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# An unpredictable body size response to the Permo-Triassic climate crisis

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**Abstract.** A predictive ecological response to both the present and past climate crises is that marine ectotherm species will become smaller before going extinct or fluctuate in abundance and size with environmental conditions. The problem with studying past climate events with high rates and magnitude of warming, which may serve as analogues for projected climate change, is that very few species, or even genera, survived such events. Here, we utilized one of the few records of marine bivalves that spans the Permian-Triassic climate crisis with specimen-level data and at a high resolution. These measurements come from the Bellerophon and Werfen formations of the Dolomites in Italy, representing relatively shallow marine environments. At the species-level, there is almost a complete turnover, and the newly evolved species are typically significantly smaller, but not unusually small, whereas the three surviving species do not show a significant body size change. Our results clarify that the observed temporary size reduction at the genus-level is primarily driven by the preferential evolution of smaller species after the extinction, rather than, as often assumed, by a size decrease within existing species; this challenges the universal validity of the 'Lilliput effect' in the sense of direct intra-species dwarfing, but confirms it as a consequence of faunal turnover. Subsequently, there are two pulses of genus-level body size recovery determined by different mechanisms. The first phase (late Griesbachian) is driven by the size-increase of the existing species, whereas the second phase (early Spathian) is also due to the evolution of larger species. The effects of abiotic and biotic factors in controlling these body size dynamics are superimposed during the Early Triassic. These results suggest a mechanism to explain size reductions during climate crises, but does not find a species-level body size reduction to be a forecastable response to extreme climate warming.

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## 1 Introduction

If scientists want to use past climate crises to forecast the potential ecological response of marine ecosystems to different projections of a modern-day climate and biodiversity crisis, then they must uncover predictive or forecastable responses of marine ecosystems to the main threats to biodiversity. One way to do this is to use past climate change events to test hypotheses related to the forecasted responses. It has, however, been suggested that the evolution of marine ecosystems has altered how climate change manifests, meaning it is difficult to uncover consistent ecological responses to climate crises (Payne et al., 2016; Foster et al., 2023a). For example, the evolution of siliceous and calcareous plankton, as well as past collapses in their productivity, would have affected how the oceans could buffer increased influxes of carbon dioxide (Kump et al., 2009; Isson et al., 2020; Rauzi et al., 2024). On the other hand, there are some consistent ecological responses observed at multiple hyperthermal events that may be considered forecastable during a projected climate and biodiversity crisis, with a key predictive response being the reduction in body size of marine ectotherms (Rita et al., 2019; Monarrez et al., 2020; Pörtner et al., 2023; Nätscher et al., 2025).

The consistent body size response, a temporary reduction in the size of ectotherms, in evolutionary studies of hyperthermals has been coined the “Lilliput effect” (Urbanek, 1993; Twitchett, 2007). This means that a predictive response to projected climate change would be an expected decrease in body size, but this finding is not unanimous and there has been an increasing number of studies suggesting that a body size decrease for past hyperthermal events is not always going to be observed (Brayard et al., 2010, 2015; Payne et al., 2016; Nätscher et al., 2023). In addition, the mechanism(s) that explains a body size decrease is often debated, e.g., is it the size-reduction at the species-level or genus-level that is being observed (Brayard et al., 2010, 2015), is it the preferential loss of larger species (Nützel et al., 2010), or is no body size reduction actually observed at all (Nätscher et al., 2023). There is also a clear lack of data when trying to understand the body-size response of marine ectotherms during and between different climate crises. This means that at best some studies have only been able to look at the body size response at a coarse temporal or coarse taxonomical scale (e.g., Rego et al., 2012; Payne et al., 2016), which can lead to some conflicting results (Monarrez et al., 2020), because they do not capture species size dynamics during the event. It is, therefore, critical that if we want to better understand a predictable ecological response to climate change, then we need high-resolution datasets that span these past climate crises.

The debate surrounding the body size response for marine ectotherms could not be greater than for the Permian-Triassic climate crisis, a 10-12°C hyperthermal event (Gliwa et al., 2023) resulting in the highest extinction rates of marine taxa of the Phanerozoic (Kocsis et al., 2018). This high turnover took place not only at the species-level, but also at higher taxonomic levels, particularly in phyla that dominated marine ecosystems prior to the extinction event (e.g., brachiopods, crinoids and bryozoans). This is, however, a general global trend; in shallow marine ecosystems bivalves, foraminifera, ostracods and gastropods were already dominant aspects of the marine ecosystem prior to the extinction, e.g., in the Dolomites (Italy) (Prinoth and Posenato, 2024; Mette and Roozabani, 2012; Gómez Correa et al., 2025), Antalya and Aldag Nappes (Türkiye) (Karapunar et al., 2025), and Spitzbergen (Svalbard) (Nakazawa et al., 1999; Bond et al., 2015). High-resolution studies from those regions and groups could, therefore, provide key insights into the response of ectotherms during a high magnitude climate crisis. Here, we have utilized a novel bivalve record of the Dolomites (Italy) to understand the bivalve body size response, if any, to the Permian-Triassic climate crisis. The Dolomites are often regarded as one of the best-studied regions in terms of palaeontological and geochemical records for the Permian-Triassic crisis, owing to the numerous exposures of a Permian-Triassic succession representing a range of water depths (Kustatscher et al., 2019) and the evolution of Triassic carbonate platforms (Stefani et al., 2004). Yet, it is only recently that an extensive bivalve collection spanning the Permian-Triassic event has been produced (Prinoth and Posenato, 2024) and there is a relative dearth of robust proxy evidence for environmental changes, even at the best studied sections.

## 2 Geological Setting

The Dolomites are a mountain area, classically considered bound by the Puster Valley to the North, Valsugana Valley to the South, River Eisack and Adige to the West and Piave Valley to the East. The UNESCO World Heritage Dolomites includes also the Brenta Group to the West and the Friulian Dolomites to the East. The Dolomites are part of the Southern Limestone Alps, where the sedimentological and ecological evolution of the Dolomites extends in other tectonic blocks from the same palaeogeographic region, e.g., Gemer-Bükk-Zagorje Unit (Kovács et al., 2011). During the Permian-Triassic transition, the western Palaeotethys was being subducted to the north and the Neotethys was opening to the south, separated by the Cimmerian microcontinent. The Dolomites were being deposited on the Adria tectonic block, in the western Palaeotethys around 15°N, which was drifting north as it became increasingly detached from the northern Africa plate (Deccourt et al., 2000). Contemporaneously, the Adria block is one of many tectonic blocks in the western Palaeotethys and northwestern

Neotethys, which record extensive shallow water carbonate deposition during the late Permian and the Triassic, from the Arabian shield across the northern Africa plate, and from the Iberian massif to Dobrogea (Deccourt et al., 2000; Muttoni et al., 2009; Pérez-Valera et al., 2023). The Adria block thus represents part of a broad epicontinental shelf and substantial habitable area for shallow marine ecosystems. Tectonically, the Dolomites experienced limited deformation during the Permian–Triassic, allowing for exceptional preservation of coastal to platform-basin transitions (Brandner et al., 2009).

