between brachiopod- and bivalve-dominated samples is significantly different for both dataset (exhaustive: homogeneity of dispersion $p = 0.8966$; npMANOVA $p < 0.001$; restrictive: homogeneity of dispersion $p = 0.9533$; npMANOVA $p < 0.001$).

Brachiopods and bivalves seem to independently describe biotic gradients, because the gradients are more or less perpendicular to each other. However such pattern is probably an artifact caused by the extreme ends of each possible gradient, while most taxa are indeed distributed in a non-lineal pattern. Independent analyses of brachiopods and bivalves confirm that there is no clear linear trend in either case (results not shown).

5.2.1. Environmental distribution

To further understand if the ordination is related to an environmental gradient, we plotted depositional environments in the ordination space. In Fig. 4A we can observe that there is high superposition between samples coming from different depositional environments. Nevertheless, shallow subtidal samples tend to have higher values of the second axis, suggesting a possible though weak environmental gradient along that axis. Taxonomic composition, however, is not statistically different between all three depositional environments (npMANOVA $p = 0.171$). Analyzing brachiopods and bivalves independently also fails to indicate a relationship between depositional environments and biotic gradients, as the nonparametric MANOVA indicates that in both cases there are no compositional differences between depositional environments (brachiopods npMANOVA $p = 0.42$, bivalves npMANOVA $p = 0.11$).

5.2.2. Geographical and temporal distribution

We also analyzed compositional differences between the different basins and zones. In Fig. 4B–C we can observe that samples coming from both basins and zones are largely superposed in the ordination space. Nonetheless, the npMANOVA indicates that there are compositional differences between basins (homogeneity of dispersion $p = 0.7082$; npMANOVA $p = 0.032$), but not between zones (npMANOVA $p = 0.089$).

Despite these differences in composition, both basins still show the segregation between bivalve and brachiopod genera and between bivalve and brachiopod sample groups (Table 1).

5.2.3. Epifauna vs. infauna

Fig. 5A shows that there is substantial superposition between epifauna and infauna in the ordination space. Moreover, the nonparametric MANOVA does not show a significant segregation between infauna and epifauna (Fig. 5A; npMANOVA $p = 0.393$).

On the other hand, when we restrict the study to the epifauna, the results still show the differentiation between brachiopods and bivalves and between the brachiopod and bivalve sample groups (Fig. 5B–C). Again, the npMANOVA confirms the significance of these differences between taxa (Fig. 5C; homogeneity of dispersion $p = 0.708$; npMANOVA $p < 0.001$) and sample groups (Fig. 5B; homogeneity of dispersion $p = 0.896$; npMANOVA $p < 0.001$).

5.2.4. Storm reworking

For the analyses of taphonomical sorting we followed the methodology proposed by Tomašových (2006b). The rational is that if an original community was sorted by storm reworking, then reworked and non-reworked samples should differ in composition, hence in a multivariate compositional space (e.g., NMDS) they should not overlap (Tomašových, 2006b). Because reworking was not determined based on the taxonomic composition of the fossil concentration but on taphonomic attributes (Sterren, 2008), it is possible to test for compositional differences between reworked and non-reworked concentrations avoiding any circular argument.

In Fig. 6A we can observe that there is no correspondence between bivalve and brachiopod sample groups and reworked and non-reworked assemblages. Compositional difference between concentrations clearly showing reworking and those showing either very little or no reworking is marginally significant (homogeneity of dispersion $p = 0.12$, npMANOVA $p = 0.045$). Nevertheless, if we restrict the analysis to non-reworked samples, the differentiation between brachiopod and bivalve sample groups is still clearly present (Fig. 6B; homogeneity of dispersion $p = 0.46$; npMANOVA $p = 0.001$).

Neither the brachiopod nor the bivalve sample groups show evidence of significant sorting as there is no compositional differences between reworked and non-reworked samples in each sample group. In Fig. 6C–D we can observe that in the case of the brachiopod sample group compositional differences are virtually absent (npMANOVA $p = 0.31$), while in the bivalve sample group there are some weak insignificant differences (npMANOVA $p = 0.06$).

