Thermal and non-thermal controls on benthic foraminiferal Mg/Ca, Sr/Ca, B/Ca, and Mg/Li: global core-top compilation, revised calibrations, and application to the geologic record

Andressa Nauter-Alves[1], David Evans[2], Miriam E. Katz[3,4], William R. Gray[5], James W. B. Rae[6], Chiara Borrelli[1]

[1] Department of Earth and Environmental Sciences, University of Rochester, Rochester, NY, USA
[2] School of Ocean and Earth Science, University of Southampton, Southampton, UK
[3] Department of Earth and Planetary Sciences, Rutgers, The State University of New Jersey, Piscataway, NJ, USA
[4] Geosciences Department, Union College, Schenectady, NY, USA
[5] Laboratoire des Sciences du Climat et de l'Environnement (LSCE/IPSL), Gif-sur-Yvette, France.
[6] School of Earth and Environmental Sciences, University of St Andrews, St Andrews, UK

Abstract

Benthic foraminiferal Mg/Ca, Sr/Ca, B/Ca, and Mg/Li data are used to reconstruct deep-sea temperature and seawater carbonate chemistry. However, the concurrent influence of various environmental parameters on these proxies is not fully understood. Here, we compile published and unpublished element/Ca core-top data from *Cibicidoides mundulus*, *C. pachyderma, Lobatula wuellerstorfi*, *Oridorsalis umbonatus*, *Nuttallides umbonifera*, and *Uvigerina* spp. to determine the sensitivity of these species' Mg/Ca, Sr/Ca, B/Ca, and Mg/Li to temperature, calcite saturation state ($\Omega_{calcite}$), dissolved inorganic carbon (DIC), and salinity. By applying multivariate linear regression analysis, we disentangle the effects of these environmental parameters on the element/Ca incorporation into these species. As a result, we provide multivariate element/Ca calibrations with temperature and $\Omega_{calcite}$ sensitivities for all species-elemental system combinations. Overall, our analysis reveals that: 1) the Mg/Ca-sensitivity to temperature is substantially lower compared to most previous approaches when accounting for the effect of $\Omega_{calcite}$; 2) Sr/Ca is driven dominantly by $\Omega_{calcite}$; 3*)* B/Ca can be linearly related to $\Omega_{calcite}$; and 4) Mg/Li-temperature calibrations have substantially lower degrees of unexplained variance compared to Mg/Ca. Our calibrations offer a statistically robust approach that also allows us to quantify the uncertainties in the reconstruction of temperature and carbonate chemistry when these element/Ca proxies are used. Finally, we develop a user-friendly data processing software ('ElCaRBenthic') that can simultaneously solve up to two benthic foraminiferal element/Ca datasets for temperature and $\Omega_{calcite}$ (e.g., Mg/Ca and Sr/Ca), while providing the ability to correct for long-term changes in seawater elemental chemistry and propagating all sources of uncertainty.

Plain Language Summary

The ratios of magnesium (Mg) to calcium (Mg/Ca) and Mg to lithium (Mg/Li) measured in benthic foraminifera shells are commonly used to reconstruct deep-sea temperature, whereas the ratios of strontium (Sr) and boron (B) to Ca (Sr/Ca and B/Ca) are used to reconstruct ocean chemistry. However, the application of these elemental ratios is not straightforward. In this study, we compiled and analyzed a dataset including Mg/Ca, Sr/Ca, B/Ca, and Li/Ca collected from five benthic foraminiferal species and one genus to understand how each elemental ratio responds to different environmental parameters (i.e., temperature, carbonate chemistry, salinity). The results of our statistical analyses show that the benthic foraminiferal Mg/Ca is less sensitive to temperature when $\Omega_{calcite}$ (a measure of how saturated seawater is with respect to calcite) is taken into account, and that Mg/Li provides more consistent temperature reconstructions compared to Mg/Ca. Benthic foraminiferal Sr/Ca and B/Ca are mainly influenced by changes in $\Omega_{calcite}$. To support paleoceanographic reconstructions, we develop a software called ElCaRBenthic. This software allows users to solve for temperature and $\Omega_{calcite}$ using paired elemental ratios, while also propagating uncertainties.

Key Points

- We compile ~1500 core-top benthic foraminiferal Mg-Sr-B-Li/Ca measurements from five species and one genus to produce new calibrations
- Many benthic foraminiferal elemental systems require multivariate calibrations to account for temperature and seawater carbonate chemistry
- We present data processing software that can simultaneously solve for temperature and $\Omega_{calcite}$ and fully propagate uncertainty

1. Introduction

The ratio of magnesium to calcium (Mg/Ca) in the tests of foraminifera provides one of the most widely applied proxies to reconstruct ocean paleotemperatures. Rooted in thermodynamics, this proxy is based on the fact that higher temperatures will be recorded as higher Mg/Ca ratios in foraminifera (Chave, 1954; Izuka, 1988; Morse and Bender, 1990; Nürnberg et al., 1996; Rosenthal et al., 1997; Lea et al., 1999; Branson et al., 2013), a feature also observed in inorganic calcite (e.g., Katz, 1973; de Choudens-Sanchez & Gonzalez, 2009).

Benthic foraminiferal Mg/Ca (Mg/Ca_{bf}) has become a useful tool in the investigation of past deep-sea temperatures (e.g., Rosenthal et al., 1997; Martin et al., 2002; Elderfield et al., 2006; Bryan and Marchitto, 2008; Tisserand et al., 2013; Lear et al., 2015; Lo Giudice Cappelli et al., 2015; Kubota et al., 2015), in particular, because few other methodologies are available for quantitative environmental reconstruction in this realm (e.g., organic geochemical proxies are limited to the upper part of the ocean). In addition, Mg/Ca_{bf} can be used in combination with benthic foraminiferal oxygen isotopes ($\delta^{18}O_{bf}$) to determine the $\delta^{18}O$ of seawater and thus reconstruct sea level and ice volume changes throughout the Cenozoic (e.g., Cramer et al., 2011; Lear et al., 2000; 2015; Miller et al., 2020).

Notwithstanding the impact that benthic Mg/Ca data had on our understanding of past climates, the application of Mg/Ca_{bf} is complicated by additional nonthermal controls. For example, Martin et al. (2002) analyzed *Lobatula* (*Cibicidoides*) *wuellerstorfi* Mg/Ca and observed that specimens collected at the deepest Atlantic and Pacific sites were characterized by Mg/Ca values that were not in agreement with the overall Mg/Ca-temperature relationship for this species. Based on this finding, different relationships between Mg/Ca_{bf} and seawater carbonate chemistry were proposed, usually parameterized as a function of carbonate ion saturation $\Delta[CO_3^{2-}]$ ($\Delta[CO_3^{2-}] = [CO_3^{2-}]_{in\ situ} - [CO_3^{2-}]_{saturation,}$ where $[CO_3^{2-}]_{saturation}$ is that which would yield $\Omega_{calcite} = 1$). Subsequent studies established a Mg/Ca_{bf} species-specific sensitivity to $\Delta[CO_3^{2-}]$, suggesting that species-specific calibrations ideally should be used where possible (Elderfield et al., 2006, Healey et al., 2008, Raitzsch et al., 2008; Yu and

Elderfield, 2008). In practical terms, the impact of [CO_3^{2-}] in down core records has been addressed by applying region-specific calibrations (e.g., Sosdian & Rosenthal, 2009) with the assumption that temperature and [CO_3^{2-}] covaried through time to the same degree as the calibration dataset. In situations where this is unlikely to have been the case, Mg/Ca data were corrected for changes in seawater carbonate chemistry by independently estimating the degree to which this factor has changed. For example, Cramer et al. (2011) parameterized deep ocean Δ[CO_3^{2-}] as a function of the calcite compensation depth (CCD). However, this approach suffers from the likely inter- and intra-basinal variability in Δ[CO_3^{2-}] given that the dataset drew on globally distributed sites, as well as the uncertainty in deriving Δ[CO_3^{2-}] from a CCD record (Greene et al., 2019).

