

ENVIRONMENTAL PREFERENCES OF BRACHIOPODS AND BIVALVES ACROSS MAJOR CLIMATIC CHANGES DURING THE LATE PALAEOZOIC ICE AGE (PENNSYLVANIAN, WESTERN ARGENTINA)

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Abstract: During the late Palaeozoic ice age (LPIA), ice-proximal marine regional communities record contrasting responses to climate change compared to ice-distal communities. However, there is still much to be understood in distal regions in order to fully understand the palaeobiological consequences of the LPIA. Here, we analyse brachiopod and bivalve environmental preferences along the bathymetric gradient during a major glacial event and the subsequent non-glacial interval in western Argentina. Median environmental breadths did not change with the reassembly of communities during the non-glacial interval. Moreover, bivalves and brachiopod immigrants show similar environmental breadths although they tend to have immigrated from different palaeogeographical regions. These patterns reinforce the idea that the worldwide marine fauna was probably culled of stenotopic taxa during the LPIA. On the other hand, analysis of the preferred depths of survivors and immigrants sheds light on the

substantial modification of the bathymetric diversity gradient. Among different possible explanations, the immigration of taxa with affinities for deep environments is the only one supported. In addition, results underscore the observation that the higher turnover in the offshore environment was probably driven by immigration rather than extinction. Finally, stability in environmental preferences at a regional scale is not mirrored by stability in survivors' individual preferences, because survivors' preferred depth is not correlated during the glacial and non-glacial intervals. Moreover, the amount of change in survivors preferred depth is not related to their environmental breadth, nor to their occupancy. These patterns suggest: (1) instability in realized niches; and (2) individual responses of survivor genera.

Key words: environmental preferences, late Palaeozoic ice age, climate, brachiopods, bivalves, environmental breadth.

DURING the late Palaeozoic there were significant global changes (e.g. climatic, oceanographic and palaeogeographic) and large-scale biotic responses are recorded worldwide (Shi & Waterhouse 2010). One of the most important events was the late Palaeozoic ice age (LPIA), which is currently understood as a complex scenario of many geographically variable discrete glacial/non-glacial cycles (Fielding *et al.* 2008; Rygel *et al.* 2008; Birgenheier *et al.* 2009). Environmental changes that occurred during the LPIA, and the resulting ecosystems dynamics, have been thoroughly studied at different geographical scales (Powell 2005, 2007; Bonelli & Patzkowsky 2008; Clapham & James 2008, 2012; Heim 2009; Sterren & Cisterna 2010; Balseiro 2016a). Among the most important biotic consequences in the marine realm during the LPIA was the

establishment of an alternate marine state dominated by broad-niche taxa with large geographical ranges, that in turn redounded in a depression of macroevolutionary rates and global diversity (Stanley & Powell 2003; Powell 2005; Aberhan & Kiessling 2012). Further evidence from palaeotropical regions have shown that these global patterns were, at least partially, observable at regional scales (Bonelli & Patzkowsky 2008, 2011; Heim 2009; Badyrka *et al.* 2013). In ice-proximal regions, however, compositional turnover and changes in hierarchical diversity and the bathymetric diversity gradient, contrast with the previously recognized pattern of regional ecological persistence in LPIA communities (Balseiro 2016a). Such a discrepancy sets the question of how much did these glaciated regions differ from palaeotropical regions. In this

contribution, we intend to go further by analysing the assembly of ice-proximal regional communities during the LPIA from a taxon perspective, focusing on environmental preferences of taxa along the bathymetric gradient. We compare the consequences of differential survival, extirpation and immigration in western Argentina during and after the most radical climatic event in that region, as well as stability in survivors' environmental preferences across the glacial–non-glacial transition.

GEOLOGICAL SETTING

The localities studied include a variety of small and genetically related outcrops representing the palaeoclimatic and environmental heterogeneity recorded in the sedimentary rocks from the Callingasta–Uspallata, Río Blanco and Paganzo Basins of western Argentina during the Pennsylvanian (Fig. 1).

In western Argentinian basins, abundant glacio-marine deposits provide evidence of the geographic expansion of continental ice centres during the Early Pennsylvanian (López Gamundí 1997; Montañez & Poulsen 2013). The clockwise rotation of Gondwana during the Carboniferous drifted the western gondwanan margin to progressively lower latitudes, causing a major climatic amelioration in the region towards the Middle–Late Pennsylvanian (Iannuzzi & Rösler 2000; Balseiro *et al.* 2009; Gulbranson *et al.* 2015). Such a set of alternating glacial and non-glacial episodes have been described and sequentially analysed by previous authors (López Gamundí & Martínez 2003; Limarino *et al.* 2006; Desjardins *et al.* 2009). Available information allows recognition of two major Pennsylvanian marine transgressions (Fig. 2), one related to the major glacial episode at the beginning of the Bashkirian; and a second during a non-glacial interval occurring during the Moscovian and early Kasimovian (Gulbranson *et al.* 2010; López Gamundí & Buatois 2010; Limarino *et al.* 2014). Both transgressions (Fig. 2, sequences 7 and 9) can be clearly identified and are separated by a thick section of continental beds (sequence 8).

The Bashkirian records the most significant glacial event registered in Western Gondwana (López Gamundí & Martínez 2000). Its diamictite deposits are followed by, or alternate with, siltstones, medium-to-fine sandstones and mudstones bearing abundant bivalves, brachiopods, gastropods, crinoids and bryozoans. This has been interpreted as a glacio-marine episode (Henry *et al.* 2008, 2010; Cisterna & Sterren 2010, in press; Taboada 2010; Alonso-Muruaga *et al.* 2013). The later Moscovian–Kasimovian transgression can be recognized in marginal continental to marine environments, overlying previous continental beds (Desjardins *et al.* 2009, 2010; Buatois *et al.* 2013; Limarino *et al.* 2014). Facies range from