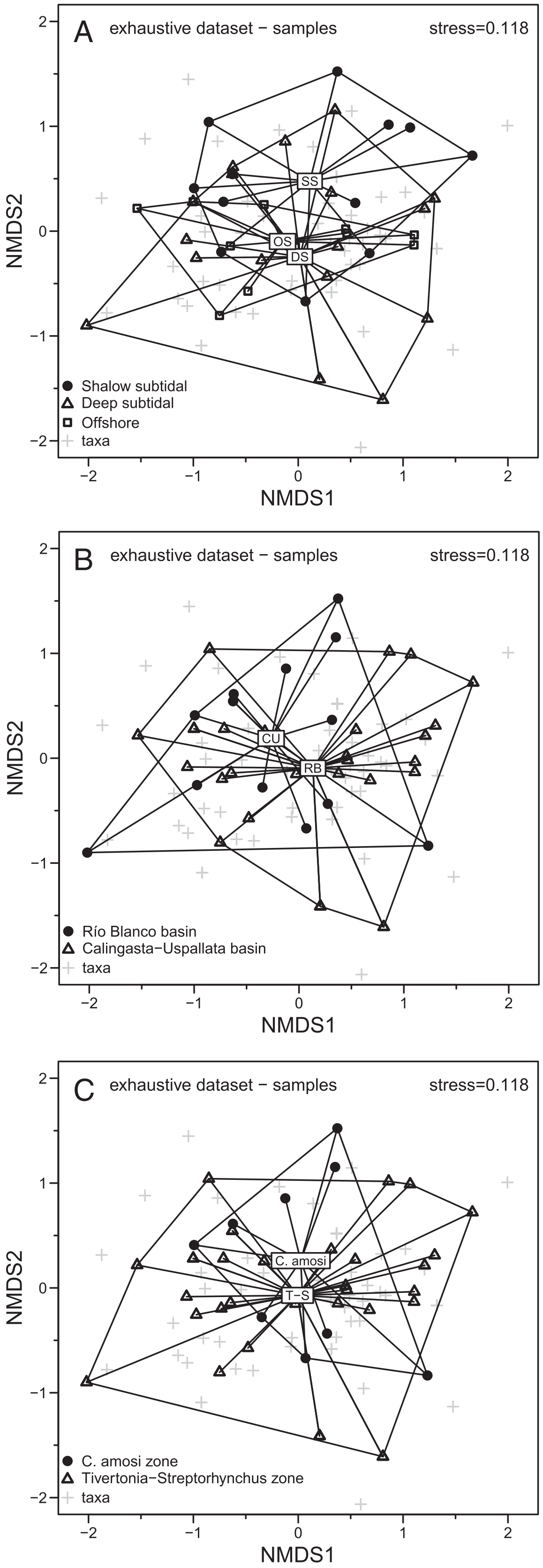

Fig. 4. NMDS of the exhaustive dataset showing A) depositional environments, B) basins, and C) zones. SS: shallow subtidal, DS: deep subtidal, OS: offshore, CU: Calingasta Uspallata basin, RB: Río Blanco Basin, C. amosi: *Costatumulus amosi* zone, T–S: *Tivertonia–Streptorhynchus* zone.

Table 1
npMANOVA for segregation between brachiopods and bivalves within basins.

Basin	Comparison	Homogeneity of dispersion	npMANOVA
Río Blanco–Western Paganzo	Genera	$p = 0.611$	$p < 0.001$
	Sample groups	$p = 0.217$	$p < 0.001$
Calingasta–Uspallata	Genera	$p = 0.4914$	$p < 0.001$
	Sample groups	$p = 0.3694$	$p < 0.003$

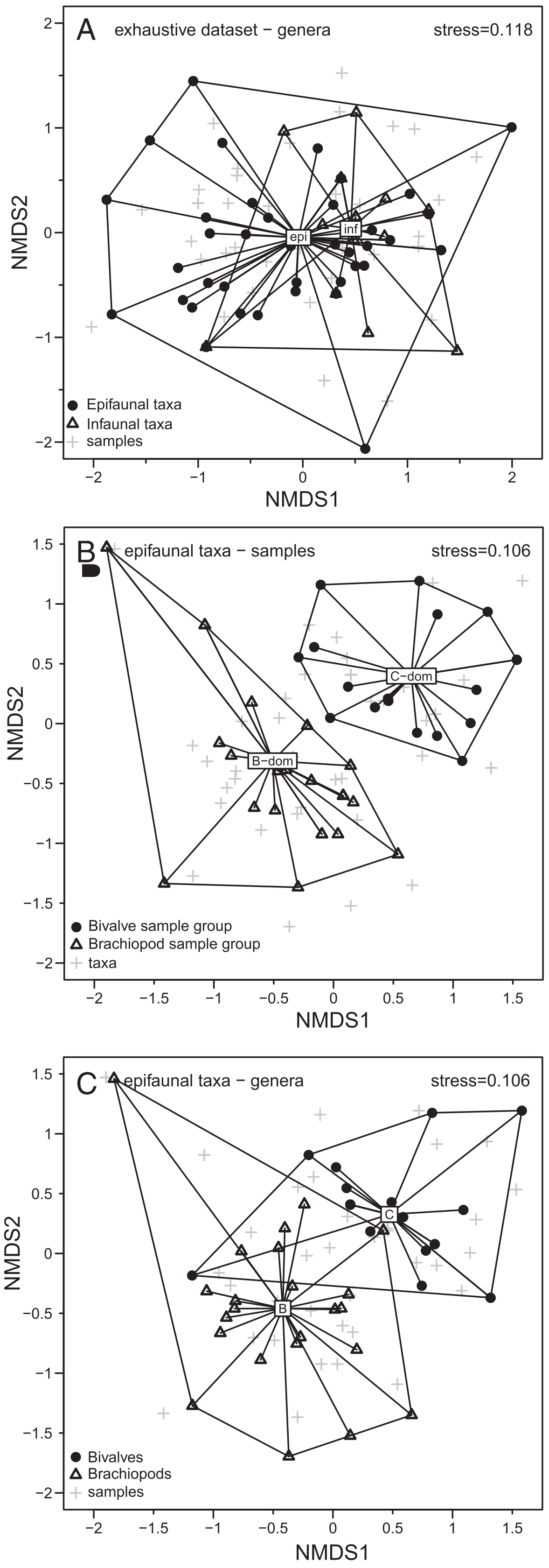

Fig. 5. A) NMDS of the exhaustive dataset showing overlap between epifaunal and infaunal genera. B–C) NMDS of the epifaunal taxa only showing segregation of B) sample groups and C) clades.