Other approaches to correcting Mg/Ca_{bf} for changes in deep ocean carbonate chemistry focused on other element/Ca ratios in foraminiferal $CaCO_3$. Bryan & Marchitto (2008) showed that normalization of benthic foraminiferal Mg to lithium (i.e., Mg/Li_{bf}) resulted in a proxy that combined the temperature sensitivity of Mg incorporation while removing the (presumably) biologically-driven impact of seawater carbonate chemistry. The basis of the approach lies in the fact that, while Li incorporation into calcite is also sensitive to temperature (e.g., Marriot et al., 2004b; Hall and Chan, 2004, Bryan and Marchitto, 2008), it can also be influenced by changes in deep water saturation, which is supported by the overall decrease in foraminiferal Li/Ca with water depth (e.g., Lear and Rosenthal, 2006; Doss et al., 2018). Therefore, the use of Mg/Li_{bf} can account for the impact that Δ[CO_3^{2-}] changes have on biological calcification processes that ultimately influence Mg/$Ca_{\underline{bf}}$, such as Ca^{2+} utilization at the calcification site (Rayleigh distillation) and growth rate (Marchitto et al., 2018). A number of studies have since built on this. For example, Lear et al. (2010) combined *O. umbonatus* Mg/Ca and Li/Ca data to subtract the seawater carbonate chemistry effect from the Mg/Ca_{bf} temperature signal (see also Dawber and Tripati, 2011; Lear and Rosenthal, 2006). The development of boron to Ca (B/Ca_{bf}) as a proxy for seawater carbonate chemistry offers an alternative tool to directly reconstruct changes in Δ[CO_3^{2-}] (e.g., Yu & Elderfield, 2007; Yu et al., 2010; Rae et al., 2011; Brown et al., 2011; Raitzsch et al., 2011).

Benthic foraminiferal strontium to Ca (Sr/Ca_{bf}) has also been suggested as an alternate proxy to reconstruct $\Delta[CO_3^{2-}]$ in geological records (Dawber & Tripati, 2012 Yu et al., 2014; Lo Giudice Capelli et al., 2015; Keul et al., 2017; Lawson et al., 2014). However, several studies have shown that Sr/Ca_{bf} can also be influenced by temperature, pH, salinity, and ontogenetic effects (Rathburn and Deckker, 1997; Reichart et al., 2003; Rosenthal et al., 2006; Dissard et al., 2010; Lo Giudice Capelli et al., 2015). In addition, the influence of temperature on the Sr/Ca_{bf} of species commonly used in paleoenvironmental investigations remains unclear (Rosenthal et al., 1997; Rathmann & Kuhnert 2008; Yu et al., 2014).

As a result, while much progress has been made over the last few decades in the development and application of (trace) element systems in benthic foraminifera, much remains to be understood in terms of the relative influence of temperature and the seawater carbonate chemistry on these proxies. For example, previous work suggested a wide range of Mg/Ca_{bf}-temperature sensitivities for the same species depending on how nonthermal influences were treated, and the degree to which temperature and carbonate chemistry varied in the underlying dataset (e.g., Lear et al., 2002; 2010; Yu & Elderfield, 2008; Raitzsch et al., 2008; Lo Giudice Capelli et al., 2015).

In this study, we compile published and unpublished globally distributed core-top Mg/Ca, Sr/Ca, B/Ca, and Li/Ca. Our dataset includes *Cibicidoides mundulus*, *C. pachyderma*, *Lobatula wuellerstorfi*, and *Nuttallides* umbonifera, described as epifaunal species (e.g., Lutze and Thiel, 1989; McCorkle et al., 1990; Rathburn and Corliss, 1994), as well as *Oridorsalis umbonatus* and *Uvigerina* spp., described as shallow infaunal species (e.g., McCorkle et al., 1990; Rathburn and Corliss, 1994) (Table 1). We analyze this compilation using multivariate linear regression models for all proxy system-species combinations with sufficient data and determine the potential influence of temperature, carbonate chemistry, and salinity on these systems. Finally, we present a Matlab script ('ElCaRBenthic') for the calculation of temperature, $\Omega_{calcite}$, and $[CO_3^{2-}]$ from benthic foraminiferal Mg/Ca, Sr/Ca, B/Ca, or Mg/Li data. This software: 1) simultaneously solves for temperature and seawater carbonate chemistry when provided with sufficient data; (2) fully propagates all sources of uncertainty; and (3) can be applied on timescales across which the elemental composition of seawater has changed.

2. Material and methods

2.1 Core-top data compilation

We compiled core-top Mg/Ca, Sr/Ca, B/Ca, and Li/Ca data for five benthic foraminiferal species (*Cibicidoides mundulus*, *C. pachyderma*, *Lobatula wuellerstorfi*, *Nuttallides umbonifera, Oridorsalis umbonatus*) and one benthic foraminiferal genus (*Uvigerina* spp.) (Fig. S1) from the Arctic, Atlantic, Indian, and Pacific Oceans (Figure 1; Table 1) from 25 published studies (Rosenthal et al., 1997; Martin et al., 2002; Lear et al., 2002; Rathmann et al., 2004; Lear and Rosenthal, 2006; Elderfield et al., 2006; Marchitto et al., 2007a; Yu and Elderfield, 2007; Yu and Elderfield, 2008; Bryan and Marchitto, 2008; Healey et al., 2008; Raitzsch et al., 2008, 2011; Lear et al., 2010; Brown et al., 2011; Rae et al., 2011; Rae, 2011; Tisserand et al., 2013; Yu et al., 2014; Gray, 2015; Kubota et al., 2015; Lo Giudice Cappelli et al., 2015; Gussone et al., 2016; Stirpe et al., 2021; Lawson et al., 2024) and two PhD theses (Gray, 2015; Rae, 2011; see Table 1). The compiled dataset can be found in Pangaea (Nauter-Alves et al., XXXX; doi:XXXXXX).

The compiled data span a temperature range from -1.15 to 18.6°C, a $\Delta[CO_3^{2-}]$ range from -35.4 to 161 µmol/kg (as reported in the original publications but recalculated here, see Sec. 2.2), and a water depth range of 151 to 5159 m. Sediment samples below 2 cm core depth and all outliers as flagged in the original publication (e.g., those resulting from analytical error or diagenetic alteration) were excluded from our analysis.

We note that in some publications, *L. wuellerstorfi* is reported as *Cibicidoides wuellerstorfi.* According to Hayward et al. (2025) (WoRMS database; https://www.marinespecies.org/index.php), this species is currently classified as *L. wuellerstorfi*. Given this and considering the distinct element/Ca signature of this species compared to the other *Cibicidoides* species considered in this study (see Sec. 3), we decided to follow the current nomenclature and therefore do not analyze *L. wuellerstorfi* data together with *C. mundulus* and *C. pachyderma* when investigating this genus-specific portion of the dataset.