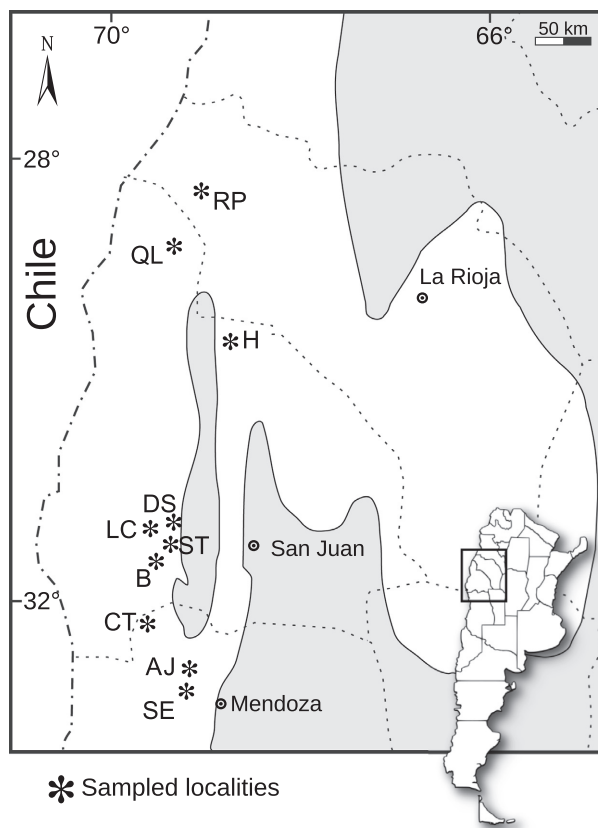


FIG. 1. Location map of the study area depicting the basin palaeogeography. Grey areas indicate positive topography. Sampling localities: RP, Río Blanco Anticlinal; QL, Quebrada Larga; H, Huaco area (Quebrada La Herradura and Quebrada La Delфина); DS, Quebrada del Salto; LC, La Capilla area (Las Cambachas and Las Juntas); ST, Sierra del Tontal. B, Barreal area (Barreal Anticlinal, Leoncito, Quebrada Majaditas, Cordón del Naranjo); CT, Cordillera del Tigre; AJ, Agua de Jagüel; SE, Quebrada Santa Elena. Based on Balseiro (2016a).

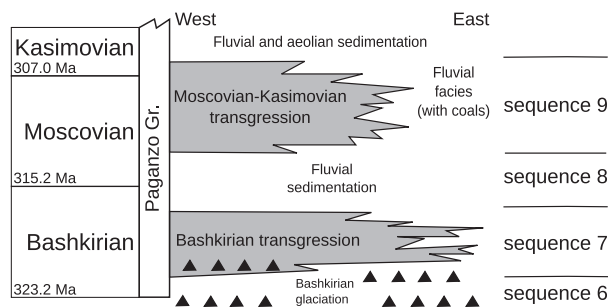


FIG. 2. Stratigraphical framework, sequence stratigraphy and chronostratigraphy of the studied region. Modified from Limarino *et al.* (2006), Césari *et al.* (2011), Cisterna *et al.* (2011) and Balseiro (2016a).

siliciclastic marine sandstones to shales, and record a diverse faunal assemblage that differs compositionally from the Bashkirian fauna (Sterren & Cisterna 2010;

Taboada 2010; Balseiro 2016a). Moreover, geochemical, faunal and stratigraphical evidence supports climatic amelioration during the Moscovian–Kasimovian interval (Sterren 2004; Cisterna 2010; Sterren & Cisterna 2010; Taboada 2010; Limarino *et al.* 2014; Gulbranson *et al.* 2015).

DATA

We used the data set previously published by Balseiro (2016a), which is freely accessible from the Dryad Digital Repository (Balseiro 2016b). In brief, the data set is based on the literature and consists of brachiopod and bivalve occurrences from 99 bed-level samples coming from 15 different localities (Fig. 1). Of these, 48 samples come from the Bashkirian, while 51 samples come from the Moscovian–Kasimovian. Genus was used as the taxonomic level for the analysis; whenever this taxonomic identification was not possible, taxa were assigned to their suprageneric level (family, superfamily or order); but, in all cases, they represent different but unidentified genera. The data set includes 88 genera and 481 occurrences.

Based on sedimentological and ichnological aspects (Henry *et al.* 2008, 2010; Desjardins *et al.* 2009, 2010; Alonso-Muruaga *et al.* 2013; Buatois *et al.* 2013), all samples were assigned to one of three environments: shallow subtidal (above fair weather wave base), deep subtidal (between fair weather wave base and storm wave base) or offshore (below storm wave base). Environmental coverage is evidently uneven within and between intervals (Fig. 3).

A detailed taphonomic analysis of a large part of the data set was performed by Sterren (2008), while further taphonomic biases were tested by Balseiro *et al.* (2014) for the Moscovian–Kasimovian part. Neither storm reworking nor time averaging seems to have had significant consequences for the composition of samples (Balseiro *et al.* 2014). Biases related to sequence stratigraphy can be disregarded as sampling in both intervals is mostly restricted to the early transgressive systems tract (Limarino *et al.* 2006; Desjardins *et al.* 2009; Alonso-Muruaga *et al.* 2013).

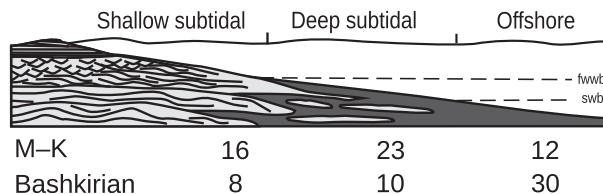


FIG. 3. Environmental sampling coverage of the studied intervals (from Balseiro 2016a). Abbreviation: M–K, Moscovian–Kasimovian.

METHOD

Environmental preferences

To quantify environmental preferences of taxa we calculated both the preferred depth (PD) and the environmental breadth. For the estimation of each taxon's preferred depth, we used the equation:

$$PD = \frac{\sum[(occu_i / \sum occu_i) \times X_i]}{x}$$

where x is the number of environments (three in our case), X_i is a constant that represents water depth, which has values of 0, 1.5 and 3 for the shallow subtidal, deep subtidal and offshore, respectively; and $occu_i$ is the taxon's occupancy in the i th environment. Occupancy is the total number of occurrences relative to the total number of samples (McGeoch & Gaston 2002) and by estimating occupancies we avoid differential sampling effects in each environment in each time bin. PD ranges from 0 if the taxon occurs exclusively in the shallow subtidal to 1 if it occurs exclusively in the offshore. A caveat of this approach is that a taxon would have a value of 0.5 regardless of whether it occurs exclusively in the deep subtidal or has a bimodal distribution with equal occupancy in the shallow subtidal and the offshore. This issue, however, is overcome by the fact that both cases would yield contrastingly different values of environmental breadth.

For the estimation of environmental breadth (EB), we used the equation proposed by Hurlbert (1978), modified for occurrences instead of abundance,

$$EB = \frac{O^2}{N \times \sum(o_i^2/n_i)}$$

where O is the total number of occurrences of the taxon, o_i the number of occurrences in the i th environment, N the total number of samples and n_i the number of samples in the i th environment. EB, however, needs to be rescaled (Hurlbert 1978),

$$EB' = \frac{EB \times N - n_{\min}}{N - n_{\min}}$$

where n_{\min} is the minimum number of samples found in any environment. The rescaled index takes values ranging from 0 when the taxon is present in a single environment to 1 when it is present in equal proportions in all environments. However, the index has a caveat, which is that values of 0 can only be achieved in the case that the taxon is specialized in the least sampled environment (Hurlbert 1978).

