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Changes in the Latitudinal Diversity Gradient during the Great Ordovician Biodiversification Event

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ABSTRACT

Near equatorial peak diversities are a prominent first-order feature of today's latitudinal diversity gradient (LDG), but were not a persistent pattern throughout geological time. In an analysis of Ordovician (485–445 Ma) fossil occurrences, an equator-ward shift of the latitudinal diversity peak can be detected. A modern-type LDG and out-of-the-tropics range shift pattern were synchronously established during emerging icehouse conditions at the climax of the Great Ordovician Biodiversity Event (GOBE). The changes in the LDG pattern and range shift trends can be best explained as a consequence of global cooling during the Middle Ordovician and of diversification in the tropical realm following a greenhouse period with temperatures too hot to support diverse tropical marine life. These results substantiate a fundamental role of temperature changes in establishing global first order diversity patterns.

INTRODUCTION

Life on earth today is most diverse at or near the equator and least diverse near the poles (Pianka, 1966; Currie, 1991; Hillebrand, 2004; Mittelbach et al., 2007; Jablonski et al. 2016). This latitudinal diversity gradient (LDG) is apparent in most groups of marine and terrestrial organisms, but was not a persistent pattern throughout geological time (e.g., Mannion et al., 2014). Strictly tropical peak diversities might be a feature of icehouse climate regimes, whereas warmer greenhouse regimes show generally shallow LDGs (e.g., Crame, 2002; Marcot et al., 2016; Jablonski et al., 2016)

These expectations can be tested against the fossil record from a time period during which one of the most dramatic and sustained Phanerozoic diversifications, the Great Ordovician Biodiversification Event (GOBE), took place. The GOBE was a ca. 40 Ma diversification interval during the Ordovician Period (485–444 m.y. ago) with a massive expansion in diversity at lower taxonomic ranks (species, genus, family level) (Fig. 1) and profound paleoecological changes within the marine biota (Servais et al., 2010). The diversification occurred against a background of changes in the physicochemical environment. In particular, it has been suggested that global cooling was one of the major driving factors, because this brought temperatures to levels more compatible with metazoan metabolism and skeletal growth (e.g., Trotter et al., 2008; Rasmussen et al., 2016). Hence, before cooling, large parts of the Ordovician seas, especially in the lower latitudes, would have been too hot to sustain highly diverse metazoan communities such as metazoan reefs (Webby, 2002). The GOBE, in this scenario, would represent a predominantly tropical diversification.

Ordovician diversity dynamics were previously analyzed mainly on a local, paleocontinent, or global scale (see e.g., Webby et al. 2004; Servais and Harper, 2013; Trubovitz and Stigall, 2016) and changes in LDG patterns can only indirectly be inferred from these data. Here, for the first time Ordovician marine diversity is analyzed across paleolatitudinal zones based on Cambrian–Silurian fossil occurrences documented in the Paleobiology Database (PaleoBioDB, https://paleobiodb.org). I reconstruct Ordovician

LDGs and their changes and ask whether the observed trends can be explained by changes in global temperatures, paleogeographical shifts, or changes in benthic habitats.

METHODS

The analysis was based on a download of the complete set of global, genus-level, Ordovician fossil occurrences from the Paleobiology Database on 26 November 2016. All accepted genus name entries in the PaleoBioDB were included in the analysis, without any additional filters set. Additionally, the complete set of 4081 genera from 773 fossil collections from the Cambrian Trempeaulean Regional Stage and the Silurian Rhuddanian Stage were downloaded. The stratigraphic data associated with each of the fossil occurrences were matched with stage level binned stratigraphic units in the RNames Database (http://rnames.luomus.fi/), resulting in 90,471 latest Cambrian to Rhuddanian occurrences (for time binning see Kröger and Lintulaakso, 2017). The genus occurrences are analyzed at stage- and stage-slice-level (Bergström et al., 2009) time resolution (average length 6.2 m.y. and 2.2 m.y., respectively).