There is also an ongoing taxonomic debate regarding the classification of *Cibicidoides pachyderma*. While the studies utilized here classified this species as *Cibicidoides*, genetic analyses disagree in the placement of this species within this genus (*Cibicidoides* versus *Cibicides*; Schweizer et al., 2009; Holzmann and Pawlowski, 2017). Considering that the debate has not yet been resolved and in the light of the broadly similar test chemistry of *C. pachyderma* and *C. mundulus* (discussed in detail below), we considered *C. pachyderma* as a *Cibicidoides* species for the purposes of our analyses.

Finally, we considered all *Uvigerina* data included here as *Uvigerina* spp. We did so because the studies utilized here were based on *U. peregrina*, which includes morphologically variable species as defined in Stirpe et al. (2021), and other species that were classified only at the genus level (i.e., *Uvigerina*, Yu and Elderfiels 2007, 2014; Gussone et al., 2016).

The compiled data were measured using different analytical methods, and samples were prepared according to different cleaning procedures. Some datasets were collected using a spatially-resolved analytical technique (laser ablation inductively coupled plasma mass spectrometry - LA-ICPMS), which differs from bulk (‘solution’) approaches in that it does not average over intra- and inter-specimen geochemical heterogeneity. In order to convert these datasets to a form that is – as far as possible – comparable to solution approaches, where data were reported as individual laser spot measurements or as individual specimen values (Rathmann et al., 2004; Stirpe et al., 2021), we calculated the average element/Ca per site and used that value in our analysis.

2.2 Hydrographic data extraction

Seawater hydrographic parameters (temperature, seawater carbonate chemistry, salinity) were recalculated from each original study to establish consistency across datasets. We based all calculations on the 0.25° resolution World Ocean Atlas (WOA) 2018 temperature and salinity datasets (Locarnini et al., 2018; Zweng et al., 2019) and the 1° resolution GLODAP gridded total alkalinity (TAlk) and pre-industrial dissolved inorganic carbon (DIC) datasets (Lauvset et al., 2016). Data were extracted from the nearest available grid cell by first extracting the closest matching depth in the gridded datasets to a given sample record, subsequently converting sample locations and the gridded datasets at that depth to cartesian coordinates, and finally deriving the closest match using the minimum distance between the sample site and all available grid cells. In the vast majority of cases, this yielded temperature and salinity datasets that agreed with the value given in the original publication within ±1°C and ±0.2 units. However, in five cases, the WOA-derived temperature used here was offset by more than 2°C. In these instances, we reverted to the value given in the original publication, on the assumption that the originally reported value better represents the sample site (e.g., given the resolution of the gridded data products).

Table 1: Sources of the benthic foraminiferal element/Ca datasets used in this study.

Species	Mg/Ca	Sr/Ca	B/Ca	Li/Ca
Cibicidoides mundulus	(Elderfield et al., 2006; Healey et al., 2008; Raitzsch et al., 2008; Rae, 2011; Tisserand et al., 2013)	(Rae, 2011; Yu et al., 2014; Lawson et al., 2024)	(Yu and Elderfield, 2007; Rae et al., 2011)	(Rae, 2011)
Lobatula wuellerstorfi	(Russell et al., 1994; Rosenthal et al., 1997; Lear et al., 2002; Martin et al., 2002a; Elderfield et al., 2006; Healey et al., 2008; Raitzsch et al., 2008; Yu and Elderfield, 2008; Rae, 2011; Tisserand et al., 2013; Kubota et al., 2015; Lo Giudice Cappelli et al., 2015; Gussone et al., 2016)	(Rae, 2011; Yu et al., 2014; Lo Giudice Cappelli et al., 2015; Gussone et al., 2016; Lawson et al., 2024)	(Yu and Elderfield, 2007; Brown et al., 2011; Rae et al., 2011; Raitzsch et al., 2011)	(Rae, 2011)
Oridorsalis umbonatus	(Rathmann et al., 2004; Elderfield et al., 2006; Healey et al., 2008; Lear et al., 2010; Rae, 2011; Tisserand et al., 2013; Gussone et al., 2016)	(Rae, 2011; Gussone et al., 2016)	(Brown et al., 2011; Rae et al., 2011)	(Lear and Rosenthal, 2006; Rae, 2011)
Nuttallides umbonifera			(Brown et al., 2011)	

Cibicidoides pachyderma	(Rosenthal et al., 1997; Lear et al., 2002; Marchitto et al., 2007a; Bryan and Marchitto, 2008)	(Lawson et al., 2024)		(Bryan and Marchitto, 2008)
Uvigerina peregrina	(Elderfield et al., 2006; Bryan and Marchitto, 2008; Rae, 2011; Gray, 2015; Gussone et al., 2016; Stirpe et al., 2021)	(Rae, 2011; Gray, 2015; Gussone et al., 2016;)	(Rae et al., 2011; Gray, 2015)	(Bryan and Marchitto, 2008; Rae, 2011; Gray, 2015; Stirpe et al., 2021)
Uvigerina spp.	(Gussone et al., 2016)		(Yu and Elderfield, 2007)	

Seawater carbonate chemistry parameters were calculated with co2sys (Lewis et al., 1998), MATLAB version V3.1.2, using the closest available TAlk, pre-industrial DIC, temperature, and salinity estimates as described above. To accomplish this, we applied: 1) the carbonate system dissociation constants of Mehrbach et al. (1973) refit by Dickson and Millero (1987), as recommended by Wanninkhof et al. (1999); 2) the HSO_4^- dissociation constant of Dickson (1990); 3) the HF dissociation constant of Perez and Fraga (1987); and 4) the total boron value of Lee et al. (2010). Our carbonate system calculation results in broadly but not unanimously good agreement with the values reported in the original publications. Specifically, ~5.5% of the reported $\Delta[CO_3^{2-}]$ values (n = 68) are offset from our internally consistent calculation by more than 25 µmol/kg, typically to lower $\Delta[CO_3^{2-}]$. While investigating the sources of this discrepancy is beyond the scope of this study, it likely stems from different choices of dissociation constants, calculation routines, and other parameters required to perform this calculation between studies, and/or between this study and the original publication. To ensure consistency in dissociation constants and parameters across the dataset, we used the recalculated $\Delta[CO_3^{2-}]$ in all instances.