The depositional setting during the Changhsingian-Early Triassic of the Dolomites was a homoclinal, mixed carbonate-siliciclastic ramp (Broglio Loriga et al., 1988). Locally, the palaeocoastline was situated to the west and outcrops of the Permian-Triassic successions towards the east of the Dolomites and into the Carnic Alps generally show a deepening (Kustatscher et al., 2019) (Fig. 1). The Lopingian sedimentary succession is represented by the terrestrial Gröden Formation (aka., Val Gardena Sandstone) and shallow marine Bellerophon Formation, which overlays Permian Porphyry volcanics, basal conglomerates and a Brixen quartzite basement (Bosellini et al., 2003).

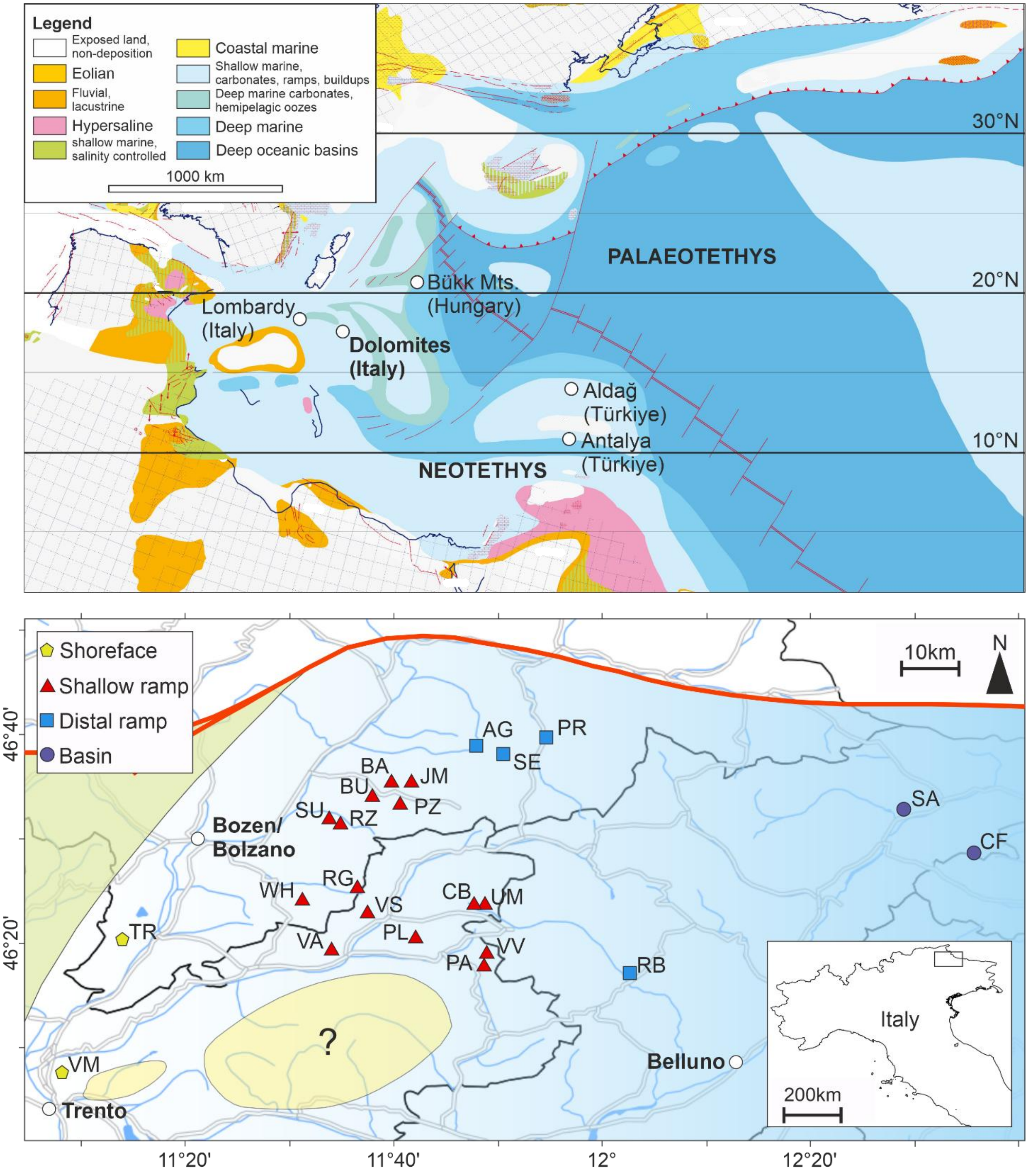

Figure 1. Palaeogeographic setting of the Dolomites, Italy. Upper panel) Palaeogeographic map of the western Palaeotethys after the Ladinian reconstruction of Dercourt et al. (2000). The location of the Dolomites and other

mentioned regions are indicated. Lower panel) The locations of the investigated sections from the Dolomites (Italy), and a palaeodepostional map overlain emphasizing the onshore-offshore water depth gradient. Abbreviations: AG – Alferer Geisler, BA – Balest, BU – Pufels/Bulla, CB – Costabella, CF – Casera Federata, JM – Jmueia, PA – Punta Rolle, PL - , PR – Preroman, PZ – Ruf di Piz, RB – Rova-Baches, RG – Rosengarten/Catinaccio, RZ – Ratzes, SA – San Antonio, SE – Seres, SU – Seis/Siusi, TR – Tramin/Termeno, UM – Uomo/l’Om Picol, WH – Weißhorn/Corno Bianco, VA – Val Averta, VM – Vigo Meano, VS – Val Sorda, VV – Val Venegia.

The extinction interval and Early Triassic is found within the Werfen Formation. The timing of the mass extinction event is yet to be quantitively constrained, with some studies recognizing multiple events starting with the Bellerophon/Werfen formation boundary (e.g., Farabegoli et al., 2007), and others recognizing a pulse within the Tesero Member (Werfen Formation) (e.g., Groves et al., 2007). Lithologically and palaeogeographically, the Dolomites succession is similar to the Antalya and Aldağ Nappes (Turkey), where the extinction has been quantitatively interpreted as an interval spanning the onset of ooid deposition up to the Permian/Triassic boundary (Karapunar et al., 2025b). This corresponds to the interval from Bed BU7B to Bed BU12A at the Bulla section, the parastratotype section for the Dolomites, which also corresponds with a globally recognised carbon isotope excursion (Farabegoli et al., 2007; Farabegoli and Perri, 2012). This interval also corresponds to a species decline and mix of autochthonous and allochthonous Permian microfossils and sedimentological changes associated with the extinction drivers.