PaleoBioDB collections are assigned to lithological and environmental classes. Based on these data I further classified all collections with sufficient lithology and environmental information into carbonate/siliciclastic and shallow/deep depositional environments (total = 13085 and 5739, respectively) and calculated their relative abundance (see the GSA Data Repository[1]). Additionally, I used the PaleoBioDB data on lithology and environment for calculation of environmental heterogeneity using the HRel statistics of Wilcox (1973), (see the Data Repository).

All PaleoBioDB collections are explicitly attributed to paleoplates and are linked to paleogeographic latitudinal/longitudinal coordinates based on GPlates (https://www.gplates.org/) rotations (Wright et al., 2013). The collections were binned into 15° and 30° paleolatitudinal zones without distinguishing between northern and southern paleo-hemispheres, because in most cases sample size for the northern paleo-hemisphere was not sufficient for analysis.

I estimated genus range shifts across paleolatitudinal zones and distinguished between “active” and “tectonic” shifts. The observed shift of a genus from one paleolatitudinal zone into another can be either a result of a tectonic shift of the genus location through time or can be caused by a active migrations or a range expansion of the genus, or both. Active shifts can be neutralized or reinforced by tectonic shifts of occurrences.

For distinction between tectonic and active range shift, I binned all genus occurrences into one-degree latitude/longitude quadrants and tracked their paleogeographical shift. Occurrences with identical quadrants in one stage (t_i) and its previous stage (t_{i-1}) and with different paleolatitudinal zones are interpreted as tectonically shifted. Occurrences with different latitude/longitude quadrants and different paleolatitudinal zones are interpreted as active range shifts.

Tectonic and active range shifts from one paleolatitudinal zone to another for times t_{i-1} to t_i, were counted with a unit length of ±1 depending on the direction, such that positive values indicate pole-ward directions and negative values indicate equator-ward directions. In order to eliminate boundary effects, I compared the distance from the mean value of each latitudinal zone.

The diversities were estimated using Shareholder Quorum Subsampling (Alroy, 2010) (herein D_{SQS}), Shannon Entropy Hill number (Chao et al., 2014) (herein D_{Chao}), and the capture-mark-recapture (CMR) method (Liow and Nichols, 2010) (herein D_{CMR}). These three methods were chosen because they represent independent approaches to account for sampling and preservation bias, which in their entirety give an estimate on the robustness of the estimated diversity pattern (Liow and Nichols, 2010; Chao et al. 2014, see the Data Repository). Because all three diversity measures, D_{SQS}, D_{Chao}, and D_{CMR}, exhibit a robust trend (Fig. DR1 in the Data Repository), only the D_{CMR} trends are described in detail in the main article, which additionally produced the most realistic (= largest) 95% confidence intervals. The downloaded data from the PaleoBioDB and the R code of the analysis are available at https://doi.org/10.5281/zenodo.197057.

RESULTS: CHANGING LDGs DURING THE COURSE OF THE DIVERSIFICATION

Ordovician diversity exhibits a trend with relatively low estimates for the first ~18 m.y. (Tremadocian–Dapingian), a steep increase during the remaining Middle Ordovician (Darriwilian), a Late Ordovician plateau, and a drastic decrease during the terminal Ordovician (Fig. 1). When partitioned into four 15° paleolatitudinal zones it becomes apparent that the bulk of the Ordovician diversity increase took place within the tropical realm (0–30°, Fig. 2). In temperate latitudes the GOBE is hardly visible.

This predominance of the tropical diversification can be interpreted as real because it is apparent in all diversity estimates explored herein (Fig. DR1), and it does not reflect changes in the relative abundance of carbonate/siliciclastic and shallow/deep depositional environments, in environmental and lithologic heterogeneity, or in paleogeographical shift (Fig. 3; Fig. DR5). However, although the pattern is not restricted to a specific organismal clade because it is apparent in e.g., brachiopods, mollusks, and trilobites, it is less pronounced or absent in planktic graptolites (Figs DR2 and DR3).

When comparing the per-time-bin diversity estimates against their paleolatitudinal zone, an Ordovician LDG trend becomes apparent, the most important features of which are an Early to Middle Ordovician (Tremadocian–Darriwilian) peak at the 15–45° zone, a Late Ordovician (Sandbian-Katian) change toward higher tropical diversities with a peak at 0–30°, and again a 15–30°-zone peak during the terminal Ordovician (Hirnantian) (Fig. 2; Fig. DR4). Notably, the Darriwilian marks not only the climax of the diversification, but also a major pattern shift in Ordovician LDGs toward maximum values in the tropics.