2.3 Multivariate linear regression analysis

We determine the sensitivity of the proxy systems considered here to a number of environmental parameters using least-squares multivariate linear regression models. We used this approach to disentangle the effects of temperature and seawater carbonate chemistry on element incorporation into benthic foraminiferal calcite. This carbonate chemistry effect is often ascribed to $[CO_3^{2-}]$ or $\Delta[CO_3^{2-}]$ (e.g., Elderfield et al., 2006; Yu et al., 2014), with the rationale that some of the apparent sensitivity of (e.g.) Mg/Ca to temperature mechanistically reflects the impact of seawater carbonate chemistry on test chemistry or vice versa, as is the case for planktonic foraminifera (see Gray et al. (2018) and Gray and Evans (2019) for discussion). Here, we alternatively use the saturation state of seawater with respect to calcite, defined as:

$$\Omega_{calcite} = [Ca^{2+}]_{sw} \bullet [CO_3^{2-}]_{sw}/K^*_{sp},$$

Where K^*_{sp} is the stoichiometric solubility product of calcite. We decided to do so for two reasons: 1) In the modern open ocean, $[Ca^{2+}]_{sw}$ is characterized by extremely little spatial heterogeneity (Zeebe and Wolf-Gladrow, 2001). While pressure and temperature impact carbon speciation and calcite solubility to different degrees, $\Omega_{calcite}$ and $\Delta[CO_3^{2-}]$ are – in broad terms - a direct transformation of one another, such that this has little practical impact on the application of the calibration model (see Figure S2C-D). 2) $[Ca^{2+}]_{sw}$ has varied across multi-million-year timescales (e.g., Brennan et al., 2013; Zhou et al., 2021), which resulted in a decoupling of $[Ca^{2+}]_{sw}$ and $\Omega_{calcite}$ (or $\Delta[CO_3^{2-}]$) over the Cenozoic (Zeebe and Tyrrell, 2019), as $\Omega_{calcite}$ remained relatively constant, while $[Ca^{2+}]_{sw}$ decreased and $[CO_3^{2-}]_{sw}$ underwent a large increase from the Palaeogene to today. While it is not necessary to consider changes in $[Ca^{2+}]_{sw}$ when interpreting Pleistocene data, formulating regression models with $\Omega_{calcite}$ avoids the need to apply different calibrations to different time intervals (Dai et al., 2023). In addition, while $\Omega_{calcite}$ and $\Delta[CO_3^{2-}]$ are not exactly linearly related, they imply a similar mechanistic driver of element incorporation into foraminiferal calcite in the modern ocean, given that they are (approximately speaking) different representations of the same underlying parameters. We argue that the use of $\Omega_{calcite}$ is likely more appropriate on longer timescales, assuming that, in terms of the mechanistic impact of seawater carbonate chemistry on mineral growth kinetics or biomineralization, a lower $[CO_3^{2-}]_{sw}$ is counteracted by a higher $[Ca^{2+}]_{sw}$ (Dai et al., 2023).

We explored parameterizing element/Ca data as a function of both $\Omega_{calcite}$ and $1/\Omega^2_{calcite}$ (Tierney et al., 2019), which accounts for the possibility that element incorporation into foraminiferal calcite becomes less sensitive to seawater carbonate chemistry under more highly oversaturated conditions. Our preferred regression models are those based on $\Omega^{-2}_{calcite}$ because these can explain a greater degree of the variance in the datasets and provide a more robust empirical fit. In addition, we note that it has been previously suggested that Mg/Ca and $\Delta[CO_3^{2-}]$ are best described by a linear relationship (e.g., Elderfield et al., 2006; Yu and Elderfield, 2008), in contrast to our preferred regression model which is linearized by log-transforming the Mg/Ca data (described below), thus implying an exponential relationship between Mg/Ca and $\Omega_{calcite}$ or $\Omega^{-2}_{calcite}$. We also tested regression models based on an exponential relationship between Mg/Ca and temperature, and a linear relationship between Mg/Ca and $\Omega^{-2}_{calcite}$, in order to assess this, and again find that linear models using log(Mg/Ca) provide better fits to the data in almost all cases. However, coefficients for all of these alternate model forms are given in the supplementary materials (Table S2) for completeness.

In the case of the other element systems analyzed (Sr-B-Li/Ca_{bf}), in which reconstructing $\Omega_{calcite}$ or $[CO_3^{2-}]$ is the primary objective, we formulated the models in terms of $\Omega_{calcite}$ rather than $\Omega^{-2}_{calcite}$ because the latter option results in models that yield prediction uncertainties that vary widely across the range of $\Omega_{calcite}$ observed in both core-top and downcore applications, even though such variability is not evident in the model residuals for these elements.

Informed by the above constraints, all element/Ca datasets were related to seawater hydrographic and carbonate chemistry parameters via a regression of the form

$$\ln(Mg/Ca) = x_1 + x_2T + x_3\Omega^{-2}calcite + x_4[DIC] + x_5S \qquad \text{(Eq. 1)}$$

in the case of Mg/Ca and

$$El_1/El_2 = x_1 + x_2T + x_3\Omega_{calcite} + x_4[DIC] + x_5S \qquad \text{(Eq. 2)}$$

in the case of Sr/Ca, B/Ca, Li/Ca, and Mg/Li). T denotes temperature, $\Omega_{calcite}$ the saturation state of seawater with respect to calcite, DIC the concentration of dissolved inorganic carbon, and S salinity. DIC and S were initially included in the model to explore whether the inclusion of these parameters could explain a greater proportion of the variance in the elemental datasets, as suggested for planktonic species

(Kısaküreket al., 2009; Haynes et al., 2023). This was broadly found not to be the case here. For this reason, all preferred models discussed below include only the first three terms of Eqs. 1 and 2 (see Eq. 3 and Eq. 4) with alternative models including a DIC and salinity component given in the supplementary information (Table S3). Specifically in the case of Mg/Ca:

$$\ln(Mg/Ca) = x_1 + x_2T + x_3\Omega^{-2}\underline{_{calcite}} \qquad \text{(Eq. 3)}$$

And for all other elements:

$$El_1/El_2 = x_1 + x_2T + x_3\Omega\underline{_{\ calcite}} \qquad \text{(Eq. 4)}$$

Element/Ca datasets were retained as raw proxy values in all regressions except Mg/Ca, which was first log-transformed to linearize the model, accounting for the thermodynamic expectation that the partitioning of Mg into $CaCO_3$ is logarithmically related to temperature (e.g., Lea et al., 1999). While this is also the case for other (trace) elements in solid substitution with $CaCO_3$, the more minor or absent resolvable impact of temperature on element partitioning in most other cases means that this transformation is unnecessary.

The above analysis is complicated to a degree by the broad covariance of temperature, $\Omega_{calcite}$, and DIC in the modern ocean (Fig. S2). Pearson's correlation coefficients between temperature and $\Omega^{-2}_{calcite}$ are -0.38, -0.70, - 0.51, -0.68, and –0.79 for the *L. wuellerstorfi*, *Uvigerina* spp., *O. umbonatus*, *C. mundulus*, and *C. pachyderma* datasets, respectively, and 0.63, 0.83, 0.51, 0.60, and 0.95 for $\Omega^{-2}_{calcite}$ and DIC (in the same order). As such, while the dataset overall is reasonably well suited to disentangling the effects of temperature and $\Omega_{calcite}$ (although this is more challenging in the case of *Uvigerina* spp. and *C. pachyderma*), it is not possible to distinguish between a $\Omega_{calcite}$ and DIC control on *C. pachyderma* test chemistry based on the data currently available. However, we consider this latter issue to be of minor importance given that the inclusion of DIC in the regression analysis does not substantially improve the predictive power of the model (Table S4).