As a proxy for abundance, we used two different but related parameters. First, we analysed the taxon occupancy in its preferred environment (OPE), which was measured simply as the highest occupancy found in an environment. Second, we calculated the mean occupancy of the given taxon in all three environment (O_{all}), which is highly correlated with raw occupancy (Kendall correlation test: Bashkirian $\tau = 0.793$, $p < 0.0001$; Moscovian–Kasimovian $\tau = 0.928$, $p < 0.0001$). Occupancy has been shown to be a good estimator of abundance both in ecological (Holt *et al.* 2002) and palaeoecological (Ivany *et al.* 2009) data sets.

A different method that quantifies similar parameters of environmental preferences but based on a Gaussian model and multivariate analysis, was put forward by Holland *et al.* (2001; see also Holland & Zaffos 2011; Patzkowsky & Holland 2012). Unfortunately, because in our analysis multivariate biotic gradients do not follow environmental gradients (Balseiro *et al.* 2014; Balseiro 2016a), this method was not able to indicate actual environmental preferences of taxa.

Survivors, immigrants and extirpations

To evaluate environmental preferences, all taxa were assigned to three categories according to their temporal distribution (Bashkirian or Moscovian–Kasimovian) namely: survivors, extirpations and immigrants. Survivors are represented by those taxa present in both intervals; extirpated taxa represent regional extinctions (i.e. present in the Bashkirian but not in the Moscovian–Kasimovian); while immigrants consist of those taxa recorded in the studied region in the Moscovian–Kasimovian but not in the Bashkirian. Although this last category includes both immigration and origination, we prefer to name it immigrants given that only a small group of brachiopods did actually originate at this interval, while most other brachiopods and all bivalves had their first appearances earlier elsewhere (Sterren 2004; Cisterna 2010; Sterren & Cisterna 2010).

In previous analyses, brachiopods and bivalves showed contrasting patterns of turnover and immigration (Balseiro 2016a). Therefore, in order to understand immigration, extirpation and survival in depth, we further compared environmental preferences of brachiopods and bivalves.

To avoid biases due to undersampled rare taxa, we restricted the analysis to taxa having a minimum of three occurrences. However, given the limited number of brachiopods that survive from the Bashkirian to the Moscovian–Kasimovian (Balseiro 2016a), analyses comparing immigration among clades were performed with taxa having at least two occurrences.

All analyses were carried out in R v. 3.2.2 (R Core Team 2015). The median was used as the measure of central tendency in all cases. For pairwise comparisons of medians we used the non-parametric Wilcoxon rank test performed with the `wilcox.test()` function in R, while for comparisons of more than two groups we used the non-parametric Kruskal–Wallis rank test with the `kruskal.test()` function in R. As a measure of dispersion we used the difference between the third and first quartile. Homogeneity of variances among two or more groups were tested using the Levene’s test with median as central value. Levene’s test was carried out with the `leveneTest()` function available in the `car` package for R (Fox & Weisberg 2011), while correlation analyses were carried out with the non-parametric Kendall correlation test with the `cor.test()` function in R (R Core Team 2015).

RESULTS

Environmental preferences of Bashkirian and Moscovian–Kasimovian genera

Bashkirian and Moscovian–Kasimovian assemblages differ in their preferred depth (PD) distribution, both in its median (\overline{PD}) and dispersion (Fig. 4A). The Bashkirian assemblage has a lower (i.e. shallower) median preferred depth ($\overline{PD} = 0.46$) than the Moscovian–Kasimovian assemblage ($\overline{PD} = 0.62$; Fig. 4A). This difference is marginally insignificant (Table 1). The variance of the PD distribution also shows slight differences between the Bashkirian (dispersion = 0.5339) and the Moscovian–Kasimovian (dispersion = 0.2837; Fig. 4A), indicating that genera differed more in their PDs during the older interval. Differences in variances are, however, statistically insignificant (Levene test, $F = 1.182$, $df_1 = 1$, $df_2 = 49$, $p = 0.282$).

The environmental breadth (EB’) distribution shows only small differences between Bashkirian ($\overline{EB'} = 0.6$, dispersion = 0.6613) and Moscovian–Kasimovian assemblages ($\overline{EB'} = 0.63$, dispersion = 0.472; Fig. 4B). Differences in EB’ (Table 1) are insignificant, although there are significant differences in variance (Levene test, $F = 1.85724.94$, $df_1 = 231$, $df_2 = 2649$, $p = 0.031$) between intervals.

In contrast to the other two parameters studied, occupancy in the preferred environment (OPE) does show a difference between intervals. Median OPE is significantly higher in the Bashkirian ($\overline{OPE} = 0.375$) than in the Moscovian–Kasimovian ($\overline{OPE} = 0.25$; Fig. 4C; Table 1). However, the higher occupancies of Bashkirian genera are only observable in their preferred environments, because median occupancy across all environments ($\overline{O_{\text{all}}}$) shows no difference between intervals (Fig. 4D; Table 1).

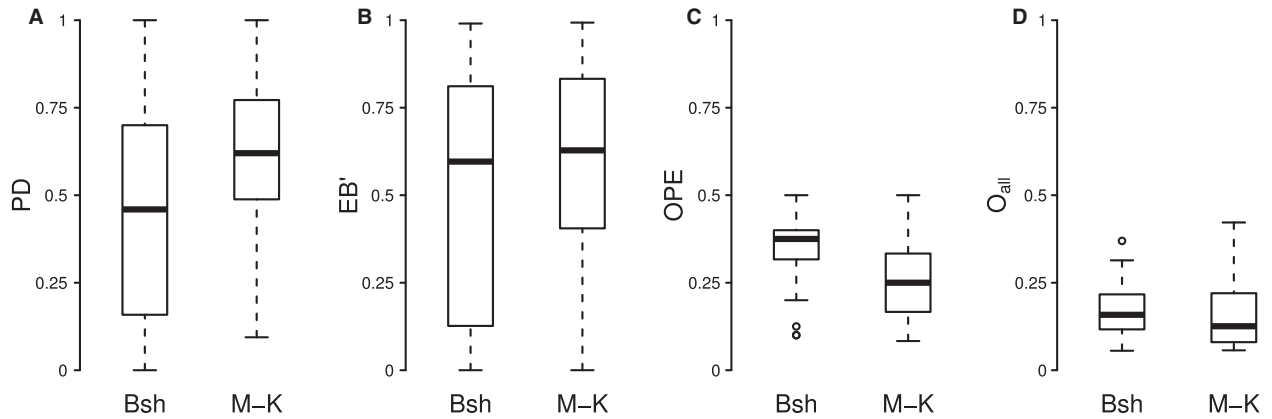


FIG. 4. Boxplots of Bashkirian and Moscovian–Kasimovian parameters of environmental preferences. A, preferred depth (PD). B, environmental breadth (EB'). C, occupancy in preferred environment (OPE). D, mean occupancy in all environments (O_{all}). *Abbreviations:* Bsh, Bashkirian; M–K, Moscovian–Kasimovian. Boxplots represent medians, first and third quartiles and whiskers extend to 1.5 interquartile range.