## 3 Materials and Methods

The bivalves that were measured in this study were primarily from Prinoth and Posenato (2024) with additional specimens from Broglio Loriga and Mirabella (1986), Hofmann et al. (2015) and Foster et al. (2020). Additional specimens were collected during targeted fieldwork on the Mazzin Member of the Werfen Formation, and measurements from figured specimens in Neri and Posenato (1985) and Posenato (2009) were additionally included. Some species which were found in Permian rocks of the Dolomites could not be found in the post-extinction succession, but are known from other European locations, in particular the Bükk Mountains in Hungary. Therefore, the body size data from the basal beds of the Gerennavár Limestone Formation at the Bálvány-North section reported by Posenato et al. (2005) were also included in the dataset. The species identifications were standardised to ensure taxonomic consistency and avoid synonymy. For example.,

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*Stutchburia* sp. A from Hofmann et al. (2015) was re-identified as *Stutchburia tschernyschewi*, making *S. tschernyschewi* a survivor species, and *Claraia orbicularis*, *C. wangi-griesbachi*, and *C. aurita* from the Mazzin Member were recombined as *Claraia* sp., as the different species names represent different taxonomic opinions rather than different species (see also Foster et al., 2020 for a discussion). For each specimen, the height and the width were measured to the nearest 0.1 mm using digital callipers. The geometric mean of each specimen was calculated where: the square root of the product of shell height and shell length, and these were then log transformed so that proportional deviations are represented consistently.

Combined, bivalve measurements come from 27 different localities across the Dolomites (Fig. 1) and correlating the sections is difficult due to the lack of lithological marker beds. Therefore, the specimens were pooled based on the sequence stratigraphic profile of the Permian-Triassic succession (following Posenato, 2008; Foster et al., 2017; Prinoth and Posenato, 2024), where: three stratigraphic sequences (Lo3-Lo5) are identified from the Lopingian Bellerophon Formation; two sequences from the Induan (In1-In2); and three sequences from the Olenekian (O1-O3). The stratigraphic sequence In1 starts with the uppermost Bulla Member of the Bellerophon Formation, prior to the extinction event (sensu Farabegoli et al., 2007), but no bivalve measurements were recorded from the Bulla Member, and the body sizes of In1 represent exclusively post-extinction body sizes. All raw taxonomic, stratigraphic, locality and measurement data can be found in the supplementary dataset.

In the analysis, bivalve specimens in open nomenclature were included. All specimens were disarticulated and given the variability in left and right valve measurements, it is unlikely that measurements from a left and right valve both originated from the same individual. Therefore, all specimen measurements were included in the analysis. To determine if differences between the time intervals were significant, we used the non-parametric Kruskal-Wallis test and Mann-Whitney U pairwise tests with a significance level of 0.05.

To investigate the drivers of body size changes, we utilised the within- and among-taxa approach by Rego et al. (2012) using the modified version of Rita et al. (2019). This method allows division of the assemblage body-size shift into three components: a disappearance of taxa effect, within-lineage effect and appearance of new taxa effect (see Rita et al., 2019). The analysis by Rego et al. (2012), Rita et al. (2019) and Nätscher et al. (2023) re-classifies all taxa into the different assemblage components and then calculates the median body sizes for each component. That means that changes in the components are sensitive to changes in the relative abundance of different species within the time interval. I.e., an assemblage component can record significant changes in size, even if all the taxa stay the same size, due to changes in the taxon abundances. Here, to avoid the impact of taxonomic composition dynamics in understanding body-size dynamics, the median size of each species was first calculated before being categorized into the different assemblage components. A comparison between the two different approaches shows the same body size dynamic patterns, except our approach shows fewer extreme fluctuations. All statistical analyses were made in R (R Core Team, 2019) and the code and data is available at https://github.com/wjf433/DBiv.

## 4 Results

3983 body sizes of 70 species from 25 genera were investigated from the Dolomites, Italy. In this region, only two species, *Stutchburia tschernyschewi and Bakevellia ceratophaga*, survived the extinction event. Both species show an increase in median size from the middle Changhsingian into the Triassic, but no size data from the upper Changhsingian are available for these species and only one specimen of *Stutchburia tschernyschewi* was measured from the Triassic (Fig. 2A). A third species that survived the extinction event is *Eumorphotis lorigae*, which is recorded from the upper Changhsingian of the Dolomites (Posenato, 2009, Prinoth and Posenato, 2024) and from the deeper water setting of the Bükk Mountains, Hungary (Posenato et al., 2005). During the extinction event and when the pre-extinction sizes are compared, this species also shows a size increase during the extinction event (Fig. 2A). At the genus-level, however, six (50%) genera survived, with five genera showing a significant body size decrease (*Eumorphotis*, *Pernopecten*, *Stutchburia*, *Towapteria* and *"Unionites"*). Only *Bakevellia* shows a significant body size increase, owing to an earlier size decrease in the upper Changhsingian (Fig. 2B). In addition, when the measurements of the closely related genera *Schizodus* and *Neoschizodus* are combined, they show a significant size decrease across the extinction event (Fig. 2B).