LDG trends are an effect of changes in evolutionary rates and dispersal (see Jablonski et al. 2016). Dispersal dynamics are driven by differential rates of active and tectonic range shifts (see Methods). These dispersal factors are not correlated in the Ordovician data, and tectonic shift appears to play a minor role in the overall picture (Fig. 3). The relative range shift pattern exhibits considerable variation during the Ordovician with different trends near the equator and in temperate paleolatitudes (Fig. 2). In the high tropics (0–15°), pole-ward shifts were relatively rare during the Early Ordovician but became abruptly more common during the late Middle and Late Ordovician. In contrast, in low tropical and temperate paleolatitudes, the trend exhibits initial (Tremadocian) high rates of pole-ward shifts, relatively high rates of equator-ward shifts during the Floian-Dapingian and an abrupt change toward moderate rates of pole-ward and equator-ward shifts during the Darriwilian.

These trends reveal an intricate change in the general migration dynamics of the Ordovician world with shifting diversity sinks and sources (Fig. 4). One prominent feature of this pattern is the change of the high tropics from a sink during the Early Ordovician toward a source during the latter part of that period. This pattern is consistent with a change toward a modern-type “out of the tropics” scenario (Jablonski et al., 2006) during the Darriwilian concurrent with the main diversification pulse of the GOBE.

DISCUSSION: CHANGING LDGs AND GLOBAL COOLING

Previous analysis of Ordovician diversity trends below global level have focused on paleocontinents or paleo-oceanic regions that range across paleolatitudinal zones and often revealed heterogenous diversity pattern that are difficult to interpret (Miller, 1997; Webby et al., 2004). Only recently have synchronous Darriwilian diversification peaks within low paleolatitude regions of Baltica and Laurentia been detected in brachiopods; these results were used to infer global drivers, such as climatic cooling, intensified sea-water circulation, greater oxygenation and increased primary production (Trubovitz and Stigall, 2016). Here, I show that, although the Darriwilian peak diversification affected all latitudinal zones, it had by far the most profound impact and highest amplitude within the high tropics (Fig. 2). Combined with escalating rates of ex-tropical range shifts during the Middle Ordovician, this tropical diversification appears to be primarily caused by in situ origination, and in turn this tropical in situ origination must have been the quantitatively most important driver of the GOBE.

If this pattern is realistic, then tropical in situ origination is crucial to understanding the GOBE and hence the question of how this high tropical diversity was produced comes into focus. In a recent study and review this question was addressed with respect to the GOBE in general with oscillations between events of immigration and geographic differentiation suggested as one effective “speciation dynamo” (Stigall, 2017). Therein, geographic differentiation, conceptualized as tectonically induced regional isolation (e.g., Harper, 2010) and habitat heterogeneity (e.g., Miller and Mao, 1995) were considered to be key factors in promoting origination (Stigall, 2017). However, the habitat heterogeneity trends estimated herein are not related to the diversity pattern and generally the heterogeneity is not higher in the tropics (Fig. DR5). Because it is currently not known if regional differentiation was more intense in the tropics during the GOBE, these two factors, although not in conflict, cannot explain the LDG pattern detected herein.

Alternatively, geographic differentiation can be more generally conceptualized as ecological niche differentiation, including biologically-induced niche differentiation (*sensu* Sepkoski, 1988). With this more general conceptualization it is possible to set the GOBE into context with the temperature and evolutionary speed (TES) hypotheses of e.g., Allen et al. (2002), Clarke and Gaston (2006), and Brown (2014), which link ecological and evolutionary rates with temperature and predict highest diversities in the tropics. Generally, the Ordovician diversity trend is contrary to naive expectations from TES hypotheses, because they would predict decreasing ecological and evolutionary rates, and diversities and flattened LDG amplitudes under climatic cooling (Tittensor et al., 2010; Brown, 2014; Tittensor and Worm, 2016). This mismatch, however, can be best explained by the existing range limits of the published diversity-temperature dependencies. All published TES hypotheses are based on empirically observed positive diversity-temperature dependencies. These dependencies are constrained by Recent sea surface temperatures with a maximum of ~30 °C (e.g., Brown, 2014). Estimated Early Ordovician tropical sea surface temperatures are well beyond today’s maximum values

