

UC Santa Cruz

UC Santa Cruz Electronic Theses and Dissertations

Title

Brachiopod paleoecology during Late Paleozoic climate change (Pennsylvanian-Early Permian, Bolivia)

Permalink

<https://escholarship.org/uc/item/3tq5q87k>

Author

Badyrka, Kira Anna

Publication Date

2012

Peer reviewed|Thesis/dissertation

UNIVERSITY OF CALIFORNIA
SANTA CRUZ

**BRACHIOPOD PALEOECOLOGY DURING LATE PALEOZOIC
CLIMATE CHANGE (PENNSYLVANIAN-EARLY PERMIAN, BOLIVIA)**

A thesis submitted in partial satisfaction
of the requirements for the degree of

MASTER OF SCIENCE

in

EARTH SCIENCES

by

Kira Badyrka

December 2012

The Thesis of Kira Badyrka
is approved:

Professor Matthew Clapham, Chair

Professor Paul Koch

Professor James Zachos

Tyrus Miller
Vice Provost and Dean of Graduate Studies

Table of Contents

Abstract	v
Introduction	1
Methods	5
Results	7
Age, Lithology, and Environment	7
Taxonomic Composition	10
Richness	12
Preferred Temperatures and Biogeographic Affinity	15
Body Size	18
Discussion	21
Taxonomic Composition	21
Diversity	24
Biogeographic Affinity	26
Body Size	26
Conclusions	30
References	32

List of Figures

Figure 1: Late Paleozoic Ice Age glaciations and temperature records	3
Figure 2: Locality map	6
Figure 3: Composite section	9
Figure 4: Cluster-abundance diagram	11
Figure 5: Non-metric multidimensional scaling	13
Figure 6: Genus richness of clusters	14
Figure 7: Preferred latitude of genera in clusters	16
Figure 8: Preferred latitude of specimens in clusters	17
Figure 9: Cluster provinciality	19
Figure 10: Body size trends in clusters	20
Figure 11: Gradual trends	23
Figure 12: Faunal boundary fluctuation	27
Figure 13: Sea level fluctuations	28

Brachiopod paleoecology during Late Paleozoic climate change

(Pennsylvanian-Early Permian, Bolivia)

Kira Badyrka

Abstract

Studies of modern ecological communities demonstrate that climate change may trigger changes in diversity and taxonomic composition; however, these studies are fundamentally limited to short timescales and therefore cannot demonstrate the full impact of major climate change. Understanding the ecological response of marine invertebrate communities to the Late Paleozoic Ice Age (LPIA), the last complete transition from icehouse to greenhouse, can establish a more complete picture of the climate-faunal relationship. We analyzed brachiopod community structure in Moscovian-Sakmarian (mid-Pennsylvanian to Early Permian) samples spanning the greatest extent of the LPIA, collected from four localities of the Copacabana Formation in Bolivia: Ancoraimes, Yaurichambi, Cuyavi, and Yampupata. Cluster analysis reveals three main groups that appear to coincide with pre-, syn-, and post-glacial times. Genus richness was significantly greater in samples during the Asselian glacial episode; however, the difference may be due to a combination of smaller body size and time averaged mixing of genera from different depths during more rapid glacioeustatic sea level change. Genera present in Bolivia consistently had warm-water affinities, even during the main glaciation, but warm-water taxa increased in abundance over time and the samples became increasingly dominated by characteristically North American genera. Overall mean body size and the size of

particular genera were smaller in the Asselian cluster. These size changes likely reflect variations in substrate because marine invertebrates should be larger at cooler temperatures due to oxygen limitation at higher temperatures. The monotonic increase in abundance of warm-water genera and increasingly North American biogeographic affinity imply that community change was most likely the result of the northward drift of Bolivia rather than a response to late Paleozoic glacial-nonglacial cycles. This lack of climate related faunal change was probably a result of Bolivia's mid-latitude location during the late Paleozoic because both the rate of temperature change and its magnitude were likely smaller at lower latitudes, reducing the impact of climate change on marine communities.

Introduction

Temperature is one of the basic controls on both marine and terrestrial community composition through its influence on organism physiology, geographic distribution, and interactions. Changes in temperature can force physiological changes in organisms' respiration, metabolic rate, and ability to perform critical biological functions, which can lead to death (Peck *et al.* 2004; Pörtner 2001). As temperature increases a rise in metabolic rate leads to a mismatch between oxygen supply and demand, which progressively lowers long-term fitness by causing tissue hypoxia and eventually forcing organisms to anaerobic metabolism (Pörtner 2010; Melzner *et al.* 2007; Somero *et al.* 2012). It is possible for organisms to withstand higher temperatures using heat shock proteins, however, this is an energy intensive process and leaves less energy for feeding and reproduction (Somero *et al.* 2012). Studies have shown that temperature limits for long-term survival occur at much lower values than those which cause rapid death (Peck *et al.* 2009). In addition to these direct physiological consequences, temperature change can cause changes in the relative abundance of species in communities, range shifts, altered species interactions, and extinction, all of which can have profound consequences for the overall structure and functioning of communities (Clarke 1993; Harley *et al.* 2006; Petchey *et al.* 2004). Many of these temperature driven ecological changes are already evident in modern species (Peck *et al.* 2004), including range shifts and disruptions in the coordinated life cycles of interacting species (Parmesan 2006; Walther *et al.* 2002). These physiological and ecological changes lead to a greater

possibility of extinction for many species, which could have further ecological consequences.

The fossil record provides evidence that faunal change has occurred in conjunction with climate change throughout geologic history. Studying ancient episodes of climate change can help to establish the biotic response to long term natural warming, thereby providing a baseline from which to assess more extreme events such as modern anthropogenic climate warming. During Pleistocene glacial-interglacial transitions faunal turnover in the Sea of Japan occurred when warm-water mollusk species migrated into the area, accompanied by a northward contraction of ranges of both warm-water and cool-water taxa and extinction of cool-water species (Kitamura *et al.* 2000). Similar faunal change has also been observed at the end of the Late Paleozoic Ice Age (LPIA), the last glacial period before the Pleistocene. Dramatic shifts in floral assemblages occurred with rapid temperature fluctuations during later LPIA glacials, with deglaciation resulting in a complete floral regime change from fern dominated to conifer dominated (Montanez *et al.* 2007; Gastaldo *et al.* 1996). Global data indicate a distinct mid-Permian diversification, especially in the tropics, due mainly to a radiation of strophomenate brachiopods (Alroy 2010) and assemblages in Australia show compositional and relative-abundance changes during deglaciation as well as potentially higher extinction rates during times of rapid climate shifts (Clapham and James 2008; Clapham and James 2012).

The LPIA was characterized by dynamic climate fluctuations lasting nearly 70 Ma from the mid-Carboniferous to the mid-Permian (Fielding *et al.* 2008) (Figure 1).

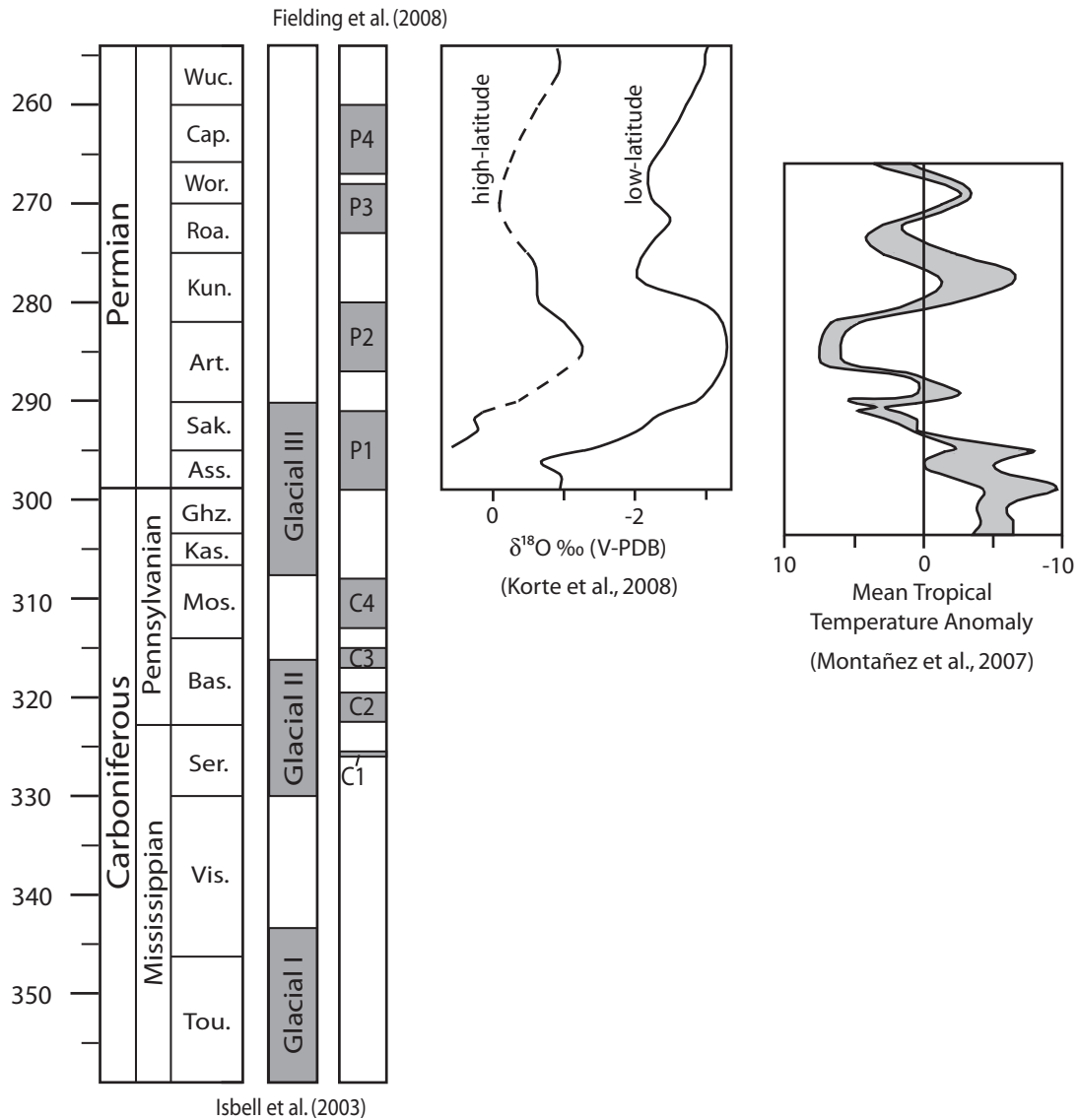


Figure 1. Summary of Late Paleozoic Ice Age glaciations and temperature records. Glacial records come from Australia (Fielding et al., 2008) and basins throughout Gondwana (Isbell et al., 2003). Permian temperature records from high and tropical latitudes show decreasing temperatures during the early Permian glacial (Korte et al., 2008 and Montañez et al., 2007).