Selectivity in extirpation and immigration

We tested whether extirpation in the Bashkirian and immigration in the Moscovian–Kasimovian were related to preferred depth or environmental breadth. Figure 5A shows differences in preferred depth between extirpated and survivor genera in the Bashkirian. The difference between extirpated ($\overline{PD} = 0.51$) and surviving ($\overline{PD} = 0.42$) genera is very small and statistically insignificant (Table 1).

Further analyses indicate that Moscovian–Kasimovian survivors differ from immigrants, having marked differences in PD (Fig. 5B). Survivors clearly exhibit higher affinity to shallower environments ($\overline{PD} = 0.5$) than immigrants ($\overline{PD} = 0.72$), and such a difference is indeed highly significant (Table 1). There is, however, no

TABLE 1. Results of Wilcoxon rank test for differences in environmental parameters of genera between intervals.

Comparison	Parameter	W statistic	p value
Bashkirian vs Moscovian–Kasimovian: all genera	PD	220	<i>0.0507</i>
	EB'	284.5	0.46
	O_{all}	392	0.2026
	OPE	465.5	0.007344
Bashkirian vs Moscovian–Kasimovian: survivors	PD	27.5	0.6742
	EB'	14	0.06496
	O_{all}	40	0.4418
	OPE	50	0.06429
Bashkirian survivors vs extirpated	PD	75.5	0.7693
Moscovian–Kasimovian survivors vs immigrants	PD	35	0.0192
	EB'	91	0.6249

Bold indicates significant results, *italics* indicate marginally non-significant results.

difference between immigrants and survivors in $\overline{EB'}$ (Fig. 5C; Table 1).

Stability in survivors' environmental preferences

Further analyses, restricted to survivor genera, show that there are interesting changes in the parameters of genera between the Bashkirian and Moscovian–Kasimovian (Fig. 6), underscoring the lack of stability in environmental preferences of surviving genera. All four correlations of survivors' parameters of environmental preference between the Bashkirian and Moscovian–Kasimovian are non-significant (Fig. 6; Table 2). However, stability in parameters' median values (Fig. 7A–B; Table 1) indicates that changes in environmental preferences cancel out; creating a final pattern of similar distributions, despite instability in environmental preferences of individual genera.

Further analyses indicate that instability in PD is not related to Bashkirian environmental breadth or occupancy, as correlation between individual shifts in PD (ΔPD) and Bashkirian EB' or O_{all} are both non-significant (Fig. 8; Table 2).

Brachiopod vs bivalve environmental preferences

As a final step in the analysis, we studied whether brachiopods and bivalves differed in their environmental preferences. The results shown in Figure 9 suggest that there is no difference between these taxa, neither between them nor among intervals in any of the two most relevant parameters (PD and EB'). A Kruskal–Wallis test confirms that differences in both parameters are non-significant between clades and among time intervals (Table 3).

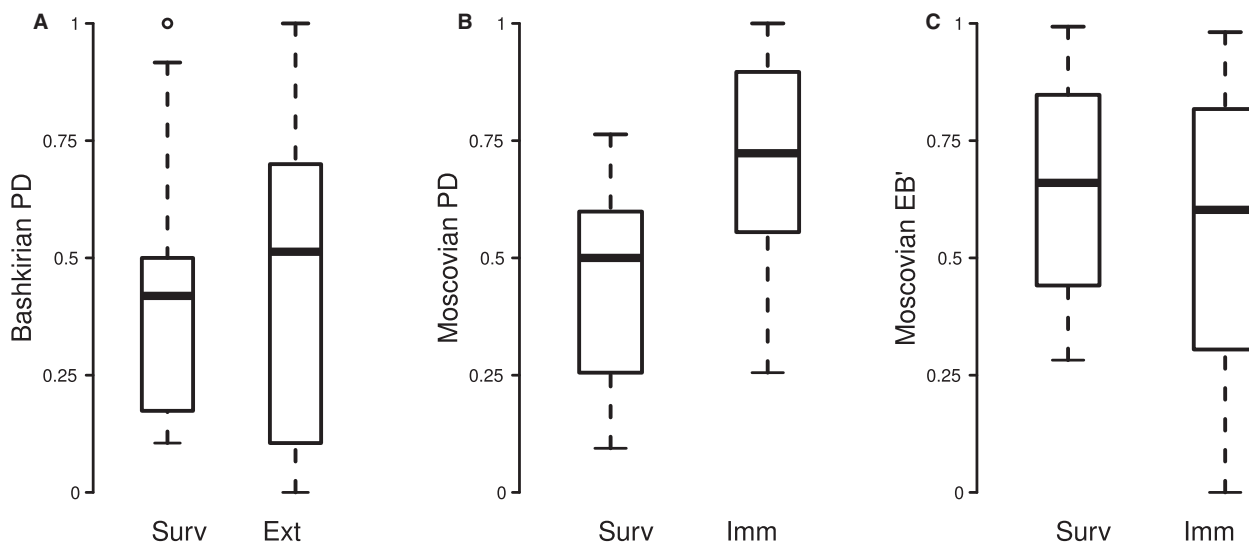


FIG. 5. Boxplots showing selectivity in extirpation, survivorship and immigrations. A, preferred depth of Bashkirian survivor and extirpated genera. B, preferred depth of Moscovian–Kasimovian survivor and immigrant genera. C, environmental breadth of Moscovian–Kasimovian survivor and immigrant genera. *Abbreviations:* Surv, survivors; Ext, extirpated; Imm, immigrants. Boxplots represent medians, first and third quartiles and whiskers extend to 1.5 interquartile range.