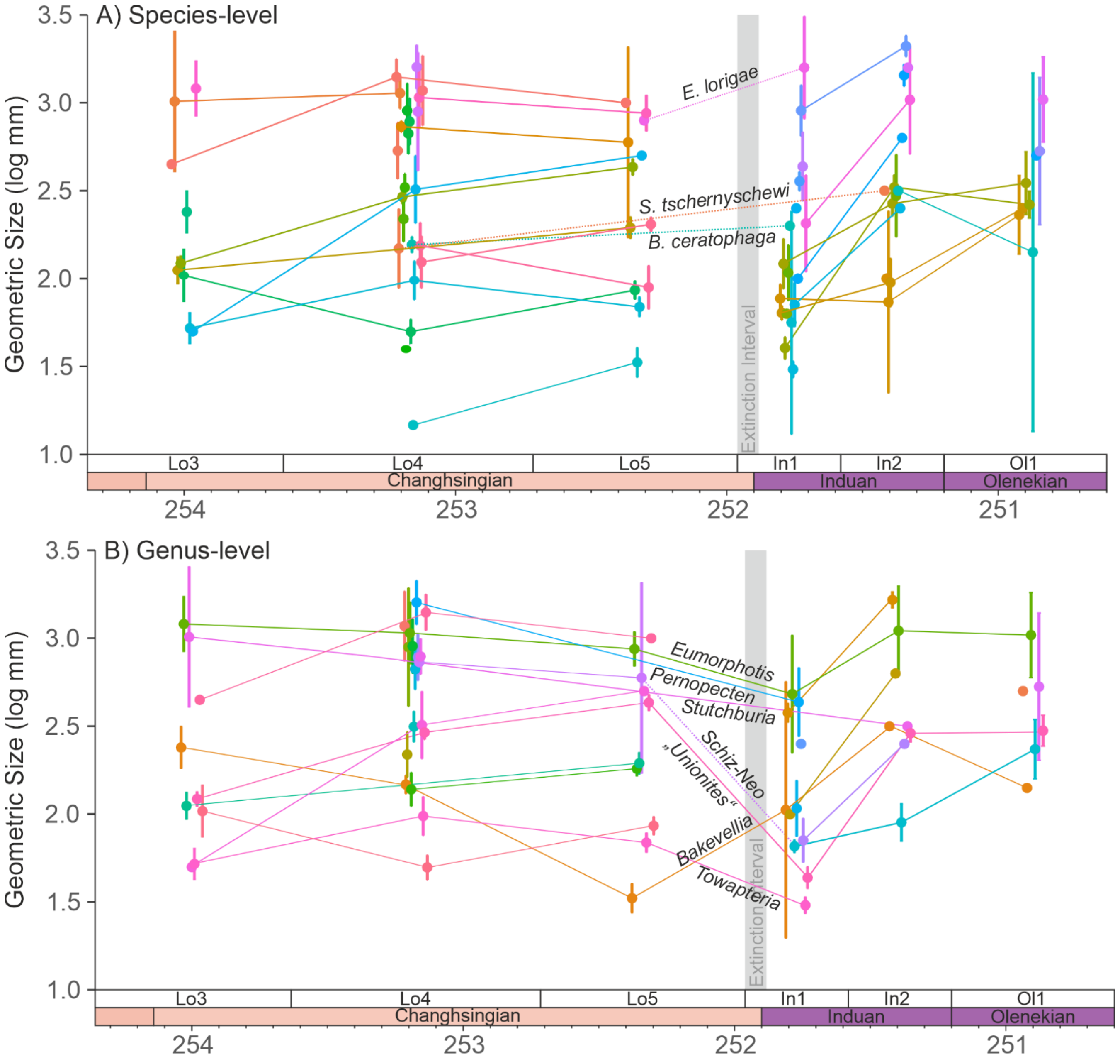

Figure 2. Changes in the mean geometric size of bivalves from the Permian-Triassic transition in the Dolomites, Italy, with 95% confidence intervals. A) Body size changes at the species-level. The samples are grouped based on their sequence stratigraphic framework to reduce lithological biases on body sizes. B) Body size changes at the genus-level. The closely related genera *Schizodus* and *Neoschizodus* are connected with a dotted line across the Permian/Triassic boundary. Schiz-Neo = *Schizodus* and *Neoschizodus*.

When the body size changes are broken down into their three different components, i.e., the effects of extinction/extirpation, within-lineage changes, and origination/immigration, four major signals appear: (1) The assemblage body size decreases, by 0.25 log units, which is a consequence of the origination of smaller species (Fig. 3A), leading to a within-genus body size decrease (Fig. 3B); (2) smaller species appear to have been selected against during the extinction event (Fig. 3A); (3) the species that evolved after the extinction show a 0.4 log unit size increase in the late Griesbachian (Fig. 3); and (4) a similar body size increase in the early Spathian is conversely driven by the origination of larger species and the increased size of existing species (Fig. 3A). The largest decline in assemblage body sizes is recorded in the late Spathian, but this can be attributed to a smaller number of body size measurements and because the stratigraphic sequence O3 does not record outer ramp lithofacies that typically has the larger body sizes (see also Foster et al., 2020). When comparing the three components of body size change across the extinction interval (Fig. 4), it turns out that, even though the median size of newly originated taxa is significantly smaller than pre-extinction data, the body sizes are not unusually different, i.e., the maximum and minimum body sizes are relatively similar (Fig. 4). The changes are driven by the increase in the number of smaller species and the abundance of smaller specimens.

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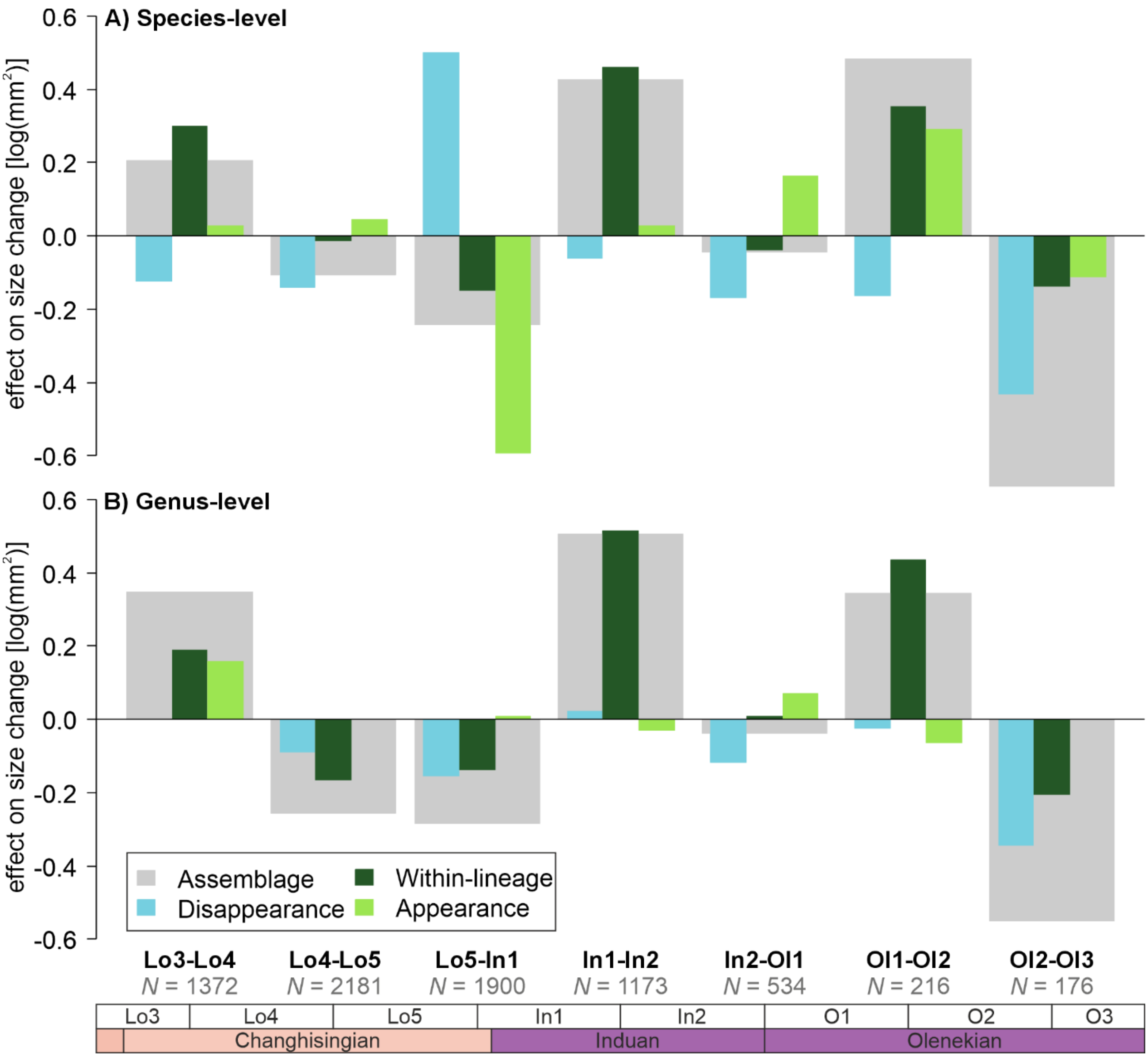

Figure 3. The effect on body-size change on bivalve assemblages and the three components of body size change from the Dolomites, Italy. A) The effects of body size changes at the species-level. B) The effects of body size change at the genus-level. The number of observations based on each comparison are shown below each comparison. The effects of the Permian-Triassic mass extinction are shown between Lo5-In1.