Our study spans the Moscovian to the Sakmarian, corresponding with the C4 nonglacial, P1, and P1 nonglacial of Fielding *et al.* (2008). The C4 glaciation waned in the Moscovian and was followed by a long, warmer nonglacial extending to the Carboniferous-Permian boundary. Asselian-early Sakmarian glaciation extended over a broader region of Gondwana, indicating that the P1 glaciation was the peak of the LPIA. Following the decline of the P1 glacial in the Sakmarian, temperature increased sharply, though cooling occurred in the beginning of the Artinskian during the P2 glacial (Montanez *et al.* 2007; Korte *et al.* 2008).

The majority of late Paleozoic geological and paleontological work has been conducted in eastern Australia (high southern paleolatitude) and North America and China (equatorial paleolatitude). The paleontology of South America has been relatively unstudied and offers a look at how glaciation, and the subsequent deglaciation, affected marine invertebrate communities in the climatically highly variable mid-paleolatitudes. The lateral and time continuity of marine and glaciogenic deposits in the basins of South America imply that steep climate gradients existed in the region (Grader *et al.* 2008). This regional climate variability is likely to result in highly variable ecological conditions, and therefore fauna, as glaciers waxed and waned throughout the LPIA.

Methods

We assessed biotic change at the end of the LPIA using data collected from four locations of the Copacabana Formation in the Lake Titicaca region of Bolivia

(Figure 2). We collected 47 bulk samples of about 100 specimens each from measured sections at Ancoraimes (31 samples), Yampupata (6 samples), Cuyavi (4 samples), and Yaurichambi (6 samples) for identification and counting in the lab. Each sample was collected from the entire exposed length of a single bed, which ranged from <1 m to >10 m. Samples consist almost entirely of strophomenate and rhynchonellate brachiopods, with trilobites and mollusks occurring rarely and mostly in the samples from Yampupata. Only brachiopods are used in our analysis. We identified specimens to genus and, where possible, species level and counted all identifiable specimens. All analyses are done at the genus level. We also measured the length, width, and height of all complete specimens. We assessed environmental conditions using standard sedimentological criteria in the field and data from Grader (2003). No sorting or grading of specimens was observed in the field and counted specimens mostly exhibit low to moderate abrasion, indicating that little transportation occurred. Sample age was determined from correlation with sections in Grader (2003) and conodont biostratigraphy of the Yaurichambi section (C. Henderson, pers. comm.). All abundance counts and size data are stored in the Paleobiology Database (reference 41985).

Multivariate analyses (cluster analysis and non-metric multidimensional scaling [NMS]) were performed in R using the Vegan package (Oksanen *et al.* 2012). We performed a square root transformation on the count data used in multivariate analyses to reduce the influence of abundant taxa, such as *Crurithyris*, which are common in most samples and could obscure trends in the data. Using global

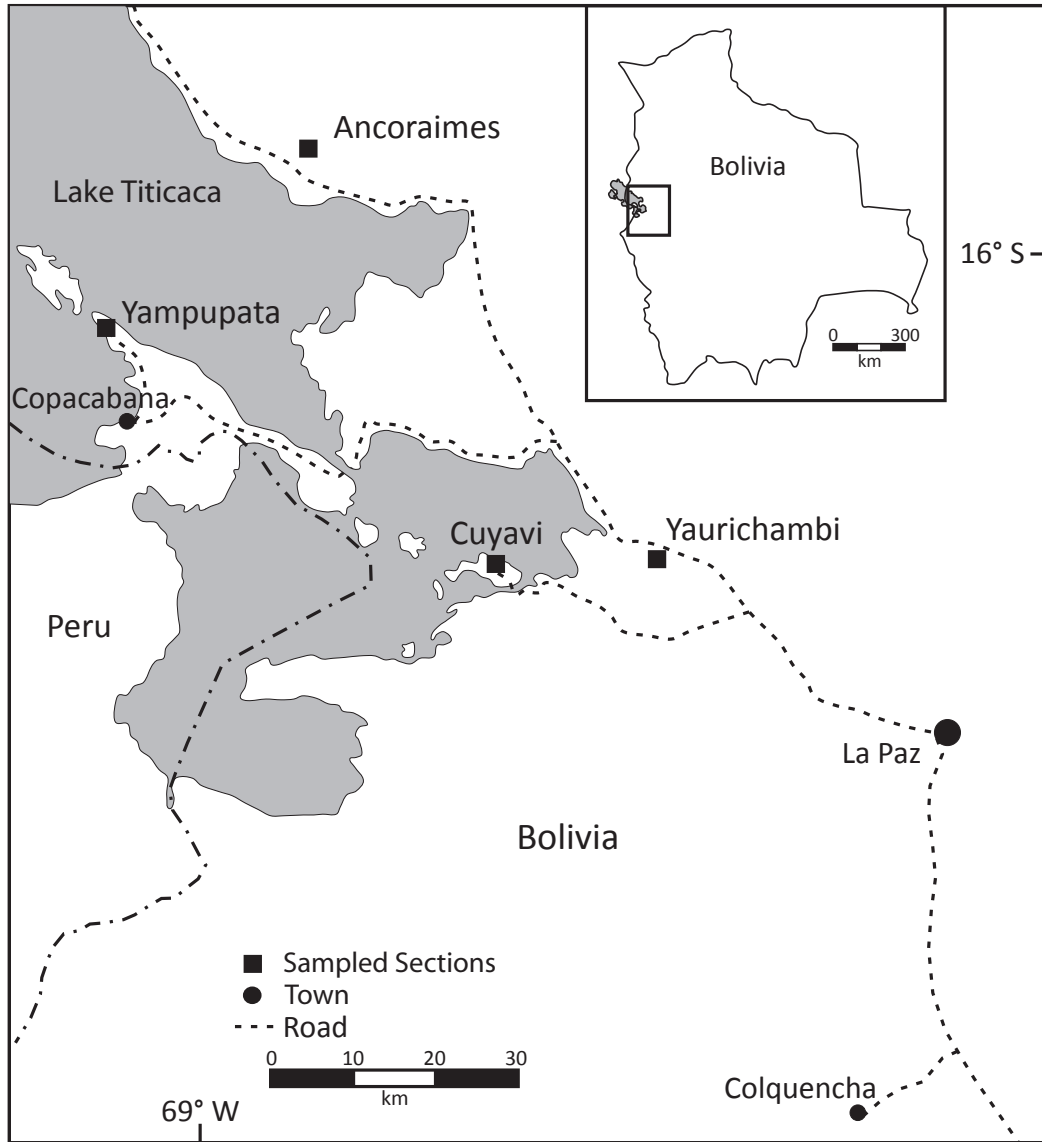


Figure 2. Map showing the location of the four sections (Ancoraimes, Yaurichambi, Cuyavi, and Yampupata) sampled for this study in the Lake Titicaca region of Bolivia.

Carboniferous and Permian occurrence data downloaded from the Paleobiology Database (PBDB; <http://paleodb.org>) on 17 May 2012, we calculated the preferred latitude of each genus found in Bolivia using the method described in Clapham (2010) and (Clapham and James 2012). Due to the high sampling frequency of the tropics a latitudinal bias may be introduced by simply using the mean latitude of all occurrences. To counteract this bias the preferred latitude of each taxon is adjusted using the latitudinal density of all occurrences (Clapham and James 2012).

We also used the PBDB data to determine the provinciality and temperature classification (warm or cool) of each genus. The globe can be divided into two cool biogeographic realms above 30° north (Boreal) and below 30° south (Gondwanan) and two tropical realms between 30° north and south: Panthalassic on the west coast of Laurentia and Tethyan surrounding the Tethys Sea. We assigned each occurrence of a genus to one of the four biogeographic realms based on its occurrences in the Paleobiology Database. We considered a genus to be characteristic of the biogeographic realm in which it was most common only if the number of occurrences in that realm was at least twice as large as the number in the next most common realm. If a taxon is not considered characteristic of a particular realm it is classified as cosmopolitan.

Results

Age, Lithology, and Environment

The four sections range in age from Moscovian to Sakmarian, spanning the greatest extent of the LPIA and its major deglaciation (Figure 3). The section from Cuyavi spans the largest amount of time (from the Moscovian to Sakmarian); however, only four samples come from this section – three from the Moscovian and one most likely from the Sakmarian. Yampupata samples are contained entirely within the Moscovian. The Yaurichambi section ranges from the Gzhelian into the Asselian with samples coming from the bottom and middle of the section. Samples from the section at Ancoraimes cover the lower two-thirds of the section, ranging in age from the Gzhelian to the Sakmarian (possibly late Asselian). The precise positions of stage boundaries are not well constrained in any of our sections.