2.4 Example down-core applications

To compare our regression models to previous approaches, we applied our calibrations to two different down-core records for which multiple element/Ca datasets were available. The first of these uses *L. wuellerstorfi* Sr/Ca (Yu et al., 2014) and B/Ca (Yu et al., 2010a, 2010b, 2014) on samples from core VM28-122 (12°N, 79°W, 3620 m, with a sill depth of 1.8 km, Caribbean Basin). Samples for B/Ca were cleaned following the 'Mg-cleaning' method (Yu and Elderfield, 2007), whereas samples for Sr/Ca were cleaned according to the oxidative and reductive methods (Boyle and Keigwin, 1985; Barker et al., 2003), prior to solution ICP-MS analysis. The dataset spans the Holocene and late Pleistocene (the last ~160 kyr). The age model was based on radiocarbon dating of planktonic foraminifera for samples younger than 30 ka. For older samples, ages were calculated based on tuning the $\delta^{18}O_{bf}$ to the global benthic foraminiferal stack of Lisiecki and Raymo (2005) (Yu et al., 2010a).

We also applied our calibrations to a second, longer record in order to investigate the degree to which reconstructions based on benthic foraminiferal element/Ca data are sensitive to nonthermal parameters that cannot be accounted for in the modern ocean (i.e., changes in the elemental composition of seawater). To do so, we used the benthic foraminiferal Mg/Ca, Sr/Ca, B/Ca, and Li/Ca records available from the Ocean Drilling Program (ODP) Site 806 (0°19.1'N, 159°21.7'E, 2521 m, Ontong Java Plateau; Lear and Rosenthal, 2006; Lear et al., 2003b, 2015a). Data were collected from specimens of *L. wuellerstorfi, O. umbonatus,* and *C. mundulus.* Samples were cleaned following Boyle and Keigwin (1985) 'Cd-cleaning' prior to solution ICP-MS analysis. Sample ages were based on the biostratigraphic events reported in the Site report (Shipboard Scientific Party, 1991), revised with the datum ages compiled by the ODP Leg 199 Shipboard Scientific Party (Lear et al., 2003a). This age model was applied to the whole Site 806 record, which ranged from 0.02 to 16.35 Ma (Pleistocene to early Middle Miocene).

3. Results

Mg-Sr-B-Li/Ca data from each species is shown as a function of *in situ* temperature, $\Omega_{calcite}$, and dissolved inorganic carbon (DIC) in Figure 2. Multivariate regression models (Eqs. 3 and 4) with two predictor terms (T and $\Omega_{calcite}$ or $\Omega^{-2}_{calcite}$) are given in Table 2. These models can explain a substantial portion of the variance in all the elemental datasets considered here (R^2 = 0.60 to 0.84; Tab. 2), with the exception of Sr incorporation into *L. wuellerstorfi* and *C. mundulus* ($R^2 = 0.37$ in both cases). In these species, we find that Sr/Ca cannot be predicted with confidence from T and/or $\Omega_{calcite}$, although the $\Omega_{calcite}$ coefficient is nonetheless significant at the 95% confidence level in both cases. The preferred models that show statistically significant coefficients only for each species element/Ca are present in Table 3.

3.1. Mg/Ca

Benthic foraminiferal Mg/Ca spans 0.5 to 10.2 mmol/mol across the dataset (Fig. 2A). All five species are characterized by a similar range of values. Instead, *Uvigerina* spp. is characterized by a narrower (~1 mmol/mol) range and offset to lower Mg/Ca for a given temperature or $\Omega_{calcite}$.

Our dataset includes sample measurements conducted following different cleaning procedures as well as samples that were not reductively and/or oxidatively cleaned prior to analysis (i.e., samples analyzed by LA-ICPMS). It was suggested that the choice of cleaning procedure (Barker et al., 2003) could impact (benthic) foraminiferal Mg/Ca, with the reductive process potentially resulting in the preferential loss of higher-Mg regions of the test (Rosenthal et al., 2004). As a result, in some cases, a ~10% correction was applied to samples that were reductively cleaned (e.g., Lawson et al., 2024). Assessing this complication is challenging because, even if the reductive cleaning may result in lower Mg/Ca, this loss of Mg may represent the desirable loss of Mg from a contaminant phase rather than the foraminiferal test. To determine the impact of reductive versus oxidative cleaning, we examined the difference in Mg/Ca resulting from these two cleaning processes using the residuals of the regression models (see Supporting Information, Figure S10), in addition to conducting statistical tests on subsets of the dataset based on cleaning procedure, and providing comparative regression models based on these subsets of the database (Table S6). As previously reported (e.g., Yu and Elderfield, 2008), we find that mean Mg/Ca is higher in the oxidative cleaning-only group by 5.5%, 10.4%, and 9.0% for *L. wuellerstorfi*, *Uvigerina* spp., and *O. umbonatus*, respectively. In the case of *C. mundulus*, the opposite is the case (6.9% lower), while insufficient data exist to test this for *C. pachyderma*. A two-tailed test was used to compare the means obtained from the two cleaning procedures. The results indicate that *C. mundulus* is not characterized by a significant difference between cleaning methods, while the opposite is true for *L. wuellerstorfi*, *Uvigerina* spp., and *O. umbonatus*. While this may support the application of a correction, we do not do so here because it is not currently clear whether it is desirable to include Mg lost during the reductive cleaning process in the average sample Mg/Ca value, i.e., reductive cleaning may remove contaminant phases as well as primary shell material characterized by higher Mg/Ca, and this is likely true to differing but poorly constrained extents between species and sample sites. Spatially resolved (e.g., laser ablation) measurements of benthic foraminifera with diagenetic coatings subjected to both procedures would be one way of addressing this issue, as has been conducted for planktonic foraminifera (Fritz-Endress & Fehrenbacher, 2020). We also note that while regression models based on only reductively and oxidatively cleaned samples do significantly differ from those based on the complete dataset in some respects (cf. Table 2 and Table S6, e.g., the *C. mundulus* Mg/Ca-T slope is nonsignificant in both cases), we cannot unambiguously attribute these differences to cleaning procedure versus differential sampling of the underlying parameter space between these data subsets. Given the minor absolute Mg/Ca offsets observed between reductively and oxidatively cleaned samples, and for the reasons outlined above, we base our discussion on the combined dataset with no reductive correction applied. However, we stress that this possible impact on benthic foraminifera shell chemistry needs to be better and mechanistically understood before this issue can be conclusively addressed.

Table 2. The relationship between element/Ca, temperature, and $\Omega_{calcite}$ ($Mg/Ca = X_1 + X_2*T + X_3*\Omega^{-2}$ and $El_1/El_2 = X_1 + X_2*T + X_3*\Omega$) for each species considered in this study. Uncertainties are reported as ±1SE (standard error), n denotes sample size. The p-value, R-squared (R^2), Root Mean Square Error (RMSE). The Ω-T column provides the coefficient of correlation between $\Omega_{calcite}$ and temperature for the subset of the overall dataset on which each individual regression model is based. *Cibicidoides* spp. refers to the regression model based on the combined *C. pachyderma* and *C. mundulus* datasets.