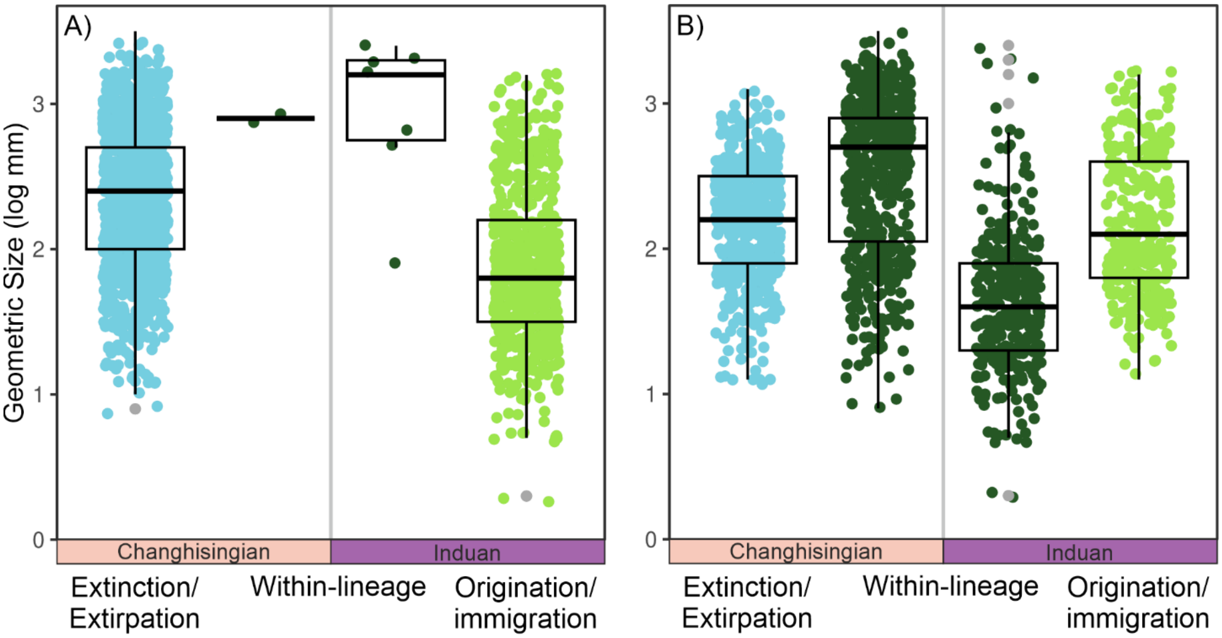

Figure 4. The geometric body sizes of bivalves between Lo5 and In1 stratigraphic sequences, i.e., the impacts of the Permian-Triassic hyperthermal event, split into the three components of size changes from the Dolomites, Italy. The jitter plot shows the individual sizes of each measured bivalve specimen, with a box plot overlain. A) At the species-level and B) at the genus-level.

It is also noticeable that within the main genera and families that survived the extinction there are differences in the body size response depending on the ecology of the bivalves. The epifaunal and semi-infaunal species of *Eumorphotis* and the Bakevellidae (Fig. 5) do not show a major size decrease across the extinction interval. The shallow-infaunal, suspension feeding genera, “*Unionites*” and a comparison between the closely related *Schizodus* and *Neoschizodus*, do, however, show a significant size decrease across the extinction interval. However , no species belonging to “*Unionites*” nor *Neoschizodus* occurred both before and after extinction (Fig. 6). Furthermore, the recovery of body size differs between “*Unionites*” and *Neoschizodus*, with “*Unionites*” recovering to pre-extinction body sizes by the late Griesbachian (Fig. 6A), but *Neoschizodus* not recording pre-extinction *Schizodus* body sizes until the early Spathian (Fig. 6B). In terms of functional morphology, *Neoschizodus* and “*Unionites*” should be ecologically similar, and it may be expected that they would mirror the same trends. The different timing in recovery, however, suggests different ecological niches between the two genera, such as optimum thermal temperatures or temperature range, may explain why “*Unionites*” typically dominates pre-Spathian communities and *Neoschizodus* dominates Spathian communities (sensu Hofmann et al., 2015; Foster et al., 2017).

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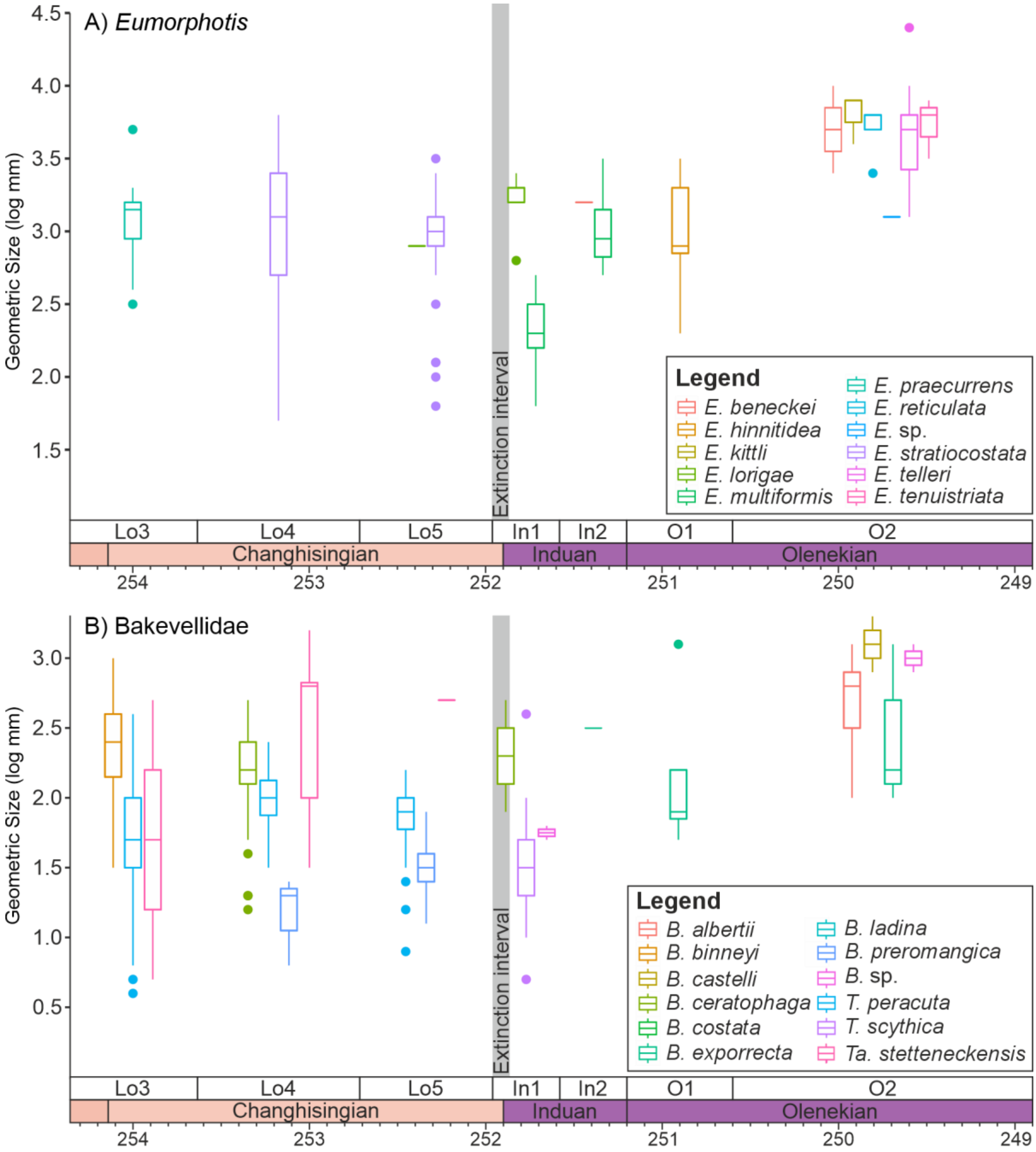