5.2.5. Aragonite dissolution

We tested if aragonite dissolution had significant effect on the observed pattern by restricting the analysis to calcite taxa. The ordination shows that even for calcite taxa the segregation between brachiopods and bivalves is still present, as well as the differentiation of brachiopod and bivalve sample groups (Fig. 7A). The nonparametric MANOVA confirms this pattern for brachiopod vs. bivalves (homogeneity of dispersion $p = 0.29$, npMANOVA $p = 0.001$) and brachiopod sample group vs. bivalve sample group (homogeneity of dispersion $p = 0.76$, npMANOVA $p = 0.001$). Moreover, if aragonite dissolution was the responsible factor for the observed pattern, we would expect a similar brachiopod richness in both brachiopod and bivalve sample groups, but this is not observed (Fig. 7B; Kruskal–Wallis test, $X^2 = 14.28$, $p = 1.6 \times 10^{-04}$).

5.3. Brachiopod and bivalve co-occurrence pattern

At regional scale bivalves are more diverse than brachiopods (35 and 26 respectively), although they have similar number of occurrences (128 and 119). The distributions of bivalve and brachiopod occurrences, however, have qualitative differences. The brachiopod distribution shows few frequent taxa and many rare ones, while the bivalve distribution is less dominated having many taxa with intermediate frequencies (Fig. 8A). Nevertheless, these differences are not significant based on a Kolmogorov–Smirnoff test ($D = 0.1543$, $p = 0.8783$). At sample scale, however, the pattern of coexistence is not evident. The histogram of proportion of brachiopod genera per sample shows that there is a clear bimodal distribution (Fig. 8B). A large number of samples have high proportion of brachiopod genera, while another large number have high proportion of bivalve genera, and fewer have bivalves and brachiopods with similar richness.

To actually test bivalve–brachiopod co-occurrence at sample scale we used a null model (Connor and Simberloff, 1979). Results from the null model indicate that genus co-occurrence is not random in our dataset. In particular the dataset shows a segregated pattern, indicating that genera co-occur less frequently than expected by chance (C-score = 9.14, $p = 0.0016$, SES = 3.14). The number of checkboard units indicates that this co-occurrence pattern is caused by species pairs that never coexist (checkboard index = 1260, $p = 0.005$).

To further understand the co-occurrence patterns we analyzed the significance of all genera-pairs (Gotelli and Ulrich, 2010) and classified them in three kinds of pairs: (1) brachiopod–brachiopod (B–B) pairs, (2) bivalve–bivalves (C–C) pairs, and (3) brachiopod–bivalve (B–C) pairs. The analysis with the simple CL criterion indicated that 44 pairs had significant co-occurrence patterns, most being aggregated (Table 2). However, the Mean Bayes and the CL Bayes approaches further restricted the number of significant pairs to 24 and 16 pairs respectively (Table 2).

When we classify each pair, a clearer pattern can be recognized On the one hand, all significant B–B and C–C pairs have aggregated co-occurrences (Table 2). This indicates that both brachiopods and bivalves tend to occur with other genera of the same clade more frequently than expected by chance. On the other hand, all significant segregated pairs were B–C pairs (Table 2). Although the number of segregated pairs is low compared to aggregated pairs, this result reinforces the one observed in the ordination analysis. Moreover, these results show that the pattern of genera pairs that never coexist found with the whole matrix checkboard analysis is driven only by the non-co-occurrence of brachiopods with bivalves.

6. Discussion

The ordination analyses and the co-occurrence null model indicate that brachiopod taxa coexisted more frequently with other brachiopods than with bivalves and vice versa. A segregated pattern between brachiopods and bivalves has also been recognized in other basins