(Trotter et al., 2008, Veizer and Prokoph, 2015). It is not known what diversity-temperature dependencies would be like in a hypothetical expanded temperature range, but thermal tolerances of complex multicellular organisms are limited, and today an upper limit for metazoans exists at ~45–47° (Ravaux et al., 2013). These limitations suggest that past diversity-temperature curves beyond modern temperature ranges had a parabolic shape with a diversity maximum in moderate temperatures and decreasing trajectories toward extreme temperatures. Past LDG's under hotter-than-today global regimes theoretically should reflect these expected trajectories with diversity peaks in temperate latitudes rather than near the equator. Data from Mesozoic and Cenozoic greenhouse intervals support this assumption (e.g., Markwick, 1998; Marcot et al., 2016) and the new data from the Ordovician are consistent with earlier assessments that tropical peak diversities are an exclusive feature of LDGs of icehouse periods (Mannion et al., 2014). Additionally, the Ordovician shift of peak LDG values toward the equator coincides with rapid initial expansion and diversification of metazoan reefs after a long period of dominance of reefs built by calcimicrobes, suggesting a (re)colonization of the low latitudes after a prolonged period of too-hot temperatures in the tropics (Webby, 2002; Kröger et al. 2017).

Hence, the mid-Ordovician cooling must have been a major factor for the diversification of the tropics. But why did this tropical diversification and LDG shift have such an overwhelming effect on global net diversity? An answer to this question is not easily found with the data at hand. The tropical mid-Ordovician diversification took place in a larger area and in regions with less intense seasonality compared with the temperate locus of the diversification during the Early Ordovician. The effects of these differences on global Ordovician diversity are currently unknown and offer great potential for future investigations. Furthermore, the tropical mid-Ordovician diversification did not affect all clades. Brachiopods, mollusks, and trilobites diversified mainly in low latitudes and during the Darriwilian, whereas the tropical diversification of graptolites occurred earlier and the Darriwilian pulse is visible only in temperate latitudes. This asynchronicity between clades was known before (e.g., Webby et al., 2004) and new studies potentially will be key to answering this question in the future.

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FIGURE CAPTIONS

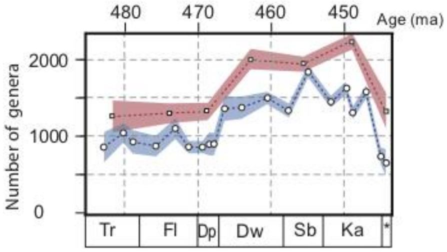

Figure 1. Global genus-level diversity trends for the Ordovician Period with stratigraphic resolution at stage level (squares) and stage slice level (circles, Bergström et al., 2009). The peak diversification of the Great Ordovician Biodiversification Event (GOBE) was during the Darriwilian Stage. Data downloaded from Paleobiology Database (PaleoBioDB, https://paleobiodb.org) on 26 November 2016. DCMR—diversity estimate from capture-mark-recapture (CMR) modeling approach with 95% confidence intervals (shaded areas). Stages: Tr—Tremadocian; Fl—Floian; Dp—Dapingian; Dw—Darriwilian; Sb—Sandbian; Ka—Katian, *—Hirnantian.