We also performed a detailed comparison of the selectivity in immigration between brachiopods and bivalves. Selectivity in immigration is not related to clade identity, as brachiopods and bivalves have comparable PD distributions for both Moscovian–Kasimovian immigrants and survivors (Fig. 10). The lack of statistical significant differences when comparing all for categories (Table 3) is surprising, because it was expected that brachiopod and bivalve immigrants should have higher values of preferred depth than survivors (Fig. 10). This insignificance could be due to the small number of genera present in some categories, particularly brachiopod survivors. A Wilcoxon rank test comparing bivalve survivors ($\overline{PD} = 0.57$) with immigrants ($\overline{PD} = 0.81$) confirms that significant differences are also present at clade scale ($W = 23$, $p = 0.0299$).

On the other hand, brachiopods and bivalves share similar EB' distributions when comparing Moscovian–Kasimovian survivors and immigrants (Fig. 10). As for community scale analyses, neither brachiopods nor bivalves record differences in EB' between survivors and immigrants (Table 3).

DISCUSSION

Habitat availability

Differences found between time intervals in median preferred depth could be explained by a loss of shallower environments after climatic amelioration, as suggested for early Miocene benthic faunas from Antarctica and south

Patagonia (Whittle *et al.* 2014). Environmental coverage, however, indicates that the Moscovian–Kasimovian shallow subtidal record is more abundant than that of the Bashkirian, while offshore is much better recorded in the Bashkirian than in the Moscovian–Kasimovian (Fig. 3). Raw data, therefore, suggest lower availability of deep environments during the non-glacial interval. This in turn could cause immigrant taxa to have lower affinity to this environment than survivors, which already inhabited the offshore region. However, the sampling-weighted indexes and previous subsampling diversity analyses (Balseiro 2016a) show the opposite trend, suggesting that habitat area or availability would not be driving changes in taxa's habitat preferences.

Environmental breadths and the glacial–non-glacial transition

Climate changes related to the late Palaeozoic ice age had major consequences for the biota, from changes in local to global diversity (Aberhan & Kiessling 2012; Badyrka *et al.* 2013; Balseiro 2016a) to changes in range size distributions and macroevolutionary dynamics (Stanley & Powell 2003; Powell 2005). From the habitat preference perspective, under cool climates, more gentle thermal bathymetric gradients cause offshore taxa to expand their ranges onshore, hence increasing the proportion of bathymetric generalists (Tomašových *et al.* 2014). In the face of the LPIA, low latitude communities from the Illinois Basin witnessed an increase in the proportion of bathymetric generalists (Bonelli & Patzkowsky 2008),

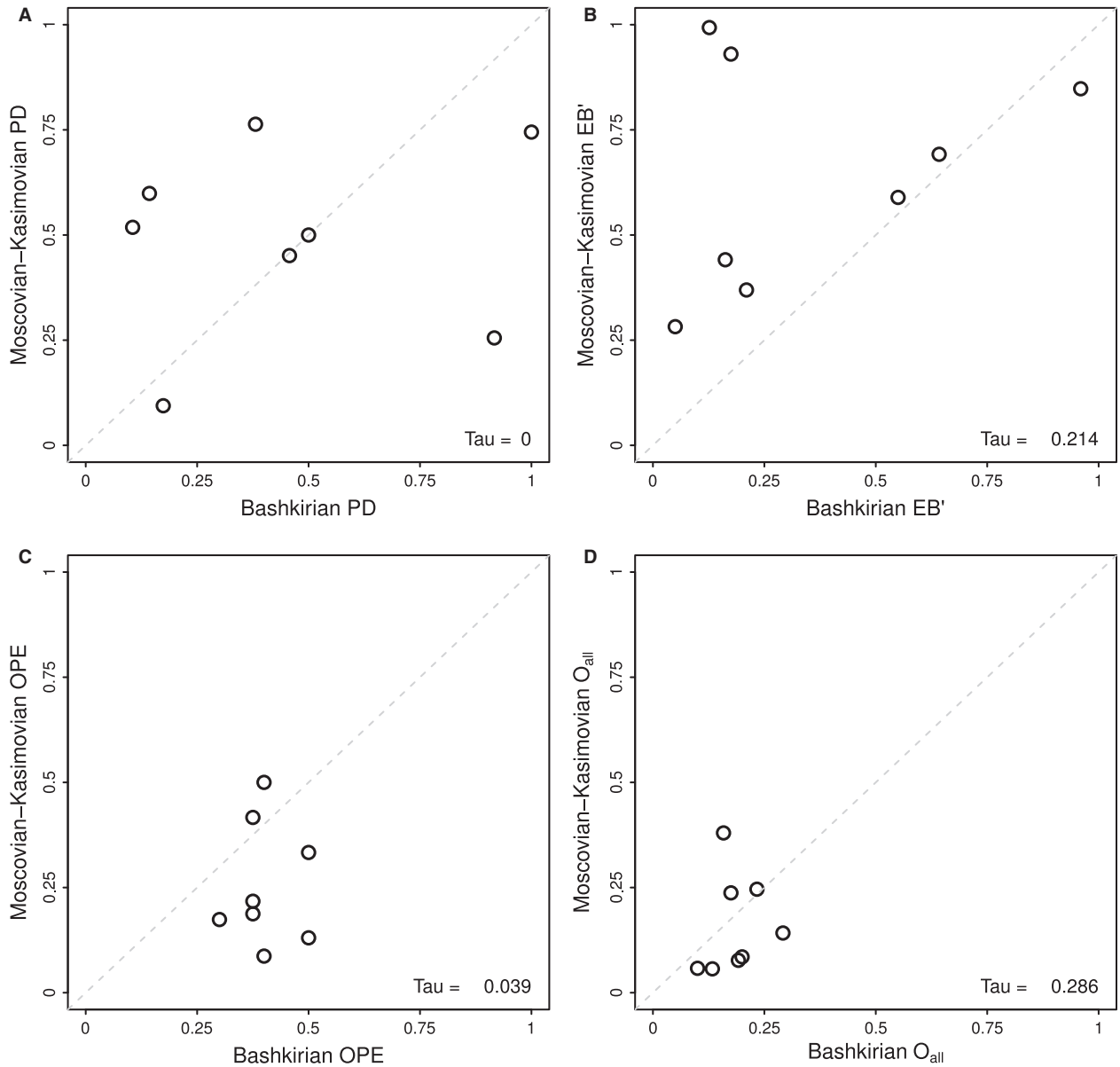


FIG. 6. Correlation of survivors' environmental preferences between intervals. A, preferred depth (PD). B, environmental breadth (EB'). C, occupancy in preferred environment (OPE). D, mean occupancy in all environments (O_{all}). Grey dashed lines depict ideal conservatism in environmental parameters.

TABLE 2. Results of Kendall's correlation test for environmental parameters of survivors.