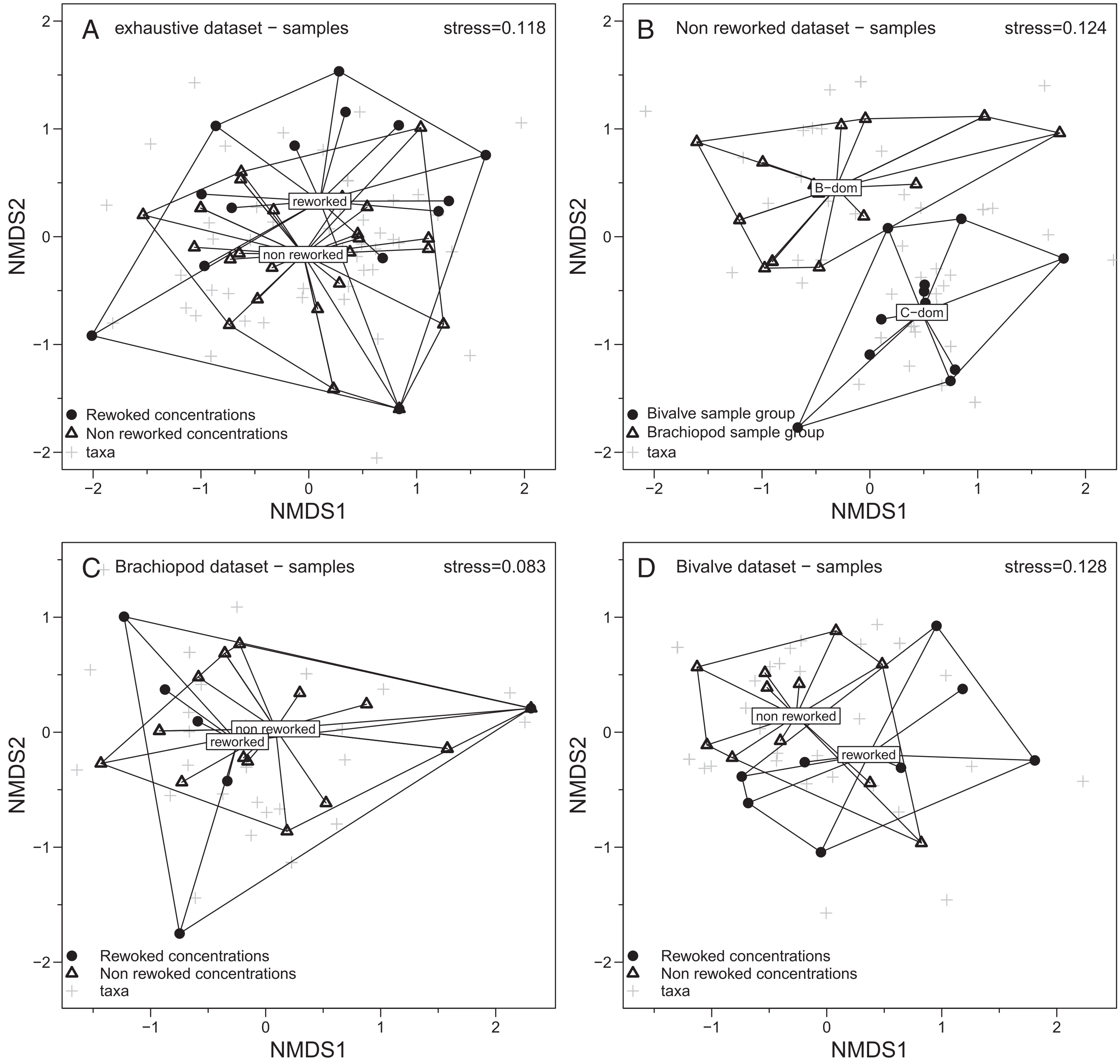

Fig. 6. A) NMDS of the exhaustive dataset showing overlap between reworked and non-reworked concentrations. B) NMDS of non-reworked concentrations showing segregation between sample groups. C) NMDS of brachiopods showing overlap between reworked and non-reworked concentrations. D) NMDS of bivalves showing overlap between reworked and non-reworked concentrations.

around the world during the Late Paleozoic (e.g., Malinky and Heckel, 1998; Olszewski and Patzkowsky, 2001; Bonuso and Bottjer, 2006) and Triassic (Tomašových, 2006a). However, there are some major differences between what is observed in Western Argentina and the pattern observed by other authors. We will first tackle some possible biases that might explain the observed pattern and then discuss other possible interpretations.

6.1. Biases in the brachiopod–bivalve coexistence pattern

6.1.1. Taphonomic biases

A possible explanation for the segregation between brachiopods and bivalves is differential sorting between them. Storm reworking could have sorted the original mixed brachiopod–bivalve community in two residual assemblages (Westrop, 1986; Tomašových, 2006b), dominated by brachiopods and bivalves respectively. Hence, the bivalve and brachiopod sample groups could actually be a taphonomic overprint instead of the original pattern. However, our results do not support this hypothesis because the multivariate analysis showed that sorting was very low or absent, and the non-reworked samples still showed the segregation between brachiopods and bivalves.

Another major taphonomic bias could be early aragonite dissolution, which has been claimed to be a major factor affecting community composition for the Paleozoic fossil record (Malinky and Heckel, 1998; Cherns and Wright, 2009). Cherns and Wright (2009) have shown that many typical Paleozoic brachiopod-dominated assemblages were actually dominated by molluscs that were later dissolved in diagenesis. It is very likely that faunas from Western Argentina were similarly skewed by diagenesis, creating the segregated pattern between brachiopods and bivalves described above. However, the high diversity of aragonite bivalves compared to calcite ones in our database is a first indication that dissolution was not strong. Moreover, our results show