Lithologically, the four sections are broadly similar and composed mainly of marly lime mudstones and wackestones, pure wackestones and packstones, and terrigenous siltstone. Samples from Cuyavi come from bioclastic-dominated wackestones, representing deposition below fair-weather wave base in a mid- to distal ramp setting, and from green calcareous sandstones from slightly shallower environments. Fossiliferous units at Yampupata are composed of mid-ramp green calcareous sandstones similar to those at Cuyavi. In contrast to the other sections, exposed units at Yaurichambi are dominated by lime mudstone and wackestone, with most of the section covered. Two samples from the base of the section are derived from light grey limestones representing deposition in a restricted inner ramp environment. Most samples are from cyclical mid- to inner ramp sediments in the middle part of the section, ranging from shallower bioclastic and fusulinid

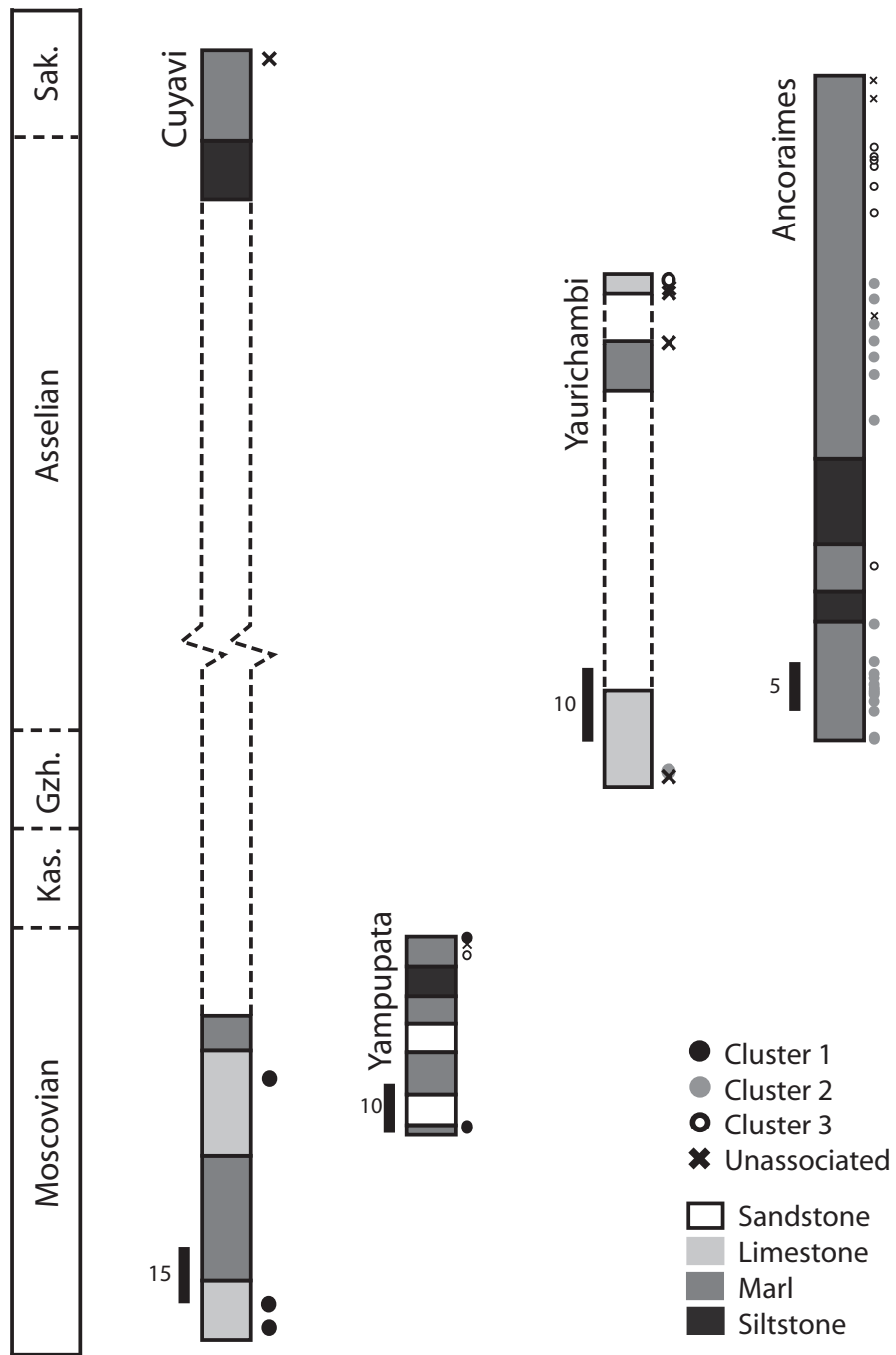


Figure 3. Composite section showing the dominant lithology, approximate age correlation of each section, and stratigraphic height of samples. Stage boundaries are approximate because the precise age of sections is uncertain. The cluster affinity of each sample is indicated and shows a fairly robust correlation of cluster with stratigraphic position.

wackestones to more distal sandstones and siltstones. The majority of the Ancoraimes section is composed of marly lime mudstone or wackestone with a few largely unfossiliferous shale-dominated intervals and increasingly high-energy packstones above our study section. Ancoraimes samples come from marly lime mudstone or wackestone beds, representing distal to mid-ramp environments close to storm wave base.

Taxonomic Composition

Cluster analysis reveals three clusters of samples: 1) Moscovian samples from before the main LPIA glaciation, 2) Asselian samples from the P1 glacial, and 3) Sakmarian samples from the end of the P1 glacial and (possibly) interglacial (Figure 4). Cluster 1 consists of the lower Cuyavi samples and the majority of the Yampupata samples. A greater abundance of *Gypospirifer condor* and *Linoproductus cora* is characteristic of this cluster, which lacks a group of taxa (*Fimbrinia cristatotuberculata*, *Orthotichia latirostrata*, *Rhipidomella cora*, *Chonetinella*, *Quadrochonetes*, *Hustedia*, and *Stenosisma thevenini*, called the *Hustedia* group) typical of cluster 2. This cluster also includes sample Ya2 in which *Isogramma* is common. Samples from the lower two-thirds of Ancoraimes and Yaurichambi make up cluster 2, which is characterized by the presence of the *Hustedia* group. This cluster also more commonly contains *Kozłowska capaci* and *Hystriculina*. Cluster 3 is mainly from the upper third of Ancoraimes and, like cluster 1, is distinguished by the lack of the *Hustedia* group. Though *Composita subtilita* and *Dasysaria inca* are present in most samples they are more common in cluster 3 samples. Three samples

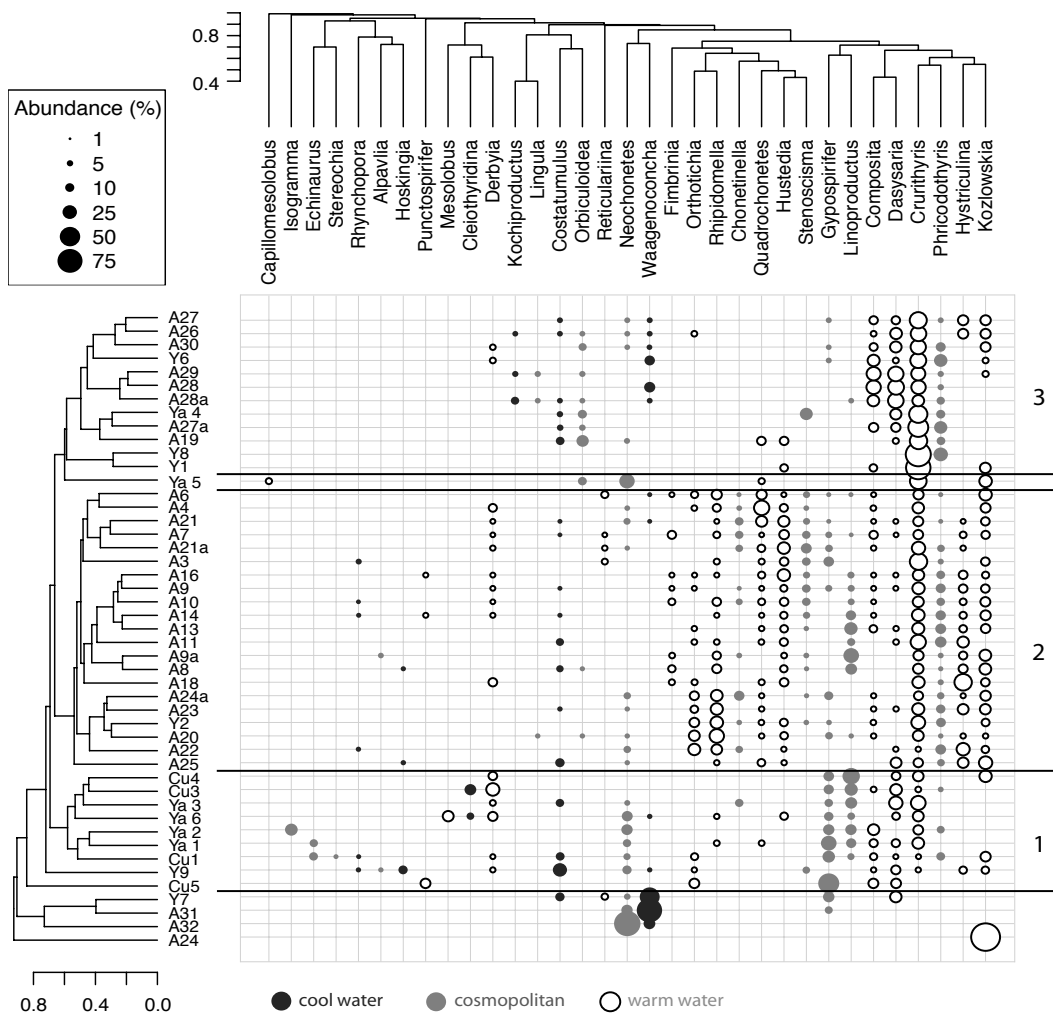


Figure 4. Cluster-abundance diagram of all samples and genera. For each genus the abundance in a sample is shown using the size of the dot and the style (black, grey, or white) indicates temperature affinity. Samples are divided into three main clusters based on the presence or absence and relative abundance of genera.

unassociated with these main clusters are of note: 1) sample A24 is composed of entirely *Kozlowskia capaci*, 2) *Waagenoconcha humboldti* makes up the vast majority of sample A31, and 3) sample A32 contains mostly *Neochonetes variolata*.