Comparison	Parameter	Kendall's τ	p value
Bashkirian vs Moscovichian-Kasimovian genera	PD	0	1
	EB'	0.214	0.54
	OPE	0.039	0.897
	O _{all}	0.398	0.285
Δ PD vs Bashkirian parameters	EB'	0.071	0.905
	O _{all}	0.214	0.548

suggesting that a similar pattern could be observed elsewhere during glacial intervals throughout the LPIA. The observed climatic amelioration during the Moscovichian-Kasimovian in western Argentina (Limarino *et al.* 2014; Gulbranson *et al.* 2015) could have gone hand in hand with an increase of stenotopic taxa. Median environmental breadth, however, did not change with the reassembly of the metacommunity after glaciers vanished in this region. Yet, evidence for reduction in environmental breadths could be restricted to survivors rather than the whole assemblage. Nonetheless, survivors do not show

any significant shift in \widetilde{EB}' but a small increase in \widetilde{EB}' towards the non-glacial interval (Fig. 7). Such stability in the number of generalist taxa and in survivors' median environmental breadths could indicate that changes in the bathymetric thermal gradient were too small to have a consequence on the biota. However, this scenario is rather improbable because different evidence suggests that high latitude oceans had important temperature fluctuations during the Middle to Late Pennsylvanian (Montañez & Poulsen 2013), and there were many ecological and compositional changes related to this climatic amelioration in western Argentina (Sterren 2004; Cisterna 2010; Sterren & Cisterna 2010; Taboada 2010; Balseiro 2016a).

The stability in median environmental breadths could also be explained if an other environmental factor, rather than temperature, was the main controlling factor on bathymetric distribution. Nevertheless, this possibility seems implausible because: (1) temperature is usually a major control on bathymetric distribution in marine organisms (Fortes & Absalão 2010); and (2) expansion of bathymetric breadths have been shown to occur related to climate changes, as for example between the Eocene and Plio-Pleistocene from the northeast Atlantic Province (Tomašových *et al.*, 2014). On the other hand, given the relationship between environmental breadth and geographical range (Heim & Peters 2011), the extinction of

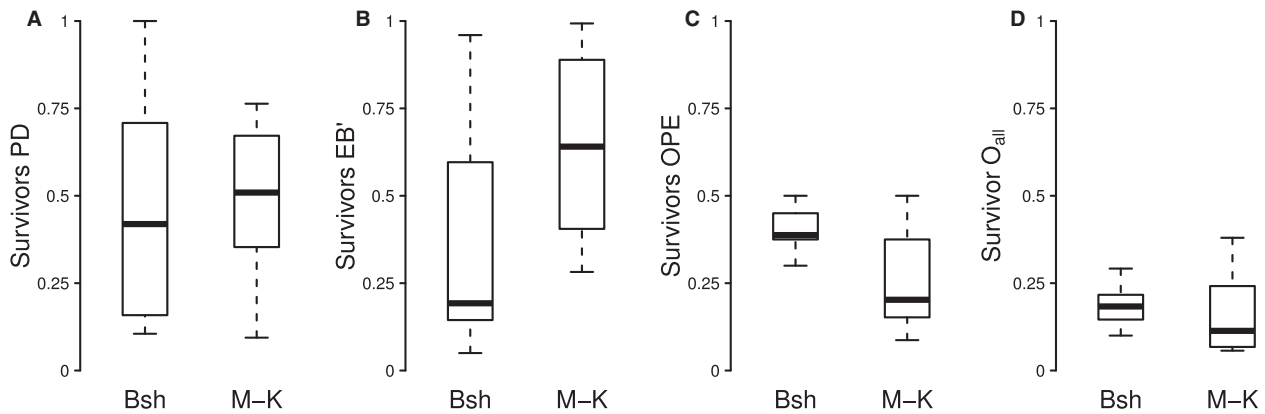


FIG. 7. Boxplots of survivors' parameters of environmental preferences between Bashkirian and Moscovian–Kasimovian. A, preferred depth (PD). B, environmental breadth (EB'). C, occupancy in preferred environment (OPE). D, mean occupancy in all environments (O_{all}). Abbreviations: Bsh, Bashkirian; M–K, Moscovian–Kasimovian. Boxplots represent medians, first and third quartiles and whiskers extend to 1.5 interquartile range.

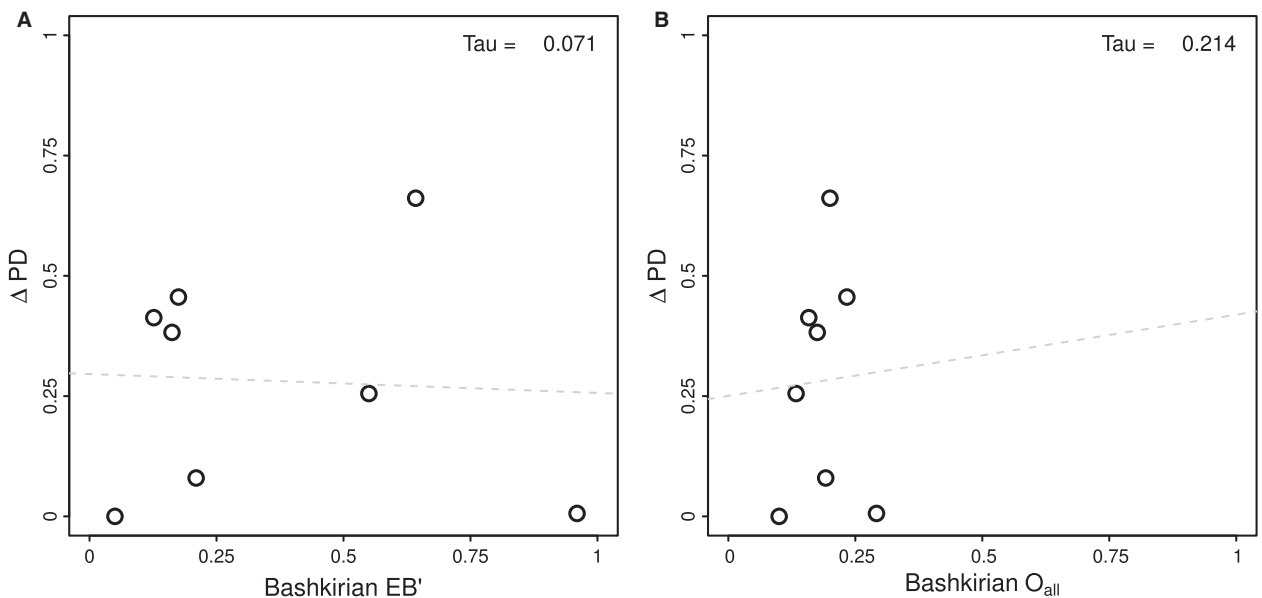


FIG. 8. Scatterplot of survivors' shift in preferred depth and environmental breadth or occupancy. A, ΔPD and EB' . B, ΔPD and O_{all} . Grey dashed lines are least squares fitted regression lines.