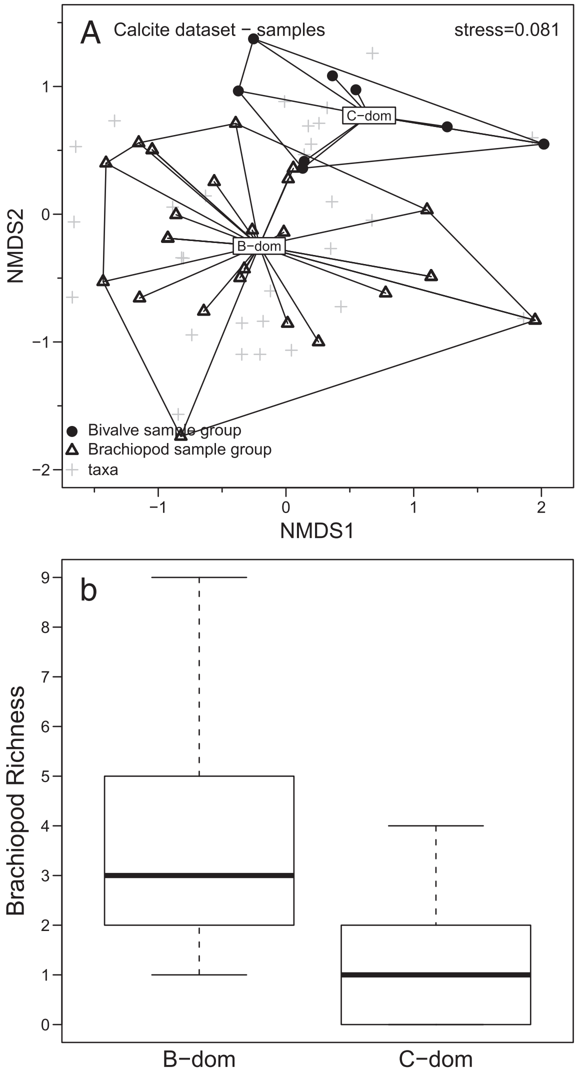

Fig. 7. A) NMDS of calcite genera showing segregation of sample groups. B) Boxplot of brachiopod richness in the brachiopod and bivalve sample groups. Box plots show medians, first, and third quartiles; whiskers extend to 1.5 times the interquartile range from the box. C-dom: Bivalve sample group, B-dom: brachiopod sample group.

that even in the analysis of calcite taxa the coexistence pattern between brachiopods and bivalve is still present, minimizing the relevance of dissolution.

6.1.2. Geographical or temporal patterns

It is also possible that the co-occurrence pattern for brachiopods and bivalves at observed sample scale is actually a pattern at a larger geographical (i.e., position along the basins) or temporal (i.e., biozone) scale. In other words, we could expect that bivalves dominated samples from one basin or temporal bin, while brachiopods from the other. In this respect, we showed that composition did not vary between biozones, disregarding the likely temporal bias. However, compositional changes between basins were present, underscoring a possible geographical bias. Nevertheless, such differences between basins might not imply that coexistence of bivalves and brachiopods was structured at this scale. It is possible that each basin held a particular composition while still maintaining the brachiopod–bivalve segregation. This latter possibility is the most plausible given that brachiopods and bivalves still do not coexist at sample scale within each region.

6.2. Segregation between brachiopods and epifaunal bivalves

6.2.1. Environmental factors

The different preferential occurrences in carbonate and siliciclastic marine shelf environments have been shown to be a major extrinsic factor controlling bivalve and brachiopod coexistence and distribution (Olszewski and Patzkowsky, 2001; Tomašových, 2006a; Peters, 2008). Unfortunately, because these two environments differ greatly in all such characteristics it has been difficult to differentiate which factor is the most important in each case (Peters, 2008; Nichols, 2009). Although there is no single environmental factor that explains this segregation, different studies indicated that brachiopods and bivalves usually occupy disparate portions of the environmental gradient (Fürsich et al., 2001; Tomašových, 2006a). Brachiopods have been shown to be dominant in either carbonate, deep (carbonate and siliciclastic), or open marine environments, while bivalves dominated siliciclastic, paralic or near-shore ones (Olszewski and Patzkowsky, 2001; Tomašových, 2006a). However in the central western Argentinian basins, the environmental segregation of brachiopods and bivalves has not been identified. Therefore, the segregated pattern observed in western Argentinian faunas has interesting contrasts to similar ones described mostly for lower