Figure 5. Changes in the sizes of epifaunal/ semi-infaunal bivalve genera that survive the mass extinction event. A) *Eumorphotis* and (B) the Bakevellidae divided into the different species that were sampled from the Dolomites, Italy. The Bakevellidae include the genera *Bakevellia* (B), *Towapteria* (T) and *Tambanella* (Ta).

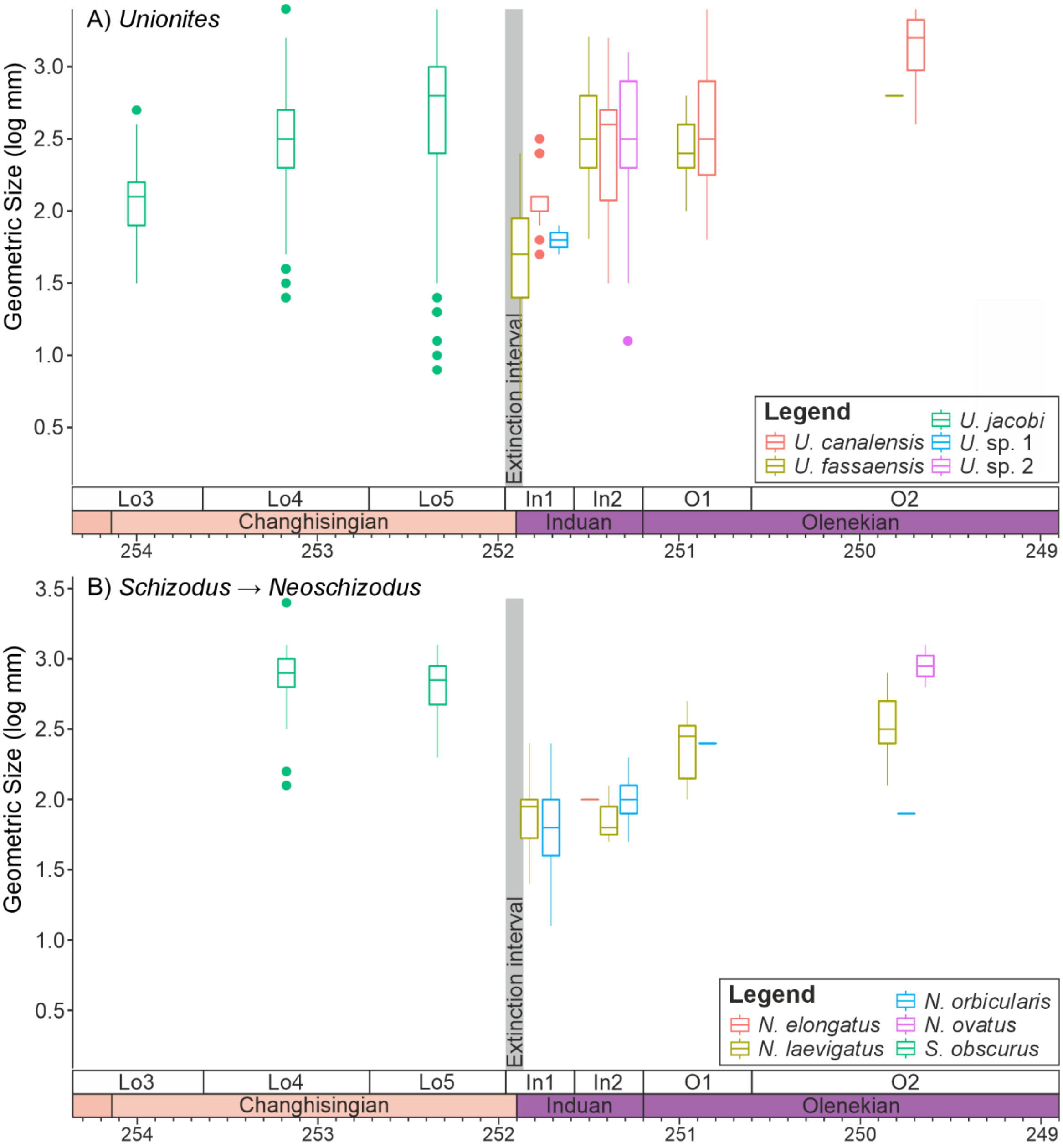

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Figure 6. Changes in the sizes of infaunal bivalve genera that survive the mass extinction event. A) *Unionites* and (B) the closely related genera *Schizodus* and *Neoschizodus*, divided into the different species that were sampled from the Dolomites, Italy.

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## 5 Discussion

### 1.1 Nature of size change

The mechanism of a body size change is a highly contested topic. Twitchett (2007) proposed four models to explain the body size reduction following mass extinction events: 1) selective loss of large taxa, 2) temporary disappearance of large taxa from the fossil record, 3) origination of small taxa, and 4) decrease within taxa. The lack of an observed decline at the species-level, the reduction in the size at the genus-level being driven by the evolution of new species, and the lack of unusually small bivalves during the climate crisis are not consistent with the proposed Lilliput effect in the strict sense (sensu Twitchett, 2007), nor the predictive response of marine ectotherms to climate warming (Pörtner et al., 2023). This then leads to two very different interpretations: at the genus-level there is a clear Lilliput effect, which is consistent with the interpretation of previous studies that were limited to genus-level dynamics (e.g., Twitchett, 2007; Metcalfe et al., 2011), but at the species-level the Lilliput effect hypothesis can be falsified.