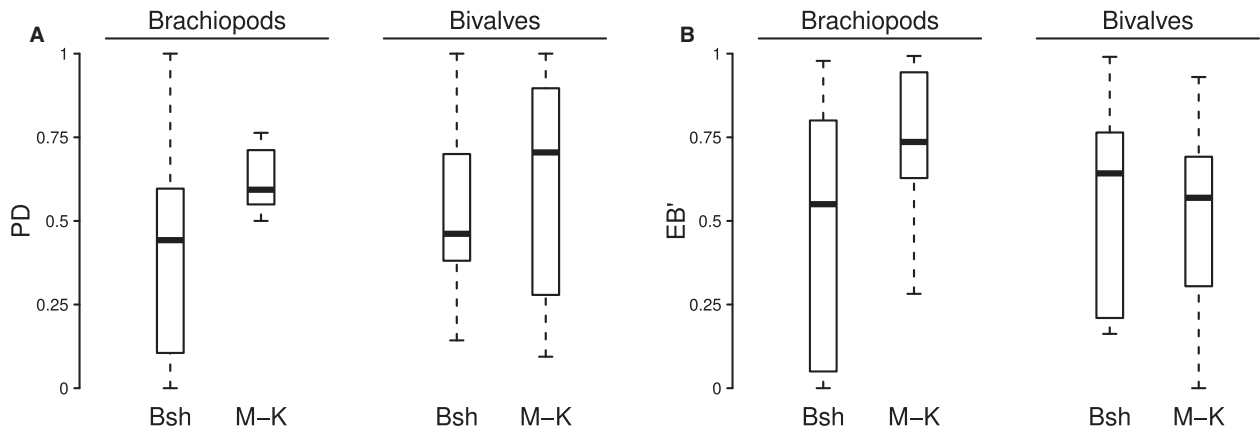


FIG. 9. Boxplots of brachiopod and bivalve parameters of environmental preferences between Bashkirian and Moscovian-Kasimovian. A, preferred depth (PD). B, environmental breadth (EB'). *Abbreviations:* Bsh, Bashkirian; M-K, Moscovian-Kasimovian. Boxplots represent medians, first and third quartiles and whiskers extend to 1.5 interquartile range.

TABLE 3. Results of Kruskal-Wallis rank test for differences in genera's environmental parameters between brachiopods and bivalves.

Comparison	Parameter	χ^2 statistic	df	p value
Bashkirian vs Moscovian-Kasimovian	PD	4.78	3	0.1882
	EB'	4.65	3	0.1988
Moscovian-Kasimovian survivors vs immigrants	PD	5.99	3	0.11
	EB'	1.51	3	0.679

narrow range taxa at the onset of the LPIA could have culled narrow environmental breadth taxa from the global biota (Stanley & Powell 2003; Powell 2005). Then, Moscovian-Kasimovian taxa would have had large environmental breadth regardless of whether they immigrated from low or high latitudes or were cold climate survivors. The similar environmental breadth of survivors and

immigrants supports this hypothesis. Moreover, it is further supported by the similar environmental breadth shown by both bivalve and brachiopod immigrants, because otherwise one would expect brachiopods to have higher number of generalists as most of them immigrated from high latitudes (Cisterna 2010), while most bivalves immigrated from low latitudes (Sterren 2004). More importantly, the observed pattern is expected even if temperature was not the controlling factor on bathymetric distribution. This is because a selective extinction of narrow range taxa should have caused a selective extinction of taxa with narrow environmental breadths as a by-product of the actual selectivity.

Furthermore, these results shed light on the explanation underlying differences in turnover intensity between low and high latitude regions during the LPIA (Balseiro 2016a). Previously, Balseiro (2016a) hypothesized that such differences could be caused either by: (1) more

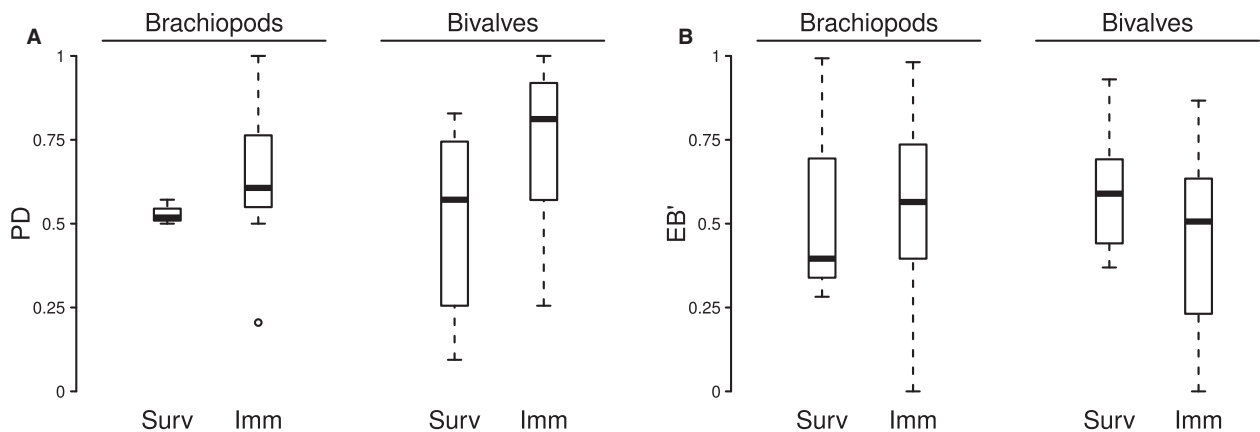


FIG. 10. Boxplot showing selectivity in immigration among brachiopods and bivalves; A, preferred depth (PD); B, environmental breadth (EB'). *Abbreviations:* Surv, survivors; Imm, immigrants. Boxplots represent medians, first and third quartiles and whiskers extend to 1.5 interquartile range.

stable ocean temperatures in the tropics (albeit a reduction in the dimension of the tropical belt); or (2) high-latitude faunas that were not culled of narrow range temperature-sensitive taxa at the onset of the LPIA and therefore their turnover dynamics were not modified through the LPIA. The temperature scenario put forward by Balseiro (2016a) supposes high climatic variability in intermediate to high-latitude basins, and therefore is opposite to the one needed to explain the stability in environmental breadth observed herein. Because changes in ocean temperatures fail to explain both the observed stability in median environmental breadth and the geographical differences in compositional turnover, our current evidence suggests the second scenario as the most plausible one.