Ratio	**X_1 (intercept)**	**p-value**	**X_2 (T)**	**p-value**	**X_3 (Ω^{-2} (Mg/Ca) or Ω)**	**p-value**	**Overall model**				
							R^2	RMSE	p-value	Ω-T	n
					L. wuellerstorfi						
Mg/Ca	0.55 ± 0.03	<<0.05	0.031 ± 0.004	<<0.05	-0.595 ± 0.028	<<0.05	0.66	0.19	<<0.05	-0.47	448
Sr/Ca	1.09 ± 0.01	<<0.05	-0.0020 ± 0.0018	0.2734	0.146 ± 0.001	<<0.05	0.37	0.06	<<0.05	0.39	305

B/Ca	99.03 ± 5.07	<<0.05	0.11 ± 1.11	0.9208	79.397± 4.290	<<0.05	0.69	14.81	<<0.05	0.34	181
***Uvigerina* spp.**											
Mg/Ca	0.23 ± 0.06	<<0.05	0.02 ± 0.01	<<0.05	-0.30 ± 0.16	<<0.05	0.68	0.16	<<0.05	-0.70	108
Sr/Ca	0.69 ± 0.03	<<0.05	0.003 ± 0.003	0.30	0.16 ± 0.03	<<0.05	0.63	0.08	<<0.05	0.80	53
B/Ca	-9.02 ± 3.53	0.020	-1.87 ± 0.56	0.002	33.24 ± 4.91	<<0.05	0.71	7.33	<<0.05	0.90	38
Mg/Li	0.059 ± 0.002	<<0.05	0.004 ± 0.001	<<0.05	-0.002 ± 0.002	0.2960	0.64	0.01	<<0.05	0.84	85
O. umbonatus											
Mg/Ca	0.38 ± 0.06	<<0.05	0.076 ± 0.008	<<0.05	-0.056 ± 0.089	0.5350	0.60	0.19	<<0.05	-0.55	96
Sr/Ca	0.77 ± 0.06	<<0.05	-0.001 ± 0.010	0.9089	0.077 ± 0.059	0.2023	0.33	0.05	0.0156	0.90	24
B/Ca	18.07 ± 22.15	0.4321	-10.10 ± 5.84	0.1113	44.72 ± 27.36	0.1305	0.21	13.87	0.2647	0.92	14
C. mundulus											
Mg/Ca	0.72 ± 0.11	<<0.05	0.036 ± 0.014	0.0085	-0.61 ± 0.12	<<0.05	0.43	0.25	<<0.05	-0.68	125
Sr/Ca	1.01 ± 0.04	<<0.05	-0.002 ± 0.010	0.8608	0.13 ± 0.05	0.0028	0.37	0.06	<<0.05	0.88	67
B/Ca	88.25 ± 6.34	<<0.05	-2.64 ± 1.57	0.0978	43.38 ± 7.46	<<0.05	0.73	9.47	<<0.05	0.94	64
C. pachyderma											
Mg/Ca	0.25 ± 0.12	0.040	0.059 ± 0.007	<<0.05	0.0796 ± 0.4310	0.8539	0.63	0.17	<<0.05	-0.75	87
Sr/Ca	1.09 ± 0.02	<<0.05	-0.016 ± 0.007	0.0176	0.1678 ± 0.0254	<<0.05	0.84	0.05	<<0.05	0.97	55
Mg/Li	0.07 ± 0.01	<<0.05	0.014 ± 0.001	<<0.05	-0.0072 ± 0.046	0.1238	0.80	0.02	<<0.05	0.62	48
N. umbonifera											
B/Ca	11.37 ± 21.55	0.60	-4.890 ± 15.479	0.7555	126.21 ± 42.13	0.0074	0.60	16.52	<<0.05	0.86	22
***Cibicidoides* spp.**											
Mg/Ca	0.62 ± 0.06	<<0.05	0.040 ± 0.004	<<0.05	-0.77 ± 0.21	<<0.05	0.64	0.23	<<0.05	-0.79	212
Sr/Ca	1.04 ± 0.02	<<0.05	0.005 ± 0.004	0.2569	0.1032 ± 0.0193	<<0.05	0.81	0.06	<<0.05	0.96	122

Table 3. Preferred models with the significant coefficient for element/Ca, temperature, and $\Omega_{calcite}$ ($Mg/Ca = X_1 + X_2*T + X_3*\Omega^{-2}$ and $El_1/El_2 = X_1 + X_2*T + X_3*\Omega$) for each species considered in this study. Uncertainties are reported as ±1SE (standard error), n denotes sample size. The p-value, R-squared (R^2), Root Mean Square Error (RMSE).

Ratio	**X_1 (intercept)**	**p-value**	**X_2 (T)**	**p-value**	**X_3 (Ω^{-2} (Mg/Ca) or Ω)**	**p-value**	**Overall model**				
							R^2	RMSE	p-value	Ω-T	n
L. wuellerstorfi											
Mg/Ca	0.55 ± 0.03	<<0.05	0.031 ± 0.004	<<0.05	-0.596 ± 0.028	<<0.05	0.66	0.19	<<0.05	-0.47	448
Sr/Ca	1.095 ± 0.015	<<0.05	-	-	0.14 ±0.01	<<0.05	0.37	0.06	<<0.05	0.39	305
B/Ca	99.09 ± 5.02	<<0.05	-	-	79.54 ± 4.01	<<0.05	0.69	14.77	<<0.05	0.34	181
***Uvigerina* spp.**											

Mg/Ca	0.23 ±0.56	<<0.05	0.023 ±0.005	<<0.05	-0.30 ± 0.04	<<0.05	0.68	0.16	<<0.05	-0.70	108
Sr/Ca	0.68 ± 0.03	<<0.05	-	-	0.19 ± 0.02	<<0.05	0.62	0.08	<<0.05	0.80	53
B/Ca	-1.85 ± 3.19	<<0.05	-	-	18.34 ± 2.42	<<0.05	0.61	8.32	<<0.05	0.90	38
Mg/Li	0.057 ± 0.002	<<0.05	0.0038 ±0.0003	<<0.05	-	-	0.63	0.01	<<0.05	0.84	85
					O. umbonatus						
Mg/Ca	0.346 ± 0.028	<<0.05	0.079 ±0.007	<<0.05	-	-	0.60	0.19	<<0.05	-0.55	96
Sr/Ca	0.76 ±0.04	<<0.05	-	-	0.08± 0.04	0.0035	0.33	0.06	0.01	0.90	24
B/Ca	47.32 ±15.47	<<0.05	-	-	-	-	0.00	14.98	0.93	0.92	14
					C. mundulus						
Mg/Ca	0.72 ±0.11	<<0.05	0.036 ±0.014	0.0085	-0.61 ±0.12	<<0.05	0.43	0.25	<<0.05	-0.68	125
Sr/Ca	1.01 ±0.03	<<0.05	-	-	0.13 ±0.02	<<0.05	0.37	0.06	<<0.05	0.88	67
B/Ca	96.64 ±3.97	<<0.05	-	-	31.53 ±2.49	<<0.05	0.72	9.60	<<0.05	0.94	64
					C. pachyderma						
Mg/Ca	0.27 ±0.06	<<0.05	0.058 ±0.005	<<0.05	-	-	0.63	0.16	<<0.05	-0.75	87
Sr/Ca	1.09 ±0.02	<<0.05	-0.016 ±0.007	0.0176	0.168 ±0.025	<<0.05	0.84	0.05	<<0.05	0.97	55
Mg/Li	0.057 ±0.012	<<0.05	0.013 ± 0.001	<<0.05	-	-	0.79	0.02	<<0.05	0.62	48
					N. umbonifera						
B/Ca	13.25 ±20.25	<<0.05	-	-	114.74± 20.91	<<0.05	0.60	16.14	<<0.05	0.86	22

Overall model (in the form of Mg/Ca = $X_1 + X_2{*}T + X_3{*}\Omega^{-2}$) root mean square error (RMSE) ranges between 0.16-0.25 (Table 2) in units of ln(Mg/Ca), equivalent to an unexplained variance of 0.26-0.40 mmol/mol for a Mg/Ca value of 1.5 mmol/mol (very approximately equivalent to a calcification temperature of 5°C). Regression models for all species yield a significant temperature coefficient (p <0.05), although there are substantial differences in the relationship between Mg/Ca and temperature. Specifically, the species investigated here broadly cluster into two groups, with *O. umbonatus* and *Cibicidoides pachyderma* characterized by sensitivities of 5.9-7.6 %/°C, while *L. wuellerstorfi*, *Uvigerina* spp., and *C. mundulus* are characterized by sensitivities of 2.3-3.6 %/°C (Fig. 3A, Tab. 2). The former group all lie within the uncertainty of the sensitivity of many species of planktonic foraminifera (Gray & Evans, 2019), whereas the latter are closer to, albeit slightly higher than, that of inorganic calcite (~2 %/°C; Burton and Walter, 1991). These sensitivities are in many cases significantly different from previous calibration approaches (e.g., Lear et al., 2002; Healey et al., 2008), broadly being offset to lower values.