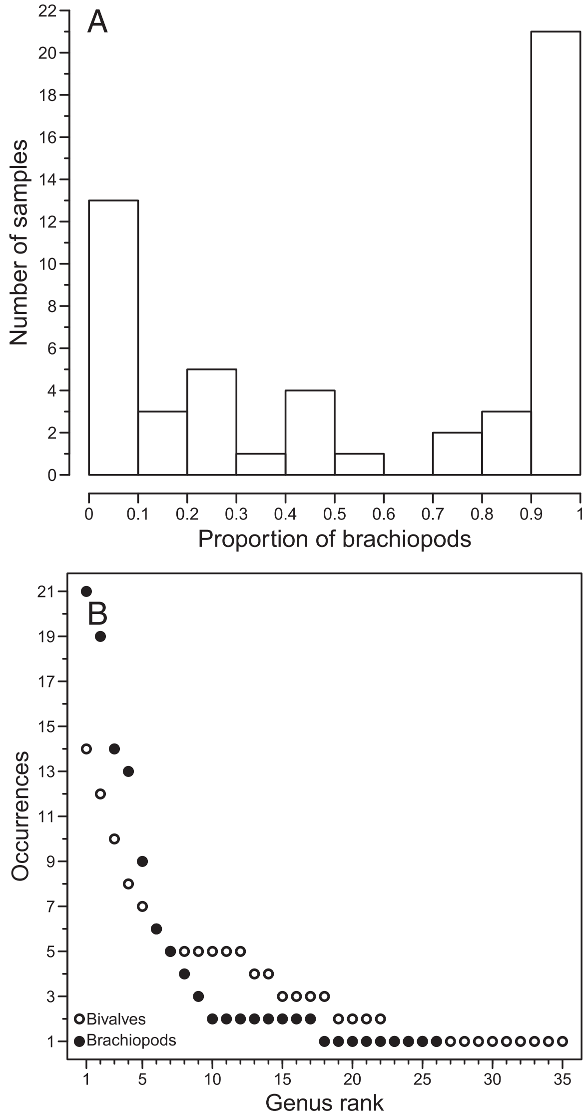

Fig. 8. A) Histogram of brachiopod proportional richness. B) Rank-occurrence plot showing the distribution of occurrences for brachiopods (black circles) and bivalves (open circles).

Table 2
Significant pairs identified by the CL approach.

Pair	Genus 1	Occs	Genus 2	Occs	Joint Occs	*P*	Pattern
B–C [a]	*Tivertonia*	12	*Phestia*	8	0	0.007	Segregated
B–C [ab]	*Tivertonia*	12	*Schizodus*	12	1	0.009	Segregated
B–C [ab]	*Modiolus*	13	*Tivertonia*	12	1	0.002	Segregated
B–C [ab]	*Precosyringothyris*	19	*Anomalodesmata*	5	0	0.007	Segregated
B–C [ab]	*Orbiculoidea*	16	*Modiolus*	13	1	0.000	Segregated
B–C [a]	*Orbiculoidea*	16	*Sanguinolites*	5	0	0.006	Segregated
B–B	*Orbiculoidea*	16	*Kochiproductus*	5	5	0.020	Aggregated
B–B	*Precosyringothyris*	19	*Tivertonia*	12	10	0.028	Aggregated
B–B [ab]	*Tivertonia*	12	*Streptorynchus*	9	7	0.016	Aggregated
B–B [a]	*Pericospira*	6	*Kochiproductus*	5	4	0.012	Aggregated
B–B	*Kochiproductus*	5	*Spiriferellina*	2	2	0.005	Aggregated
C–C	*Modiolus*	13	*Schizodus*	12	10	0.001	Aggregated
C–C [a]	*Modiolus*	13	*Aviculopecten*	10	8	0.012	Aggregated
C–C	*Modiolus*	13	*Edmondia*	5	5	0.014	Aggregated
C–C	*Modiolus*	13	*Leptodesma*	5	5	0.010	Aggregated
C–C	*Modiolus*	13	*Ptychopteria*	5	5	0.031	Aggregated
C–C	*Modiolus*	13	*Sanguinolites*	5	5	0.018	Aggregated
C–C [ab]	*Schizodus*	12	*Aviculopecten*	10	8	0.016	Aggregated
C–C	*Schizodus*	12	*Edmondia*	5	5	0.019	Aggregated
C–C	*Schizodus*	12	*Leptodesma*	5	5	0.009	Aggregated
C–C	*Schizodus*	12	*Ptychopteria*	5	5	0.007	Aggregated
C–C	*Schizodus*	12	*Sanguinolites*	5	5	0.005	Aggregated
C–C	*Aviculopecten*	10	*Edmondia*	5	4	0.022	Aggregated
C–C	*Aviculopecten*	10	*Leptodesma*	5	5	0.013	Aggregated
C–C	*Aviculopecten*	10	*Ptychopteria*	5	5	0.006	Aggregated
C–C	*Parallelodon*	7	*Acanthopecten*	3	3	0.013	Aggregated
C–C	*Edmondia*	5	*Leptodesma*	5	3	0.015	Aggregated
C–C [a]	*Edmondia*	5	*Acanthopecten*	3	2	0.015	Aggregated
C–C	*Leptodesma*	5	*Ptychopteria*	5	5	0.004	Aggregated
C–C [a]	*Acanthopecten*	3	*Nuculavus*	3	2	0.010	Aggregated
C–C	*Acanthopecten*	3	*Wilkingia*	2	2	0.001	Aggregated
C–C	*Nuculavus*	3	*Wilkingia*	2	2	0.003	Aggregated
C–C [ab]	*Myalinidae*	1	*Elimata*	1	1	0.000	Aggregated
C–C [ab]	*Myalinidae*	1	*Leiopteria*	1	1	0.000	Aggregated
C–C [ab]	*Myalinidae*	1	*Merismopteria*	1	1	0.000	Aggregated
C–C [ab]	*Netschajewia*	1	*Euchondria*	1	1	0.000	Aggregated
C–C [ab]	*Netschajewia*	1	*Merismopteria*	1	1	0.000	Aggregated
C–C [ab]	*Oriocrassatella*	1	*Elimata*	1	1	0.000	Aggregated
C–C [ab]	*Oriocrassatella*	1	*Merismopteria*	1	1	0.000	Aggregated
C–C [ab]	*Pteropectinella*	1	*Streblopteria*	1	1	0.000	Aggregated
C–C [ab]	*Elimata*	1	*Grammatodon*	1	1	0.000	Aggregated
C–C [ab]	*Elimata*	1	*Merismopteria*	1	1	0.000	Aggregated
C–C [a]	*Solemya* (*Janeia*)	1	*Merismopteria*	1	1	0.000	Aggregated
C–C [a]	*Leiopteria*	1	*Merismopteria*	1	1	0.000	Aggregated