Immigrants' preferred depth and the modification of the bathymetric diversity gradient

One of the main changes previously described as a consequence of the glacial to non-glacial transition in western Argentina was the modification of the bathymetric diversity gradient (Balseiro 2016a). During the glacial interval, diversity was higher in the deep subtidal, generating a humped gradient, while in the non-glacial interval diversity rose sharply offshore, generating a linear gradient (Balseiro 2016a). Such a change explains the small shift in PD towards deeper environments during the Moscovian–Kasimovian. Although Balseiro (2016a) proposed that the main factor related to this change was a rise in productivity in all environments, the actual mechanism for the gain in offshore diversity still remains unknown. The study of environmental preferences sheds light on such mechanisms. There are at least three possible simplistic scenarios that could account for such a change in the diversity gradient:

1. A shift in survivors' environmental preferences towards deep environments together with a homogeneous occupation of the bathymetric gradient by immigrants. A somewhat similar scenario has been described for the Late Triassic of Austria, where brachiopods retracted from their preferred habitats towards deeper environments as a consequence of an increase in siliclastic or nutrient supply (Tomašových 2006). Such a shift in environmental preferences, however, can be rejected for western Argentina. Although survivors do not show stability in their PDs, neither do they show a prevailing trend for higher values in the Moscovian–Kasimovian, which would account for a shift in their preferences towards deeper environments.
2. Selectivity in the extirpation of taxa with preferences for shallow environments, again coupled with a lack of shared environmental preference by immigrants. Higher extinction rates in onshore environments relative to offshore ones is a common pattern in the fossil record (Sepkoski 1987; Kiessling & Aberhan 2007). Indeed, possible selectivity in extirpation for inhabitants of shallow environments has already been observed in the onset of the LPIA at lower latitudes (Powell 2008), and could be expected in western Argentina as a consequence of melt-water discharge related to the retreat of glaciers (Buatois *et al.* 2013). Nonetheless, this scenario can be disregarded because western Argentinean survivors and extirpated taxa do not show differences in their preferred depth. It also seems implausible because if extirpation was concentrated in shallow taxa, then shallow subtidal turnover should have been higher than offshore turnover, which is exactly opposite to the recorded pattern (Balseiro 2016a).
3. If extirpation was not selective for shallow-water taxa and there was no shift in survivors' environmental preferences for deeper environments, the modification of the bathymetric diversity gradient could still have happened if immigrants preferentially inhabited deeper-water environments. Preference for deep settings is, for example, a common characteristic of brachiopod immigrations during the Upper Ordovician in Baltica and peri-Gondwana (Hansen & Harper 2008; Colmenar *et al.* 2012). This last possibility is the most supported scenario for western Argentina, as immigrants do show a significantly higher affinity towards deeper environments than Moscovian–Kasimovian survivors. The relevance of selective immigration as the mechanism underlying the change in the diversity gradient, is reinforced by the previously mentioned lack of extirpation selectivity and stability in survivors preferred depth.

On the other hand, environmental preferences of survivors, immigrants and extirpated taxa also helps understanding the turnover bathymetric gradient observed in western Argentina, with higher turnover rates towards the offshore (Balseiro 2016a). Although it is commonly accepted that turnover tends to be higher onshore than offshore (Tomašových *et al.* 2014), there is evidence that Palaeozoic large-scale community turnover was higher in deep environments (Bretsky 1968a, b). Sepkoski (1987), however, argued that the actual pattern during the Palaeozoic was an extinction gradient with higher rates towards the shore, and that differential extinction rates of clades inhabiting different parts of the bathymetric gradient caused the opposite trend at community scale, with higher turnover towards offshore. Although brachiopods suffered higher levels of extirpation than bivalves in western Argentina (Balseiro 2016a), both clades do not differ in their median habitat preference and they do not show any environmental trend in extirpation; hence such a

scenario could not explain the regional turnover gradient. The community-scale turnover gradient is, therefore, caused by higher immigration in the offshore and a lack of common preference to a given environment by survivors. In summary, the resulting bathymetric gradient shaped by the faunal turnover can be mainly related to immigration rather than extinction dynamics.

Stability in environmental preferences of taxa

It is reasonable to expect that the observed stability in median preferred depth and environmental breadth of survivors, is caused by niche stability, i.e. the actual stability of individual measures of environmental preference (Holland & Zaffos 2011; Brame & Stigall 2014; Hopkins *et al.* 2014). Despite the stability in median environmental parameters between intervals, niche stability can be rejected for all studied parameters, as none of the four parameters is correlated between intervals. Authors have argued that stenotopes should show a more evident pattern of stability in environmental preferences (Brett *et al.* 2007), but our results underscore that there is no relationship between previous environmental breadth and stability in preferred depth, indicating that neither stenotopes nor eurytopes have higher tendency for stability in environmental preferences. Abundance and occupancy has further been related to stability (Holland & Zaffos 2011; Balseiro & Waisfeld 2013), but again our results indicate that Bashkirian commonness is not related to shifts in preferred depth.

All in all, the whole picture underscores: (1) a lack of stability in environmental preferences; and (2) the individuality of responses. One possible explanation for such instability is that the compositional differences in the reassembly of regional communities affected the survivors. The influence of invasive species should not be underestimated as it seems likely that invasion processes directly impact individual organisms in ways that cannot necessarily be mitigated by simple lateral dispersal of larvae or adults (Stigall 2014). Evidence from the Upper Ordovician of Laurentia, suggests that taxa show much higher stability during gradual abiotic changes than when facing rapid biotic changes such as the Richmondian invasion (Malizia & Stigall 2011). Indeed, during the Richmondian invasion, communities were reorganized along different biotic gradients to those of pre-invasion communities (Holland & Patzkowsky 2007), a pattern similar to that observed in the glacial to non-glacial transition in western Argentina, where towards the Moscovian–Kasimovian the dynamics of local community assembly were modified resulting in segregation between brachiopods and bivalves (Balseiro *et al.* 2014; Balseiro 2016a). However, it is very unlikely that

instability in survivors' environmental preferences was caused by immigrants alone, because a major reason for instability in environmental preference is difference in realized environment (Jackson & Overpeck 2000), and western Argentina undoubtedly witnessed large-scale environmental changes during the glacial to non-glacial transition (Limarino *et al.* 2014; Gulbranson *et al.* 2015). Both climate change and biotic interactions were, thus, probable triggers of instability in survivors' realized niche (Jackson & Overpeck 2000) and therefore, in their estimated environmental preferences.

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