These clusters are also apparent when count data is analyzed using non-metric multidimensional scaling (Figure 5). The majority of samples occur in a single large group; however, samples from the clusters identified by cluster analysis plot together. Samples from cluster 1 plot to the right on axis one and in the bottom two-thirds of axis two, cluster 2 plots on the left on axis one and spans a greater amount of axis two than cluster 1, and cluster 3 plots at an intermediate axis 1 position but at high values on axis 2. The samples that are unassociated with any of the three clusters plot around the edges of the main group, with many of them (especially the high-dominance, low-diversity samples A24, A31, and A32) clearly separated from the rest of the samples.

Richness

Overall, mean within-sample genus richness was 10 genera, but there were significant variations among clusters (ANOVA, $p < 0.001$). Because richness is a proxy for the 'health' of a system that may have been influenced by late Paleozoic climate fluctuations it is important to look at any variations among the clusters. Cluster 2 had the highest richness, with a mean of 12.5 genera per sample, whereas cluster 1 (mean richness of 9.9 genera) and cluster 3 (mean richness of 8.2 genera) had lower diversity (Figure 6). The increase from cluster 1 to cluster 2 is weakly significant (Tukey test, $p = 0.045$), but the decrease from cluster 2 to cluster 3 is highly significant (Tukey test, $p < 0.001$). Richness did not differ significantly between

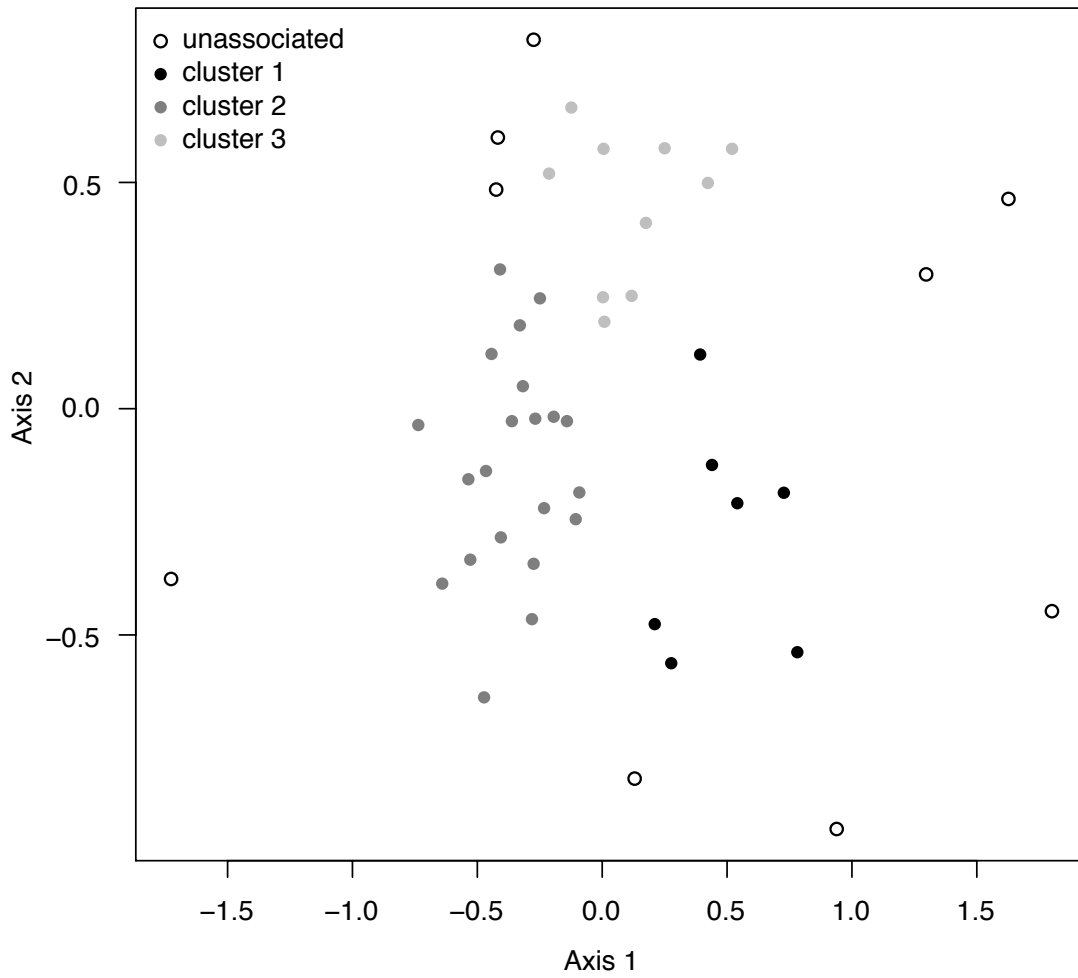


Figure 5. Non-metric multidimensional scaling showing the grouping of samples from clusters identified by cluster analysis. Samples from these clusters group together with unassociated samples scattered on the fringes of the plot.

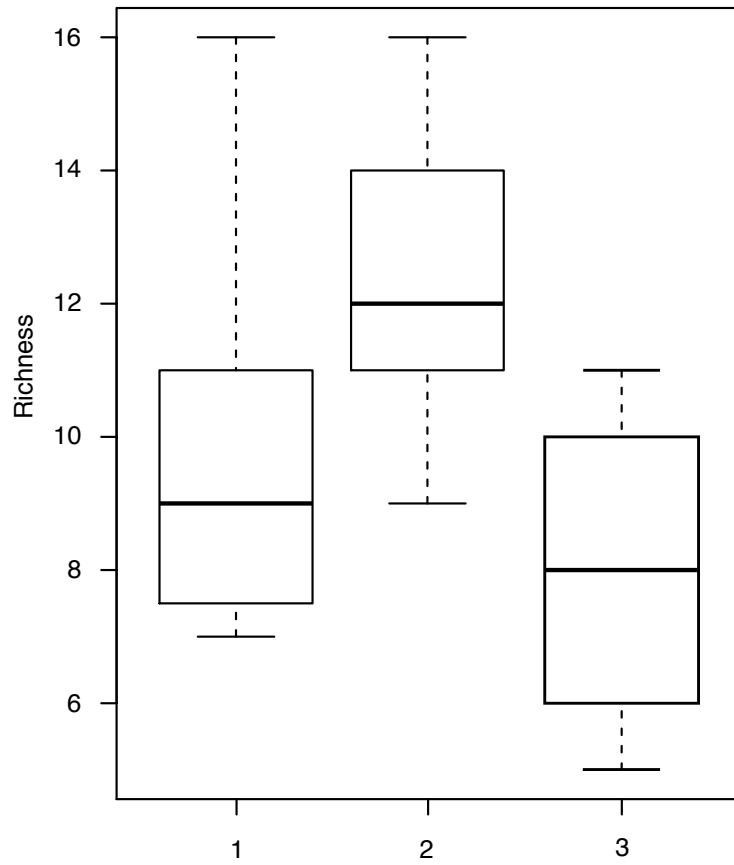


Figure 6. Box and whisker plot showing median and first and third quartiles for genus richness of samples in each cluster.

clusters 1 and 3 (Tukey test, $p=0.35$). Sample richness varied greatly within clusters of samples, including some samples containing only 1-2 genera, but no consistent trends or regular patterns can be observed among samples from single stratigraphic sections.

Preferred Temperatures and Biogeographic Affinity

If climate changes contributed to the community restructuring, the changing faunal composition of the three clusters may also have led to shifts in the proportion of warm- and cool-water genera. For each genus, we quantified its preferred temperature (warm or cool water) by calculating the mean paleolatitude of its global occurrences (termed ‘preferred latitude’). Overall, the mean preferred latitude of all genera present in each cluster was very consistent through time (25.4° in cluster 1, 26.4° in cluster 2, and 25.3° in cluster 3) and is relatively low in all clusters (Figure 7). Though the preferred latitude of genera within clusters shows very little variation, the mean preferred latitude of specimens within samples (which weights the genus preferred latitude by relative abundance) consistently decreased with time (Figure 8). Samples in cluster 1 have the highest mean preferred latitude (mean of 23.8°), followed by cluster 2 (mean of 20.4°), and finally cluster 3 (mean of 17.9°). The range of preferred latitude values remained consistent through the three clusters.