[a] Pairs identified by the Mean Bayes Criterion.
[b] Pairs identified by the CL Bayes criterion (Gotelli and Ulrich, 2010).

latitudinal settings (Fürsich et al., 2001; Olszewski and Patzkowsky, 2001; Bonuso and Bottjer, 2006; Tomašových, 2006a).

There are different major factors that have been classically discussed as governing bivalve–brachiopod distribution, namely turbidity (Steele-Petrovich, 1979; Rhodes and Thayer, 1991), productivity (Bambach, 1999; Tomašových, 2006a) and substrate stability (Fürsich et al., 2001; Bonuso and Bottjer, 2006).

Previous analyses indicate that the segregation between brachiopods and bivalves was actually segregation between infauna and epifauna (Bonuso and Bottjer, 2006), while in our results the pattern is observed between brachiopods and both epifaunal and infaunal bivalves.

Such differences have important consequences on the understanding of the factors controlling the co-occurrence pattern. Many hypotheses explaining brachiopod distribution are generalizable to other epifaunal groups such as bivalves. Thayer (1979, 1983) proposed that infaunal deposit feeders enhanced substrate disturbance limiting the development of immobile epifaunal suspension feeders mainly by bulldozing (i.e., overturning and burying them), while Tomašových (2006a) suggested that brachiopods and epifaunal (filibranch and pseudolamellibranch) bivalves could cope with low productive environments due to low metabolic rates, or higher clearance rates and retention efficiency respectively. Therefore, substrate consolidation and bulldozing (Thayer, 1983; Fürsich et al., 2001), and productivity (Tomašových, 2006a) both account for the coexistence between epifaunal bivalves and brachiopods but fail to explain the observed pattern in Western Argentina. Olszewski and Patzkowsky (2001) showed that the main factor segregating bivalve dominated communities from brachiopods dominated ones was an environmental gradient from paralic to open marine environments, being bivalves typical of the first and brachiopods of the second. In Western Argentina, however, this pattern is neither observed because there are no compositional differences along the bathymetrical gradient.

Turbidity and oxygen content are also possible factors explaining the segregation between brachiopods and epifaunal bivalves, because it has been shown that bivalves are better than brachiopods at dealing with turbidity (Rhodes and Thayer, 1991; James et al., 1992; Rhodes and Thompson, 1993), and that brachiopods could dominate low oxygen environments due to their low metabolic rates (James et al., 1992; Rhodes and Thompson, 1993; Peck, 2008). Environmental segregation between brachiopods and bivalves along turbidity or oxygen gradients is also improbable in Western Argentina because there are no facies that clearly indicate either condition. The fact that the whole marine basin corresponds to a siliciclastic shelf suggests that turbidity might have been similar in almost every environment. Moreover, if turbidity or oxygen were a major cause, we should expect brachiopods to be restricted to deep environments were sediment supply and oxygen are low (Einsele, 1992; Levin, 2003), but both brachiopods and bivalves occur along the whole bathymetric gradient in Western Argentina.

6.2.2. Biotic interactions

Competition between bivalves and brachiopods could also be causing their segregation. The results of the null model state that the pattern of co-occurrences is a non-random one (Gotelli, 2000) and such a result has been usually related to competition as an underlying process (Gotelli and McCabe, 2002). Unfortunately, although they are a very important tool, co-occurrence null models alone are not enough to confirm that competition is the main factor (Ulrich and Gotelli, 2007). Both environmental checkboards and neutral dynamics could be responsible for the non-random pattern (Ulrich, 2004). Environmental checkboard, however, is an implausible explanation for our case, because brachiopods and bivalves are not evidently segregated along an environmental gradient. On the other hand, the high value of standardize effect size (SES) found in our null model analysis is not indicative of neutral dynamics, but of competitive structured communities (Gotelli and McGill, 2006). Moreover, the brachiopod–bivalve segregation has been recognized, although with some differences, in many places around the world during the Late Paleozoic (Olszewski and Patzkowsky, 2001; Bonuso and Bottjer, 2006). Such a pattern is not expected to be recognized in disparate regions under neutral dynamics (Hubbell, 2001), because compositional structure in communities assembled by neutral processes in different regions should be uncorrelated (Ricklefs and Renner, 2012). The scale dependence pattern of coexistence further supports competition between bivalves and brachiopods. In the hypothetical scenario where bivalves and brachiopods were indifferent to each other, the coexistence should be similar at local and regional scales (Araújo and Rozenfeld, 2014). However, scale dependence pattern of coexistence is expected to be present under competition (Segurado et al., 2012; Araújo and Rozenfeld, 2014). All in all, the failure of environmental factors and neutral dynamics to clearly explain the segregation, summed to the co-occurrence null model result and the scale dependant coexistence, underscores the relevance of competition in structuring the segregated pattern at local scale.