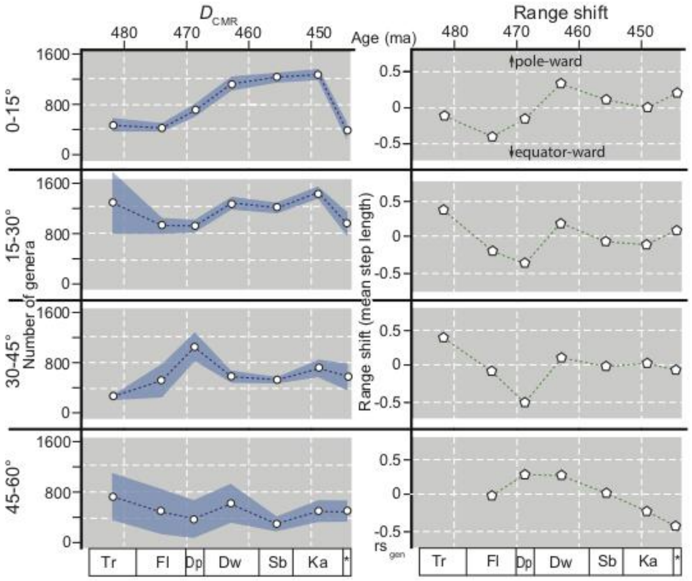

Figure 2. Ordovician diversity trends and range shift dynamics within four paleolatitudinal zones (Northern and Southern Hemispheres combined). Note the massive Darriwilian diversification pulse in low paleolatitudes. D_{CMR}, diversity estimate from capture-mark-recapture (CMR) modeling approach with 95% confidence intervals (shaded areas). n_{gen}—number of genera; rs_{gen}—mean range shift (given as distance from Ordovician mean). Positive values indicate dominance of pole-ward; negative values dominance of equator-ward shifts.

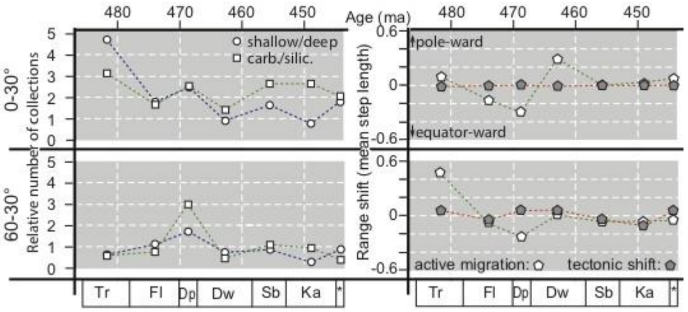

Figure 3. Trends in relative abundance of Ordovician fossil occurrences downloaded from Paleobiology Database (PaleoBioDB, https://paleobiodb.org) on 26 November 2016 from different environments and lithologies (carb.—carbonatic; silic. —siliciclastic), and direction of active/tectonic shift within two paleolatitudinal zones (Northern and Southern Hemispheres combined). Note the differences between active/tectonic shift, environmental trends, and diversity trends (see Fig. 2).

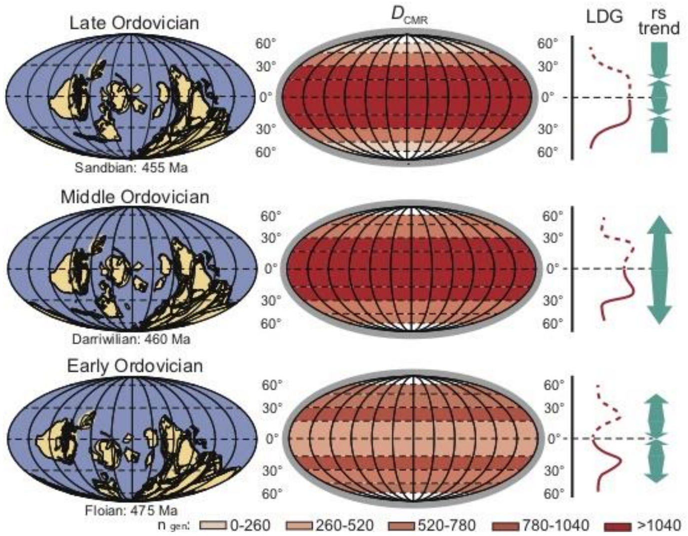

Figure 4. Summary of global change during the Ordovician. Paleogeographic reconstructions from BugPlates (http://www.geodynamics.no/bugs). Diversity estimates and range shift dynamics simplified from Figure 2 (see also Fig. DR4 [see footnote 1]). Estimates are combined for northern and southern hemisphere and are symmetrically plotted across equator for simplicity. n_{gen}—number of genera.

[1] GSA Data Repository item 2018xxx, xxxxxxxx, is available online at http://www.geosociety.org/datarepository/2018/, or on request from editing@geosociety.org.