Although the preferred latitude of genera is very stable throughout our study interval, indicating a consistently warm-water composition, the biogeographic affinity of those genera may have varied due to changing climate or oceanographic patterns. We assigned genera to five different regions (Boreal, Gondwanan, Tethyan,

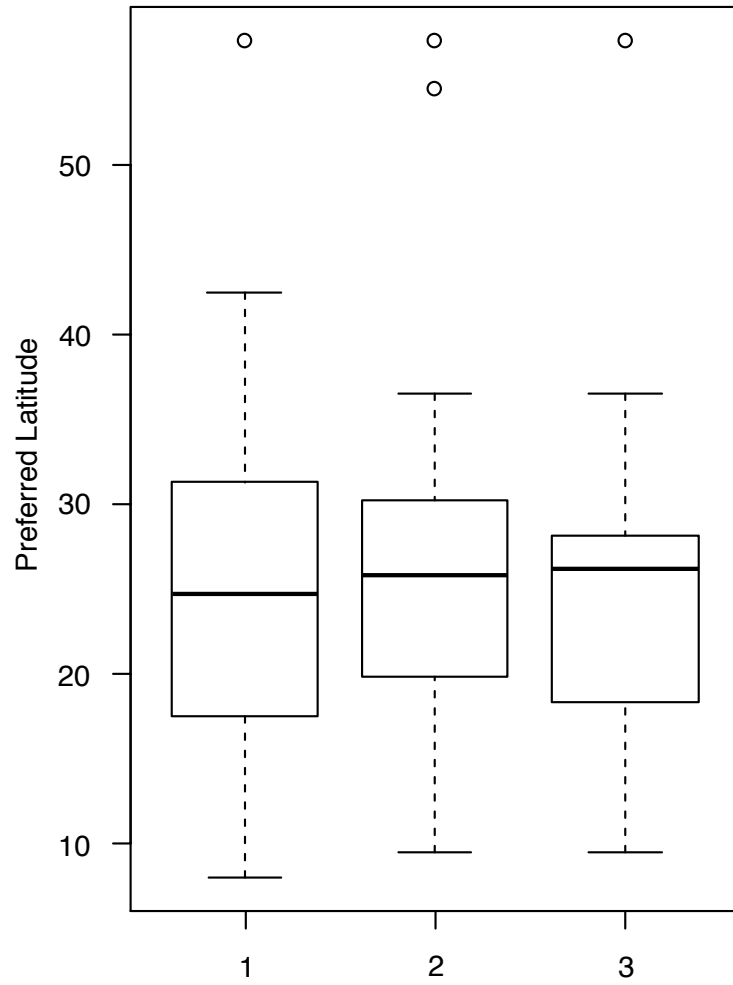


Figure 7. Box and whisker plot of the preferred latitude of genera present in each cluster.

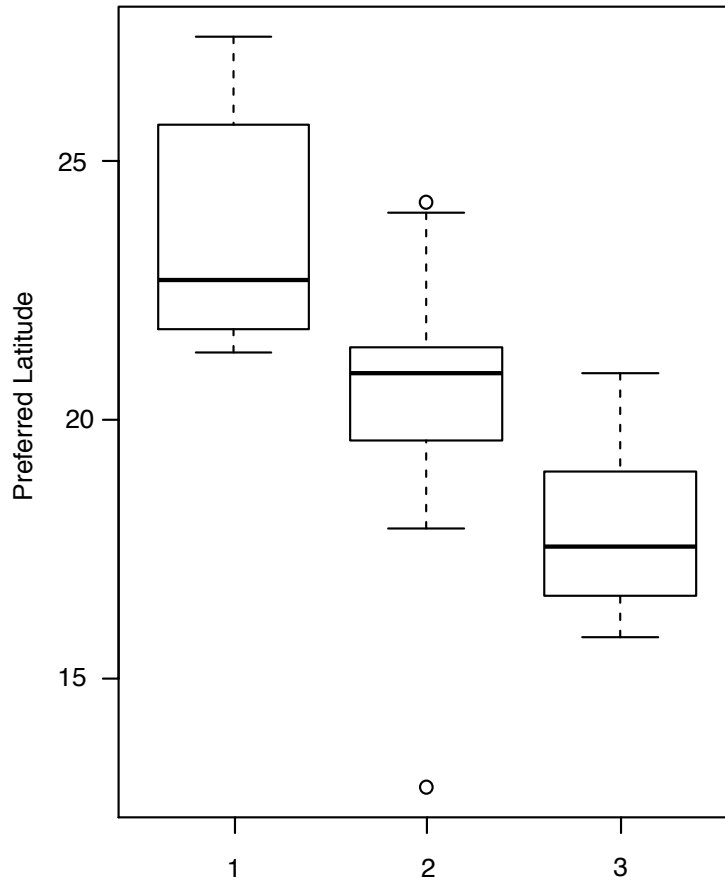


Figure 8. Box and whisker plot of the preferred latitude of specimens within samples of each cluster.

Panthalassic, and Cosmopolitan) and compared the relative proportion of specimens from each region to test for shifts in the biogeographic composition of each cluster. Biogeographic affinity shows a trend of increasing Panthalassic association with time, increasing from 36% of specimens in cluster 1 to 71% in cluster 2, and to 88% in cluster 3 (Figure 9). Cosmopolitan genera show a corresponding decrease: cluster 1 is composed of 56% cosmopolitan specimens, whereas clusters 2 and 3 contain 23% and 12%, respectively. Boreal, Gondwanan, and Tethyan genera make up a negligible percentage of each cluster, comprising no more than 5% of specimens.

Body Size

In the fossil record, changes in body size can be indicative of physiological stress. Although many factors can influence body size, maximum body size in marine invertebrates is controlled by oxygen (Pauly 2010). Due to the mismatch between oxygen supply and demand during times of ecological stress organisms can be forced to suspend non-vital functions such as growth, leading to smaller body size. The mean body size (measured by the geometric mean of shell length and width) of genera in cluster 2 is 7.3 mm, which is significantly smaller than the mean size of genera in either cluster 1 (11.5 mm; Welch t-test, $p < 0.001$) or cluster 3 (11.3 mm; Welch t-test, $p < 0.001$). Because these body size shifts may reflect changes in the relative proportion of larger- and smaller-bodied taxa or in the identity of taxa present, it is also important to assess within-genus size changes of taxa present in multiple clusters. Eleven of the 12 genera present in both cluster 1 and cluster 2 decrease in body size (exact binomial test, $p = 0.006$) (Figure 10). Ten of 13 genera

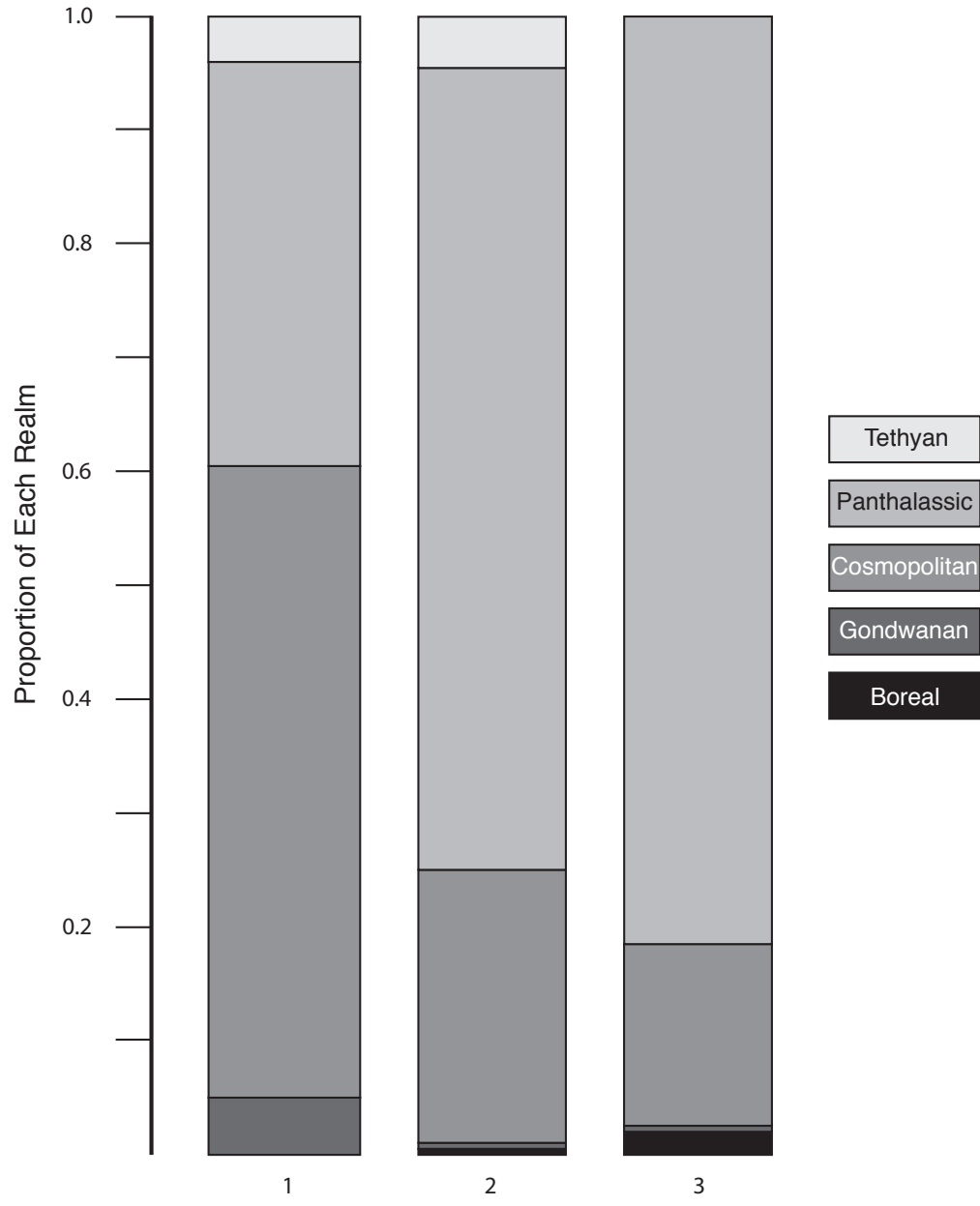
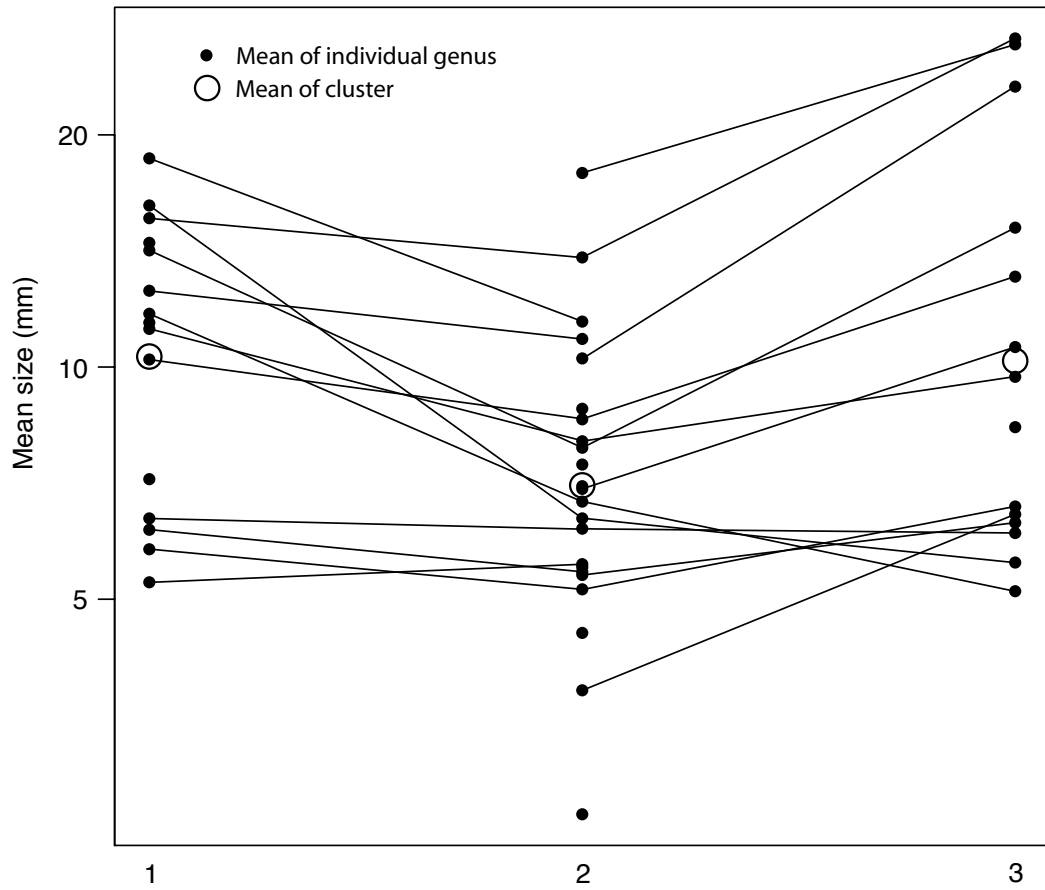