In contrast to temperature, only two species and one genus – *C. mundulus, L. wuellerstorfi*, and *Uvigerina* spp. – are characterized by a significant Mg/Ca-$\Omega^{-2}_{calcite}$ slope (m = -0.61, -0.60, and -0.30, respectively; Tab. 2), with *Uvigerina* spp. characterized by a lower sensitivity. In these species/genus, a one-unit change in $\Omega_{calcite}$ drives a Mg/Ca change equivalent to a ~10°C change in temperature, although we stress that the nonlinear parameterization of the seawater carbonate system in the regression model means that drawing a direct equivalence between the temperature and $\Omega_{calcite}$ slopes is not possible. Conversely*, C. pachyderma* and *Oridorsalis* spp. are not characterized by a significant sensitivity to the carbonate system. While this finding agrees with previous studies that have reported a strong $\Delta[CO_3^{2-}]$ effect on Mg/Ca in *L. wuellerstorfi* and *C. mundulus* (Elderfield et al., 2006; Yu and Elderfield, 2008; Yu et al., 2014), and no resolvable impact on *Oridorsalis* spp. (Rathmann and Kuhnert, 2008; Elderfield et al., 2010), we note that these datasets suffer from strong covariance between T and $\Omega^{-2}_{calcite}$ (see above and the Ω-T column in Table 2), which may mask a carbonate system control. More broadly, we acknowledge that a multiple linear regression approach cannot remove collinearity in these (or any) regressions, impacting the significance of the predictors and standard error of the overall model (e.g., Allen, 1997). Therefore, the interpretation of the influence of each variable on Mg/Ca should be made with caution where covariance in the underlying parameters is an issue (Table 2). In addition, the *C. mundulus* dataset spans a narrow $\Omega_{calcite}$ range, such that additional data are required to properly assess whether such a relationship exists in this case. Removing $\Omega^{-2}_{calcite}$ from the regression model in the case of the two species that lack a significant $\Omega^{-2}_{calcite}$ coefficient results in no significant change in the estimated Mg/Ca-T sensitivity of either *O. umbonatus* (7.9±1.3 versus 7.6±1.0 %/°C) or *C. pachyderma* (5.8±1.0 versus 5.9 ±1.0%/°C).

To assess whether our linear regression models capture the key structure of the datasets, we corrected Mg-Sr-B/Ca for the influence of all but one of the regression parameters in turn, and plotted against the parameter for which no correction was applied (see Text S1), as a means of determining whether there is any residual structure in the data. The results of this analysis are shown as a function of temperature, $\Omega^{-2}_{calcite}$, and DIC, with the alternate parameters subtracted out (Figure 4). Specifically: 1) $\Omega^{-2}_{calcite}$-corrected Mg/Ca displayed as a function of temperature shows Mg/Ca values with the effects of $\Omega^{-2}_{calcite}$ and the intercept term removed ($\Omega^{-2} \bullet x_3 + x_1$); 2) T-corrected Mg/Ca displayed as a function of $\Omega^{-2}_{calcite}$ shows test Mg/Ca with the effect of temperature and the intercept term subtracted out ($T \bullet x_2 + x_1$); and 3) T-and $\Omega^{-2}_{calcite}$-corrected Mg/Ca displayed as a function of DIC is a transformation in the direction of the y axis of a plot of the full model residuals. This latter analysis shows that while the inclusion of DIC in the regression model overall does suggest a sensitivity of Mg/Ca to DIC in *L. wuellerstorfi* and *Cibicidoides* spp. (Supporting information, Table S4), we find no significant residual relationship between corrected Mg/Ca and DIC once the temperature and $\Omega^{-2}_{calcite}$ sensitivities have been removed from these datasets, suggesting that the former finding is an artifact of (e.g.) DIC and temperature covariance in the dataset.

3.2 Sr/Ca

The overall Sr/Ca dataset clusters into two groups, with *L. wuellerstorfi*, *C. mundulus*, and *C. pachyderma* characterized by higher values than *O. umbonatus* and *Uvigerina* spp. at similar temperatures (~1.0-1.6 versus ~0.8-1.0 mmol/mol respectively; Fig. 2D). Otherwise, the most obvious difference between species is that the degree of variance at a given temperature is greater in *L. wuellerstorfi* compared to the other species, although we note that this dataset is also substantially larger (n = 305 versus 24-67).

Using the regression model described above ($Sr/Ca = X_1 + X_2{*}T + X_3{*}\Omega$), the overall model R^2 ranges between 0.33-0.84 and RMSE between 0.051 - 0.077 (in units of mmol/mol; Tab. 2). Only *C. pachyderma* is characterized by a significant Sr/Ca-T coefficient of -0.016 mmol/mol per °C (Fig. S6M). Conversely, all species investigated here are characterized by the same Sr/Ca-$\Omega_{calcite}$ relationship within uncertainty (x_3 = 0.13 to 0.17), with the exception of *O. umbonatus* (0.08). These findings are in broad agreement with previous analyses of the underlying datasets (Lawson et al., 2024; Yu et al., 2014), although we find no significant Sr-carbonate system relationship in *O. umbonatus*, in contrast to Rathmann & Kuhnert (2008). As in the case of Mg/Ca, the underlying covariance between temperature and $\Omega_{calcite}$ means that it is challenging to separate the effect of these two factors on test chemistry in the case of *Uvigerina* spp. and *C. pachyderma*. We also note that neither temperature nor $\Omega_{calcite}$ is a good predictor of *C. mundulus* Sr/Ca (overall model $R^2 = 0.37$), a result of the narrow range of sample site temperature (95% of the dataset falls between 0.5-4.5°C) and $\Omega_{calcite}$ (~1-2) in the context of the variance in the Sr/Ca data (Fig. 2; Fig. S6K).

Reformulating the regression models to exclude nonsignificant terms (i.e., removing the temperature coefficient (Fig. 3B) from the regression models for all species except *C. pachyderma*) results in no substantial change in the overall model R^2 or RMSE, but does result in an overall marginally shallower Sr/Ca-$\Omega_{calcite}$ slope (0.08-0.19 mmol/mol per unit; Fig. 3E).