The recorded survivors, *Bakevellia ceratophaga*, *Stutchburia tschernyschewi* and *Eumorphotis lorigae*, retained or slightly increased their body sizes. These species were likely pre-adapted to the harsh conditions surrounding the Permian/Triassic boundary, possessing physiological traits that allowed persistence without substantial size reduction. For instance, *E. lorigae* thrived in the extreme conditions of the Bellerophon Formation, which was characterised by high temperatures, low oxygen levels, and variable salinity (Prinoth and Posenato, 2023).

Our results are also consistent with previous studies that show a body size decrease in many different groups of marine ectotherms, but again this body size decrease is driven by the evolution of newly evolved, smaller species (Song et al., 2011; Chu et al., 2015; Chen et al., 2019; Feng et al., 2020; 2024; Huang et al., 2023). This trend has also been observed for brachiopods and bivalves from South China during the Permian-Triassic crisis (Chen et al., 2019; Huang et al., 2023), bivalves at the Triassic-Jurassic climate crisis (Atkinson et al., 2019; Opazo and Twitchett, 2022), belemnites during the Toarcian climate crisis (Rita et al., 2022), molluscs during the end-Cretaceous event (Lockwood, 2005; Jarrett, 2016) and marine organisms during extinction events in general (Monarrez et al., 2020). This suggests a consistent (i.e., predictive) response to a climate crisis is the preferential evolution of small-sized species. One hypothesis is that newly evolved species tend to be smaller (Stanley, 1973), and the vacated ecospace following the mass extinction promoted the evolution of smaller species (Twitchett, 2007). The preferential evolution of smaller species after mass extinctions as a general evolutionary rule is, however, inconsistent in the Dolomites record for two reasons: (1) the newly evolved species become larger later in the Griesbachian, and (2) newly originating species in the Spathian are preferentially large, not small.

There has been considerable debate about the duration of a body size reduction following the Permian-Triassic climate crisis (Nützel et al., 2010; Brayard et al., 2010, 2015; Fraiser et al., 2010), and even if there is a body size reduction for all marine groups at all (Forel et al., 2015; Nätscher et al., 2024). Our results suggest that there was only a short-duration decrease in body sizes, limited to the early Griesbachian for most genera (Figs. 2 & 5), but body sizes also increased again later in the Spathian. These body size data are, however, consistent with Nützel et al. (2010), who highlighted that whilst generally small, Early Triassic, or even early Griesbachian, molluscs are not unusually small as previously suggested by Twitchett (2001). The increase in the size (so-called Brobdingnag effect; Atkinson et al., 2019) of these newly evolved species during the late Griesbachian suggests that some biotic or abiotic stressor was prevalent during the Permian-Triassic transition, because a sudden within-species size increase can only be explained by a shift to more favourable conditions. A within-species size increase is also consistent with bivalves from South China (Huang et al., 2023) and bivalves from the UK following the end-Triassic mass extinction (Atkinson et al., 2019).

Pre-extinction body size reductions have often been considered a precursor signal of a mass extinction event, and one expectation is that species would have reduced their size prior to their extinction. This has been observed for ammonoids and podocopid ostraocds from Iran (Kiessling et al., 2018; Nätscher et al., 2024) and brachiopods from South China (He et al., 2010; Zhang et al., 2016). Pre-extinction changes in temperature, albeit at a slower rate and smaller magnitude, have also been recorded from South China and Iran (Wu et al., 2023; Gliwa et al., 2023). A decrease in body size prior to extinction may also, therefore, be a predictive response and warning sign for modern-day marine ecosystems. The pre-extinction body size decline is typically only visible at a very high-resolution, and for the Dolomites the lack of bivalves from the uppermost Changhsingian Bulla Member, means that an immediate pre-extinction body size decline cannot be tested here.

Summarised, our data reject the “Lilliput effect” in the sense of a temporal within-species size reduction during an extinction/hyperthermal event (Urbanek, 1993; Twitchett 2007). Rather, small post-extinction body size of bivalves in the wake of the end-Permian mass extinction in the Dolomites was the effect of the preferential evolution of small-sized species after the crisis. This evolution of small-sized species caused a decline of body size at the genus-level, which has previously been reported but now turns out to be an artefact of the taxonomic

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level. However, the question remains whether the preferential evolution of small-sized species was controlled by biotic controls, abiotic factors, or a combination of both.

### 1.2 Abiotic determinates of body size

The aerobic scope and temperature tolerance of species is paramount to an organism's growth and reproduction, with maximum growth at the $T_{optimum}$, but superimposed changes in oxygen availability would alter the aerobic scope of ectotherms at the same temperatures (Pörtner et al., 2023). The aerobic scope of marine invertebrates is thought to be mostly governed by temperature and oxygen availability, with each species having different $T_{optimum}$ and $T_{critical}$ temperatures (Penn et al., 2018; Pörtner et al., 2023). There is no robust evidence to suggest that the Dolomites (Italy) experienced anoxic conditions during the Permian-Triassic climate crisis (Brand et al., 2012; Hofmann et al., 2015; Frank et al., 2025), but the shallow marine settings may have experienced slight deoxygenation owing to a reduction in oxygen solubility as a consequence of increased temperatures and increased uptake of oxygen due to the increased metabolic activity of microbes. Increased sea surface temperatures of ~5-10°C, based on $\delta^{18}O_{calcite}$ and clumped isotopes are reported for the Dolomites associated with the extinction event (Kearsey et al., 2009; Brand et al., 2012), and are likely to have had a greater impact on the aerobic scope of marine organisms than the changes in oxygen availability. The problem is that these estimates are only based on a single data point from post-extinction sediments. Despite the rich history of Permian-Triassic investigations of the Dolomites, there is a clear lack of environmental proxy data for making ecological comparisons. When compared to the $\delta^{18}O_{calcite}$ records from South China, Iran and Pakistan (Sun et al., 2012; Romano et al., 2012; Schobben et al., 2014; Chen et al., 2016; Gliwa et al., 2022), the preferential evolution of smaller species coincides with rapid temperature increases, and the preferential evolution of larger body sizes in the early Spathian coinciding with cooler temperatures. In South China, the body sizes of two foraminifera species also appear to be closely related to the $\delta^{18}O_{apatite}$ record (Foster et al., 2024), suggesting a link between body size and temperature for marine organisms.

A meta-analysis of what environmental stressors and combination of environmental stressors determine the growth rate of bivalves demonstrates that temperature, oxygen, pH and salinity all play a vital role (Kruft Welton et al., 2023). Given the normal marine setting of the post-extinction ramp and the presence of lithofacies consistent with saturated seawater with respect to carbonate (Foster et al., 2020), it is unlikely pH played a key role in limiting the growth of bivalves. Even though there is geochemical proxy evidence for sustained ocean acidification into the Induan (Jurikova et al., 2020), this record directly conflicts with the widespread deposition of ooids and microbialites that require normal to super-saturated, with respect to calcium carbonate, conditions. In addition, the absence of echinoderms and ammonoids from the Dolomites succession in the Griesbachian (Posenato, 1992; Foster et al., 2017) could be a consequence of the changes in salinity and cannot yet be completely ruled out in the absence of robust proxy data.