Figure 9. Bar plot showing the provinciality of each cluster. Genera are assigned to Tethyan, Panthalassic, cosmopolitan, Gondwanan, and Boreal regions based on the area with the largest number of occurrences.



increase in size between cluster 2 and cluster 3; although the number of size increases is weakly non-significant (exact binomial test, $p=0.09$), the magnitude of increase is generally greater than the decrease from cluster 1 to cluster 2.

Discussion

Taxonomic Composition

Separation of samples into three primary clusters that occur during pre-, syn-, and post-glacial times is potentially consistent with the hypothesis that long-term climate change restructured marine communities. Although clusters occasionally contain samples of different ages (e.g., a Moscovian sample from Yampupata groups with primarily Sakmarian cluster 3), there is a strong relationship between age, and therefore climate, and cluster membership. It is possible that clusters reflect facies rather than time, but this seems unlikely because samples within clusters span multiple lithologies and, occasionally, come from multiple sections. For example, cluster 1 is composed of samples from both bioclastic-dominated wackestones at Cuyavi and calcareous sandstones at Yampupata. In contrast, clusters 2 and 3 are both dominated by samples from Ancoraimes (cluster 2 from the lower two-thirds of our section and cluster 3 from the upper one-third) and come from very similar lithologies and environments, yet have different faunal compositions. Both clusters are from lime mudstones and wackestones, representing distal to mid-ramp environments, but cluster 2 is dominated by the *Hustedia* group, *Kozłowska capaci*, and *Hystriculina*, whereas cluster 3 almost completely lacks the *Hustedia* group and contains

Composita subilita and *Dasysaria inca* in greater abundances. Because there are no clear patterns in either lithology or location in the composition of clusters, it seems unlikely that clusters are simply a result of differing facies.

Although the faunal change associated with the clusters seems to coincide with climate change due to the P1 glacial, the clusters are distinct but not clearly separated by MDS analysis, suggesting that cluster analysis may impose artificial breaks on a continuous gradient of gradual faunal change related to slow northward drift of Bolivia. The preferred latitude of genera in clusters was low and very consistent through time, indicating that the genera present did not dramatically change with either the onset of glaciation or deglaciation. Although the preferred latitude of genera did not change, the preferred latitude of individual samples based on specimens consistently decreased between clusters. Constant cluster-level but decreasing sample-level preferred latitude was due to an increase in the abundance of warmer-water genera rather than the replacement of cooler-water genera by warmer-water taxa. The decrease in sample preferred latitude is uninterrupted through the glacial period, when cool-water genera and therefore preferred latitude should have increased. The continuous change from cosmopolitan to Panthalassic genera is also consistent with a gradual shift rather than effects of glacial climate change (Figure 11).

In contrast, community restructuring during post-glacial warming has been observed at high latitudes in Australia (Clapham and James 2008). Similar faunal shifts may not have occurred in Bolivia, which was located at mid-latitude, because

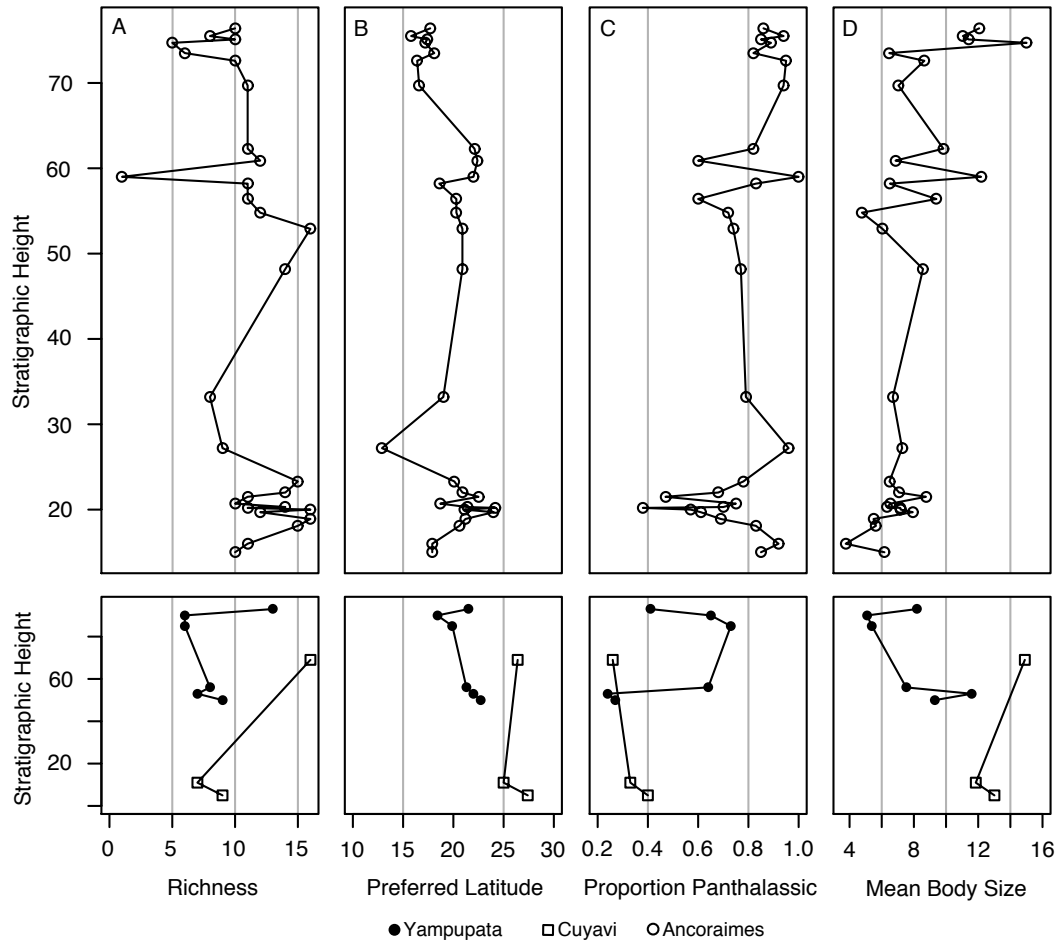


Figure 11. Richness (A), preferred latitude (B), proportion of Panthalassic taxa (C), and mean body size (D) trends of samples from Yampupata (solid circles), Cuyavi (open squares), and Ancoraimes (open circles). Yaurichambi samples are not included because they cannot be correlated precisely with Ancoraimes.

the rate or magnitude of change at lower latitudes may have been slow enough that organisms were capable of migrating, adapting, or evolving (Hofmann and Todgham 2010; Miller *et al.* 2010; Holland and Bitz 2003). Modern high-latitude organisms have low aerobic scopes because of their low metabolic rates, an adaptation to permanently cold conditions, and therefore are less able to meet metabolic oxygen demands as temperature increases (Peck *et al.* 2004). In contrast, mid- and low-latitude organisms experience greater seasonal fluctuations and are therefore more able to cope with changes in temperature (Pörtner 2001). Similarly, high-latitude Permian taxa may also have been more vulnerable to temperature changes, whereas mid-latitude taxa, such as those in Bolivia, would not have been as greatly affected.