Unfortunately, although competition at local scale can be asserted, further details are difficult to assess. Competition for food, however, can be dismissed since it has been shown that, even during the Late Paleozoic, bivalves were metabolically dominant compared to brachiopods (Payne et al., 2014). On the other hand, interaction between brachiopods and bivalves has been discussed in the context of competition for space mediated by biotic disturbances (Thayer, 1985; Tomašových, 2008). In this scenario, brachiopod–bivalve competition could be modulated by preferential predation of bivalves (Thayer, 1985) and/or lesser resistance to biotic disturbances — such as grazing on larvae — by brachiopods (Tomašových, 2008), allowing either brachiopod or bivalve to dominate depending on the intensity of these interactions. Unfortunately, with the available information we cannot yet know if the latter could have been the actual case.

6.3. Regional-local dynamics

During the Paleozoic brachiopods had a tendency to be more abundant in carbonate environments (Miller and Connolly, 2001; Olszewski and Patzkowsky, 2001; Peters, 2008). They had a well defined latitudinal gradient during the Late Paleozoic, being more diverse in low latitudinal settings (Leighton, 2005; Powell, 2007, 2009), and their global geographic and temporal diversity patterns could be explained by the availability of carbonate environments (Peters, 2008; Powell, 2009). Bivalves, on the other hand, preferred siliciclastic environments (Miller, 1988; Novack-Gottshall and Miller, 2003a) and, at least during the Early Paleozoic, they were more diverse in high latitudinal settings (Novack-Gottshall and Miller, 2003b).

At regional scale, the data from Western Argentina agrees with this first-order biogeographic pattern, because 1) bivalves are slightly more diverse than brachiopods, and 2) brachiopods and bivalves have similar occupancies, while at lower latitudes brachiopods are much more frequent than bivalves (e.g., Malinky and Heckel, 1998; Olszewski and Patzkowsky, 2001; Lebold and Kammer, 2006). Moreover, the amount of local communities dominated by bivalves is higher than in lower latitudes (e.g., Olszewski and Patzkowsky, 2001; Lebold and Kammer, 2006).

However, at local scales the pattern of coexistence is not evident. Most local communities are dominated either by brachiopods or bivalves and only a few samples have similar number of occurrences of both clades.

These patterns suggest that environmental change along the latitudinal gradient allowed regional coexistence of the two clades, by increasing bivalve occupancies and diversity relative to brachiopods. Such regional coexistence, in turn, appears to promote the amount of local communities dominated by one or the other clade, but it does not foster local coexistence, indicating that the processes acting at these two scales are, at least partially, decoupled.

Finally, the observed decoupling of local and regional processes structuring brachiopod–bivalve communities in Western Argentina supports the idea that competition was not relevant in the major transition between brachiopod–dominated (Paleozoic) and bivalve-dominated (Modern) faunas. Such transition is most probably related to processes acting at regional to biogeographic scales, because large scale temporal patterns are related to large geographical ones. Nevertheless our results underscore that the interaction between brachiopods and bivalves was occurring, being observable when studied at the proper scale (Dietl and Vermeij, 2006), and having relevance in local communities dynamics.

7. Conclusions

1. Coexistence of brachiopods and bivalves in a siliciclastic shelf developed during the Late Paleozoic of Western Argentina shows two different patterns. On a regional scale bivalves were more diverse than brachiopods, although both had similar total number and distribution of occurrences. At local scale, however, brachiopods and bivalves were segregated.
2. Multivariate analyses indicate that the coexistence of brachiopods and bivalves was significantly low, while the biotic structure is neither consistent with a bathymetric, nor a geographical or temporal gradients.
3. The low co-occurrence of brachiopods and bivalves was not caused by taphonomic factors such as storm reworking, because there are no compositional differences between reworked and non-reworked concentrations.
4. The absence of environmental segregation between brachiopods and bivalves coupled to analyses taking into account ecological guilds indicates that the main factors commonly proposed as controlling the segregation, such as turbidity, productivity or substrate stability did not play a significant role.
5. These results suggest a possible competitive interaction between these groups at local scales and suggest that the processes acting at regional and local scales are, at least partially, decoupled.

Acknowledgments

DB and AFS wish to acknowledge the assistance of the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) and the Universidad Nacional de Córdoba, both of which support facilities used in this investigation. Two anonymous reviewers provided useful comments that improved this contribution. Financial support was provided by the Consejo Nacional de Investigaciones Cientificas y Técnicas (CONICET) [PIP No. 0091 (GAC) and PIP No. 112-201101-00571 (AFS)].

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.palaeo.2014.08.022.

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