Another important factor for determining growth and life expectancy is nutrient availability, which has been hypothesised to be a key factor in shifting benthic communities in other regions (Foster et al., 2024). However, for the Dolomites there is no proxy data; in other regions, changes in primary productivity are highly debated with conflicting hypotheses (Shen et al., 2015; Zhang et al., 2018; Qiu et al., 2019). Regional variability in the degradation products of a lipid biomarkers that becomes abundant after the Permian-Triassic mass extinction and is interpreted to come from phytoplankton would, however, suggest low productivity in the Dolomites (Buchwald et al., 2025). On the other hand, what is clear from the record of the Dolomites is that there is an increased influx of sediment onto the ramp (Algeo and Twitchett, 2010; Brand et al., 2012), low amounts of TOC (Siegert et al., 2011) and the turbid conditions after the onset of extinction, which would have interfered with feeding for the filter-feeding species and availability of detritus for the deposit-feeding species, respectively, both negatively affecting growth. Therefore, whilst many environmental changes are hypothesised to have affected marine ecosystems during the Permian-Triassic climate crisis (Clapham and Renne, 2019), only limited temperature data exist for the Dolomites, and is considered here the most likely abiotic factor to explain the observed body size reduction.

### 1.3 Biotic determinates of body size

Biotic factors also play an important role in determining body sizes on evolutionary timescales that are superimposed on environmental effects (Nakazawa et al., 2007). Mass extinctions lead to a profound restructuring of marine ecosystems, primarily driven by extreme abiotic stressors. These environmental changes imposed intense selective pressures that eliminated most stenotopic species, while favouring opportunistic, r-strategist taxa characterised by high reproductive rates, short generation times, and broad ecological tolerances (Tong et al., 2007). Consequently, small-bodied bivalves became ecologically dominant due to their rapid growth, early maturity, and morphological plasticity, which enabled them to quickly colonise disturbed environments (Metcalfe et al., 2011; Hofmann et al., 2014; Hautmann et al., 2015).

Although all Early Triassic bivalve species must ultimately be derived from Permian ancestors, not all exhibit straightforward lineage continuity, and the connection to body size evolution is variable. Some Early Triassic repopulating taxa may have evolved from morphologically plastic ancestors that were predisposed to smaller body sizes under environmental stress (Prinoth and Posenato, 2023). For example, *Towapteria scythica* shows morphological similarity to the Upper Permian *T. peracuta*, and *Eumorphotis lorigae* likely represents a direct lineage from pre-existing species that retained or even slightly increased body size after the extinction. In contrast, *Claraia*, the most abundant and widespread taxon in the Early Triassic, and *Neoschizodus*, immigrated from the eastern Tethys and have morphologically distinct late Permian precursors (He et al., 2014; Nakazawa and Newell, 1968), making it difficult to assess whether their small size was inherited or evolved during the extinction crisis. *Claraia* sp. from the Mazzin Member lacks the radial ribs typical of Permian species, although *Claraia liuqiaoensis*, a smooth-shelled species, already occurred in the latest Permian and extended into the Griesbachian (He et al., 2014; Foster et al., 2019). *Neoschizodus orbicularis* and "*Unionites*" *fassaensis* also show substantial morphological divergence from their Permian counterparts. This morphological divergence could indicate either (1) the emergence of entirely new taxa adapted to Early Triassic environmental conditions, or (2) ecological and phenotypic plasticity within surviving lineages that enabled rapid morphological shifts in response to post-extinction stressors. Distinguishing between these scenarios requires further phylogenetic analysis and detailed stratigraphic correlation to assess lineage continuity. This variability indicates that size reduction may have resulted from a combination of inherited traits and evolutionary responses to post-extinction conditions of the abiotic and biotic environment.

One key biotic factor for body size reduction may have been the breakdown and simplification of trophic structures (Huang et al., 2023a). The collapse of complex ecosystems with specialised predators and prey, including durophagous gastropods, crustaceans, and fish, led to ecological release and the temporary dominance of low-level consumers and generalists (Schubert and Bottjer, 1995; McRoberts, 2001; Fraiser and Bottjer, 2007). In the absence of strong predatory pressure, smaller and thin-shelled bivalves could proliferate without investing in energetically costly defensive traits. This relaxation of size-selective predation, together with the general collapse of food webs (Chen and Benton, 2012), created conditions in which small size was selectively advantageous. However, the shift in functional traits to thicker shells and increased body size in the late Griesbachian and into the Spathian, could indicate that selective pressures gradually shifted, as predator guilds began to recover (Karapunar et al., 2025b), driving within-lineage size increases in some taxa.

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Furthermore, this recovery interval was likely characterised by what Hautmann et al. (2015) described as "competition in slow motion": a state of ecological simplicity in which interactions were weakly differentiated and resource partitioning was minimal. Communities were dominated by generalists with overlapping niches, and the dominant form of competition may have been intraspecific or density-dependent rather than shaped by complex interspecific interactions (Foster et al., 2019). Opportunistic r-strategists often formed monodominant, high-density populations where smaller individuals benefited from reduced metabolic demands and lower per capita resource requirements. In some Early Triassic assemblages of the Mazzin Member, a relatively high genus diversity suggests that multiple opportunistic taxa coexisted in crowded populations, where smaller body sizes may have conferred an energetic advantage through more efficient resource use (Hofmann et al., 2015). However, the dominance of certain highly dispersive generalists such as *Claraia* may have also suppressed ecological differentiation and delayed the establishment of larger-bodied species. This reflects a form of biotic monopolization, where early colonisers create priority effects that inhibit niche access for later-arriving taxa, even in the absence of direct competition. This dynamic could have added inertia to the recovery process and reinforced the trend toward small body sizes by precluding competitive escalation, effectively layering on a form of trophic suppression (Hautmann et al., 2015).

## 6 Conclusion

Shallow marine bivalve communities from the Dolomites in Italy show a significant reduction in body-size at the genus-level, but conversely at the species-level body sizes stay the same or slightly increase, inconsistent with the Lilliput effect hypothesis. The reduction of bivalve body-size assemblages, including at the genus-level is, therefore, driven by the preferential origination and dominance of small species. These new species are not, as has been previously suggested, unusually small. Two of the species surviving the extinction that do not show a body size decrease, were already adapted to stressful conditions prior to the climate crisis. Due to the lack of proxy data available from the Permian-Triassic succession of the Dolomites, it is difficult to understand and distinguish the role of specific abiotic factors in causing the observed body size dynamics, but an effect of high seawater temperature and nutrient supply appears likely. The impact of the mass extinction event on biotic interactions also likely played a major role in the preferential origination of small-sized species, and these biotic impacts are superimposed on the abiotic controls during the Early Triassic.

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## Code and data availability

All statistical analyses were made in R (R Core Team, 2019) and the code **and data** is available at https://github.com/wjf433/DBiv.

## Author contributions

WJF, HP and EK conceptualised the project. WJF, HP and MH collected the data. WJF carried out the analysis and data visualisation. All authors contributed to writing the manuscript draft.

## Competing Interests

The authors declare that they have no conflict of interest.