Diversity

Despite the gradual faunal change rather than climate-driven restructuring, the richness of samples in cluster 2 is higher than that of either cluster 1 or cluster 3. This higher diversity apparently coincides with the P1 glacial; however, diversity is usually higher in the tropics and the onset of cooler glacial conditions should have been accompanied by a drop in diversity (Alroy 2010; Roy *et al.* 1998). This apparent decoupling of temperature and diversity could be due to an increase in surface ocean nutrient levels from more vigorous ocean circulation during the glacial. The importance of increased nutrient levels in Bolivia is unclear because Bolivia was located in a partially enclosed basin with limited connection to wider ocean circulation during the Late Carboniferous and Early Permian.

The higher richness of samples in cluster 2 could perhaps be explained by smaller body size of taxa in the cluster. Because the size-frequency distribution of species is log-normal, many species are small (Clauset and Erwin 2008). Therefore, samples that contain smaller taxa in addition to large ones, like those in cluster 2, may contain greater diversity relative to the other clusters where small specimens are less abundant.

Mixing of warmer and cooler water faunas due to time averaging is another possible explanation for increased diversity during the glacial (Figure 12). The faunal boundary between warmer and cooler water taxa may have shifted northward and southward with climate changes (Angiolini *et al.* 2007), causing shifts in local faunal composition at Mikankovich timescales. Time averaging is a pervasive phenomenon that mixes shells over scales of hundreds to thousands of years in a single shell bed. Time averaging during deposition of the sample may have mixed genera from warm and cool water faunas and inflated the diversity of these samples relative to samples from climatically more stable time periods. This is unlikely, however, because the range of preferred latitude of samples is fairly consistent in all three clusters. The fauna of cluster 2 do not span a greater range of latitudes than the other clusters so it is unlikely that they would represent a mix of both warm and cool water faunas. The effect of faunal mixing would have been minimal because the timescales of Milankovitch cyclicity are much longer than those of time averaging.

Time averaging may have mixed genera from a greater range of depths during the glacial, which could also have caused the increased diversity in cluster 2 (Figure

13). Sea level changes would have been more rapid and of greater magnitude during the P1 glacial (Rygel *et al.* 2008), which would have superimposed a living community from one depth over recently dead shells from a different depth. These shells from different habitats would then get mixed into a single bed by time averaging.

Biogeographic Affinity

There is a shift from Cosmopolitan to Panthalassic taxa with time, with a dramatic increase occurring from Carboniferous cluster 1 to Permian cluster 2. Most of these Panthalassic taxa are genera found in the western U.S., especially west Texas. Although Texas is extremely well-sampled, this signal of increasing proportion of Panthalassic taxa is not simply a sampling bias, because we normalized each genus to the total number of occurrences in each region. Increasing dominance by Texas taxa may reflect warming sea surface temperatures in Bolivia during this time period as Bolivia drifted north from more than 35° S to close to 30° S. This sort of faunal similarity between Bolivia and the western U.S. has also been seen in corals (Wilson 1990). Studies of brachiopod biogeography have variously identified a separate Andean province based on chonetids (Archbold 1983) or were unable to group Bolivia with any defined province because of the cosmopolitan nature of the few taxa previously reported in the literature (Shen *et al.*).

Body Size

Genera are smaller in cluster 2, roughly during the LPIA glacial, than in either cluster 1 or 3. This reduction in body size is evident in both the mean body size of all

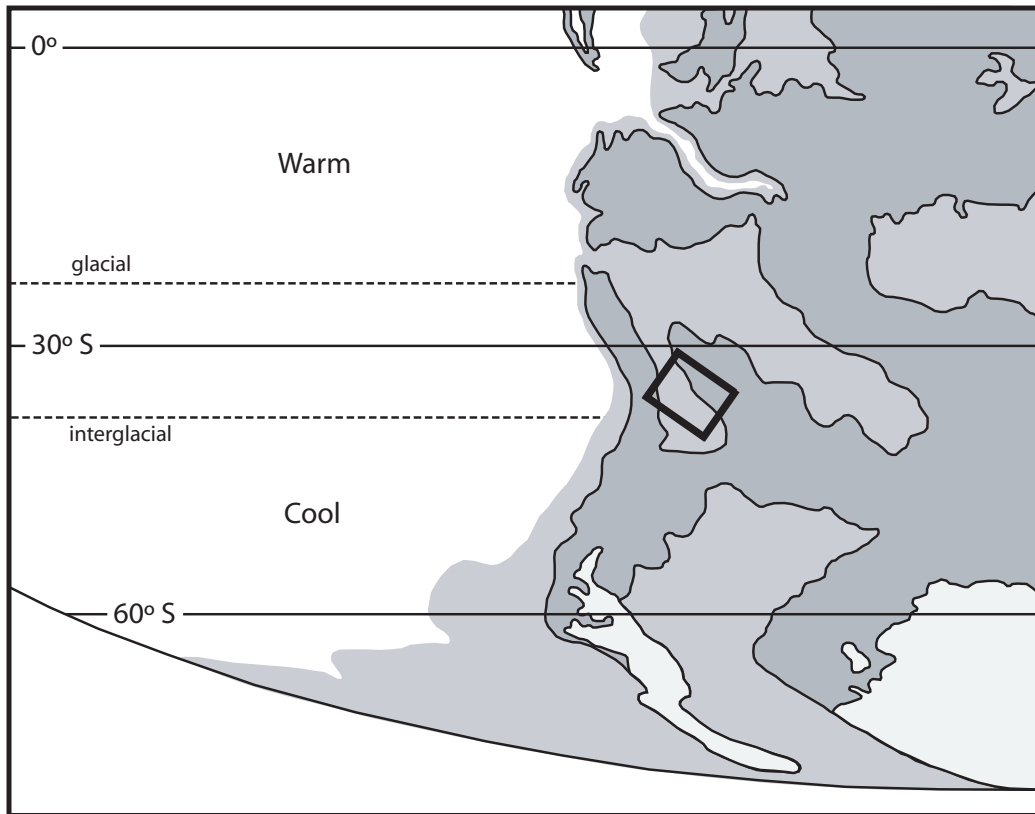


Figure 12. Base map showing hypothetical fluctuations of the faunal boundary between warm-water and cool-water faunas (dashed lines) relative to Bolivia (black box) during glacial and interglacial times. The latitudinal position of the faunal boundary is approximately based on data from Angiolini et al. (2007).

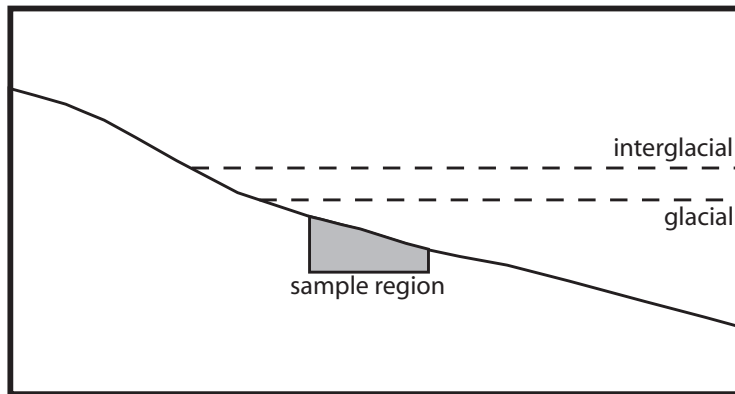


Figure 13. Cartoon showing Milankovich-scale sea level fluctuations (dashed lines) during glacial and interglacial times, illustrating their effect on water depth at a hypothetical sample locality. Time-averaged fossil samples would integrate specimens over a broad depth range.

specimens in each cluster and the within-genus size comparisons between clusters. Body size is closely related to composition because samples with a larger number of smaller taxa will have a smaller overall size. Clusters 1 and 3 are characterized by larger taxa, such as *Gypospirifer condor* and *Linoproductus cora* in cluster 1 and *Composita subtilita* and *Dasysaria inca* in cluster 3. They also lack the *Hustedia* group, which is characteristic of cluster 2 and composed of generally smaller taxa, such as *Hustedia* and the chonetids *Chonetinella* and *Quadrochonetes*. While this appearance and increase in abundance of larger genera in clusters 1 and 3 explains the larger mean sizes of those clusters, it does not explain the within-genus trend of reduced body size in cluster 2. The reduction in size during cluster 2 also cannot be explained by cooling related to glaciation, because the principles of oxygen-limited thermal tolerance would predict larger body size during cooler temperatures (Forster *et al.* 2012; Pauly 2010). The most likely explanation for reduced body size in cluster 2 is a sampling issue related to lithology, because cluster 2 comes almost entirely from the lower two-thirds of Ancoraimes, which is typically finer grained and more fissile. This fissile nature makes it easier to find smaller specimens and harder to find larger ones. Finer-grained sediments are likely to reflect softer substrates that may also have favored smaller individuals (Thayer 1975). The smaller grain size of Ancoraimes can explain the decrease in body size from cluster 1 (collected from Cuyavi and Yampupata) to cluster 2 but the increase from cluster 2 to cluster 3 (also from Ancoraimes) is less clear because Ancoraimes is lithologically and

environmentally consistent throughout our section, potentially suggesting that the increase is a real phenomenon.

Conclusions

Faunal changes are evident in Bolivia, but are most likely due to gradual northward drift of Gondwana rather than climate change related to the LPIA. The shift in sample preferred latitude towards lower latitudes and the increasingly Panthalassic biogeographic affinity are consistent with this. Diversity is higher during the glacial period, contrasting with the anticipated decline in diversity associated with the onset of cooler glacial conditions. The higher diversity in cluster 2 is likely due to some combination of the mixing of genera from different habitat depths from Milankovitch-scale glacioeustatic sea level changes during time averaging and the sampling of a greater range of body sizes, including small taxa.

This lack of climate related faunal change in Bolivia was probably a result of its mid-latitude location. Both the rate of temperature change and its magnitude were likely smaller at lower latitudes than at high-latitudes, thereby reducing the impact of climate change on marine communities. Furthermore, this lack of change implies that mid- and low-latitude organisms are less vulnerable than high-latitude organisms during climate change, which is consistent with predictions from biologists based on aerobic scope and metabolic rate. More broadly, variable responses across latitudes during slow, long-term climate change implies that geographic distribution would likely have been a significant predictor during more

severe climate change events such as the end-Permian or end-Triassic mass extinctions and suggests that high-latitude organisms are likely to be at greatest risk during modern climate change.

References

- ALROY, J. 2010. Geographical, environmental and intrinsic biotic controls on Phanerozoic marine diversification. *Palaeontology*, **53**, 1211-1235.
- ANGIOLINI, L., GAETANI, M., MUTTONI, G., STEPHENSON, M. H. and ZANCHI, A. 2007. Tethyan oceanic currents and climate gradients 300 m.y. ago. *Geology*, **35**, 1071-1074.
- ARCHBOLD, N. W. 1983. Permian marine invertebrate provinces of the Gondwanan Realm. *Alcheringa*, **7**, 59-73.
- CLAPHAM, M. E. 2010. Faunal evidence for a cool boundary current and decoupled regional climate cooling in the Permian of western Laurentia. *Palaeogeography Palaeoclimatology Palaeoecology*, **298**, 348-359.
- CLAPHAM, M. E. and JAMES, N. P. 2012. Regional-scale marine faunal change in eastern Australia during Permian climate fluctuations and its relationship to local community restructuring. *Palaios*, **27**, 627-635.
- CLAPHAM, M. E. and JAMES, N. R. 2008. Paleoecology of early-middle Permian marine communities in eastern Australia: response to global climate change in the aftermath of the Late Paleozoic Ice Age. *Palaios*, **23**, 738-750.
- CLARKE, A. 1993. Temperature and extinction in the sea: a physiologist's view. *Paleobiology*, **19**, 499-518.
- CLAUSET, A. and ERWIN, D. H. 2008. The evolution and distribution of species body size. *Science*, **321**, 399-401.
- FIELDING, C. R., FRANK, T. D., BIRGENHEIER, L. P., RYGEL, M. C., JONES, A. T. and ROBERTS, J. 2008. Stratigraphic imprint of the Late Palaeozoic Ice Age in eastern Australia: a record of alternating glacial and nonglacial climate regime. *Journal of the Geological Society*, **165**, 129-140.
- FORSTER, J., HIRST, A. G. and ATKINSON, D. 2012. Warming-induced reductions in body size are greater in aquatic than terrestrial species. *PNAS*, **109**, 19310-19314.
- GASTALDO, R. A., DIMICHELE, M. A. and PFEFFERKORN, H. W. 1996. Out of the icehouse into the greenhouse: a late Paleozoic analog for modern global vegetational change. *GSA Today*, **6**, 1-7.

- GRADER, G. W. 2003. Carbonate-siliciclastic sequences of the Pennsylvanian and Permian Copacabana Formation, Titicaca Group, Andes of Bolivia. University of Idaho.
- GRADER, G. W., ISAACSON, P. E., DÍAZ-MARTÍNEZ, E. and POPE, M. C. 2008. Pennsylvanian and Permian sequences in Bolivia: Direct responses to Gondwana glaciation. *Resolving the Late Paleozoic Ice Age in time and space. Geological Society of America Special Paper*, **441**, 143-159.
- HARLEY, C. D. G., HUGHES, A. R., HULTGREN, K. M., MINER, B. G., SORTE, C. J. B., THORNBUR, C. S., RODRIGUEZ, L. F., TOMANEK, L. and WILLIAMS, S. L. 2006. The impacts of climate change in coastal marine systems. *Ecology Letters*, **9**, 228-241.
- HOFMANN, G. E. and TODGHAM, A. E. 2010. Living in the Now: Physiological Mechanisms to Tolerate a Rapidly Changing Environment. *Annual Review of Physiology*, **72**, 127-145.
- HOLLAND, M. M. and BITZ, C. M. 2003. Polar amplification of climate change in coupled models. *Climate Dynamics*, **21**, 221-232.
- KITAMURA, A., OMOTE, H. and ODA, M. 2000. Molluscan response to early Pleistocene rapid warming in the Sea of Japan. *Geology*, **28**, 723-726.
- KORTE, C., JONES, P. J., BRAND, U., MERTMANN, D. and VEIZER, J. 2008. Oxygen isotope values from high-latitudes: Clues for Permian sea-surface temperature gradients and Late Palaeozoic deglaciation. *Palaeogeography Palaeoclimatology Palaeoecology*, **269**, 1-16.
- MELZNER, F., MARK, F. C. and PÖRTNER, H. O. 2007. Role of blood-oxygen transport in thermal tolerance of the cuttlefish, *Sepia officinalis*. *Integrative and Comparative Biology*, **47**, 645-655.
- MILLER, G. H., ALLEY, R. B., BRIGHAM-GRETTE, J., FITZPATRICK, J. J., POLYAK, L., SERREZE, M. C. and WHITE, J. W. C. 2010. Arctic amplification: can the past constrain the future? *Quaternary Science Reviews*, **29**, 1779-1790.
- MONTANEZ, I. P., TABOR, N. J., NIEMEIER, D., DIMICHELE, W. A., FRANK, T. D., FIELDING, C. R., ISBELL, J. L., BIRGENHEIER, L. P. and RYGEL, M. C. 2007. CO₂-forced climate and vegetation instability during late paleozoic deglaciation. *Science*, **315**, 87-91.

- OKSANEN, J., BLANCHET, F. G., KINDT, R., LEGENDRE, P., MINCHIN, P. R., O'HARA, R. B., SIMPSON, G. L., SOLYMOS, P., STEVENS, M. H. H. and WAGNER, H. 2012. vegan:Community Ecology Package. *R package version 2.0-3*.
- PARMESAN, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics*, **37**, 637-669.
- PAULY, D. 2010. Excellence in Ecology. *Gasping Fish and Panting Squids: Oxygen, Temperature and the Growth of Water-Breathing Animals*. International Ecology Institute, Oldendorf/Luhe, Germany, 216 pp.
- PECK, L. S., CLARK, M. S., MORLEY, S. A., MASSEY, A. and ROSSETTI, H. 2009. Animal temperature limits and ecological relevance: effects of size, activity and rates of change. *Functional Ecology*, **23**, 248-256.
- PECK, L. S., WEBB, K. E. and BAILEY, D. M. 2004. Extreme sensitivity of biological function to temperature in Antarctic marine species. *Functional Ecology*, **18**, 625-630.
- PETCHEY, O. L., DOWNING, A. L., MITTELBAACH, G. G., PERSSON, L., STEINER, C. F., WARREN, P. H. and WOODWARD, G. 2004. Species loss and the structure and functioning of multitrophic aquatic systems. *Oikos*, **104**, 467-478.
- PÖRTNER, H. O. 2001. Climate change and temperature-dependent biogeography: oxygen limitation of thermal tolerance in animals. *Naturwissenschaften*, **88**, 137-149.
- 2010. Oxygen- and capacity-limitation of thermal tolerance: a matrix for integrating climate-related stressor effects in marine ecosystems. *Journal of Experimental Biology*, **213**, 881-893.
- ROY, K., JABLONSKI, D., VALENTINE, J. W. and ROSENBERG, G. 1998. Marine latitudinal diversity gradients: Tests of causal hypotheses. *Proceedings of the National Academy of Sciences of the United States of America*, **95**, 3699-3702.
- RYGEL, M. C., FIELDING, C. R., FRANK, T. D. and BIRGENHEIER, L. P. 2008. The magnitude of late Paleozoic glacioeustatic fluctuations: a synthesis. *Journal of Sedimentary Research*, **78**, 500-511.
- SHEN, S., ZHANG, H., SHI, G. R., LI, W., XIE, J., MU, L. and FAN, J. Early Permian (Cisuralian) global brachiopod palaeobiogeography.

- SOMERO, G. N., CARLSON, C. A. and GIOVANNONI, S. J. 2012. The Physiology of Global Change: Linking Patterns to Mechanisms. *Annual Review of Marine Science*, **4**, 39-61.
- THAYER, C. W. 1975. Morphological adaptation of benthic invertebrates to soft substrata. *Journal of Marine Research*, **33**, 177-189.
- WALTHER, G. R., POST, E., CONVEY, P., MENZEL, A., PARMESAN, C., BEEBEE, T. J. C., FROMENTIN, J. M., HOEGH-GULDBERG, O. and BAIRLEIN, F. 2002. Ecological responses to recent climate change. *Nature*, **416**, 389-395.
- WILSON, E. C. 1990. Permian corals of Bolivia. *Journal of Paleontology*, **64**, 60-78.