We find a significant, albeit low slope between residual Sr/Ca and DIC (Fig. 4F) in the case of *L. wuellerstorfi*, with a slope of 3.9×10^{-4} mmol/mol per µmol/kg (Fig. S6C). However, within the context of the model R^2 (0.05) and RMSE (0.062), the uncertainty in reconstructed DIC using these slopes would be similar in magnitude to the entire modern ocean range, such that this may be of mechanistic but not practical interest.

3.3 B/Ca

B/Ca values are lower in *Uvigerina* spp. and *O. umbonatus* than the other species (~0-100 versus 100-250 µmol/mol Fig. 2G-I). B/Ca ratios appear to be positively correlated to temperature for *L. wuellerstorfi* and *C. mundulus* (Fig. S7A and J), which is almost certainly an artifact of the covariance of temperature and the carbonate system (discussed below). B/Ca ratios in *L. wuellestorfi* collected from the Norwegian Sea (Elderfield et al., 2006; Yu and Elderfield, 2007) at temperatures <0°C appear to be offset from the rest of the dataset (Fig. 2G); however, this can be reconciled by considering the unusual carbonate chemistry of these sites. We note that the majority of the *L. wuellerstorfi* and *N. umbonifera* B/Ca data come from sites characterized by a temperature <5°C, such that further data are required to unambiguously resolve whether or not temperature variability independent of seawater carbonate chemistry may play a role in B incorporation into these foraminifera.

Multiple linear regression models that include T and $\Omega_{calcite}$ can explain much of the variance in the B/Ca datasets of *L. wuellerstorfi* and *C. mundulus* (R^2 = 0.69 and 0.73 and RMSE = 14.8 and 9.5 µmol/mol, respectively; Tab. 2), as previously described (e.g., Yu and Elderfield, 2007; Rae et al., 2011). Based largely on the *Uvigerina* spp. data published in this paper, we also demonstrate that this is the case for this genus (R^2 = 0.71, RMSE = 7.3 µmol/mol). However, this is not the case for *O. umbonatus* or *N. umbonifera* (R^2 = 0.21-0.60, RMSE = 11.4-16.5 µmol/mol). This division coincides with the size of the underlying datasets, with the two species in the latter group represented by 12-22 data points (compared to 38-181 in the former group). As such, this finding may simply reflect that further data are required before boron incorporation into *O. umbonatus,* and *N. umbonifera* can be properly assessed.

None of the species considered here are characterized by a significant temperature coefficient in the B/Ca regression models except for *Uvigerina* spp., which has a temperature slope of -1.9 µmol/mol per °C. In contrast, *L. wuellerstorfi*, *C. mundulus*, and *N. umbonifera* are characterized by significant B/Ca-$\Omega_{calcite}$ sensitivities (Fig. 2H). We note that we choose $\Omega_{calcite}$ as an independent variable for the sake of ease of use and consistency in dataset treatment among elemental systems but studies on planktonic foraminifera species demonstrated that B/Ca may be more appropriately related to a more complex boron/carbon system parameter such as $[B(OH)_4^-]$/DIC (e.g., Foster, 2008); on the other hand, studies focused on low-Mg benthic foraminifera have shown that B/Ca better correlates with deep water carbonate saturation state (e.g., Yu and Elderfield, 2007). While this is discussed in more detail below, we note that there is no systematic trend in the residuals of the B/Ca-$\Omega_{calcite}$ regressions, suggesting that a more complex approach may be unnecessary for practical purposes (i.e. balancing the goal of building regressions that are mechanistically meaningful with the practicalities of constraining multiple aspects of seawater carbon and boron chemistry through time). Removing temperature from the model for all species does not substantially change the goodness of fit of the regressions, but it does result in a lower slope between B/Ca and $\Omega_{calcite}$ in the case of

Uvigerina spp. and *O. umbonatus*, this change in slope is justifiable given the nonsignificant temperature coefficient in almost all cases. On the other hand, including temperature in the model results in very similar *Uvigerina* spp., *C. mundulus*, and *O. umbonatus* B/Ca- $\Omega_{calcite}$ sensitivities (33 to 45 µmol/mol per $\Omega_{calcite}$; Fig. 3C), possibly indicating mechanistic similarity in boron incorporation when temperature is accounted for, while removing this component results in an even spread between 1 and 115 µmol/mol (Fig. 3F). However, we focus on models without a temperature component below, given the overall minor impact on the regression model statistics and nonsignificant temperature coefficient, and given that omitting it simplifies the practical application of B/Ca.

We find a significant albeit shallow residual correlation between B/Ca and DIC in *L. wuellerstorfi* and *C. mundulus*, with slopes of –0.27 and 0.091 µmol/mol per µmol/kg (Figs. 4I, S8C and L). As for the Sr/Ca-DIC relationships discussed above, these residual relationships imply possible B/Ca changes in response to DIC far smaller than the magnitude of the residuals in the overall regression, given the magnitude of the DIC variability across the modern ocean.

3.4 Li/Ca

Li/Ca data are available only for *O. umbonatus*, *Uvigerina* spp., and *C. pachyderma*, and are, in isolation, poorly or noncorrelated to temperature in all cases (Fig. 2J; note that six of the nine *C. mundulus* Li/Ca data points are from sites with a temperature range of ~1°C, and therefore we do not interpret the data). Likewise, there is no significant relationship between *Uvigerina* spp. and *C. pachyderma* Li/Ca and $\Omega_{calcite}$ or DIC (Fig. 2K, and L), although residual *O. umbonatus* Li/Ca is positively correlated with $\Omega_{calcite}$ ($R^2 = 0.52$; Fig. 2K and L, and Fig. S9E). Given the absence of a clear temperature or carbonate chemistry control on Li incorporation, as shown in previous studies, we focus on combining these data with Mg/Ca. Linear Mg/Li regression models are characterized by a far lower degree of relative residual variance compared to Mg/Ca for the two species for which sufficient data exist (*Uvigerina* spp. and *C. pachyderma*) (Fig. 5).

Specifically, *Uvigerina* spp. and *C. pachyderma* Mg/Li fit to temperature and $\Omega_{calcite}$ results in overall model R^2 of 0.64 and 0.80, and RMSE of 0.013 and 0.023, respectively (Tab. 2). We find no significant relationship between $\Omega_{calcite}$ and Mg/Li in the case of *Uvigerina* spp., while the *C. pachyderma* data come from sites spanning a range of $\Omega_{calcite}$ that is too small to test whether Mg/Li responds exclusively to temperature in less oversaturated seawater. Removing $\Omega_{calcite}$ from the regression for *Uvigerina* spp. and *C. pachyderma* does not substantially change the goodness of fit (R^2 = 0.63 and 0.79, RMSE = 1.3 and 2.4×10^{-2}), but does result in a moderately lower Mg/Li-temperature sensitivity of 0.38 and 1.27×10^{-2} rather than 0.43 and 1.39×10^{-2} mol/mmol per °C, implying a negative, albeit statistically nonsignificant $\Omega_{calcite}$ effect on Mg/Li (Table 2). There is no significant residual Mg/Li sensitivity to DIC in either species (see Fig. 5 and discussion in section 4.1).

4. Discussion

4.1 Practical considerations in the application of elemental chemistry in benthic foraminifera to paleoenvironmental reconstructions

Our regression (re)analysis demonstrates that temperature can explain the greatest portion of the variance in Mg/Ca for *O. umbonatus* and *C. pachyderma*, based on the ratio of the calibration slopes to the range of these parameters in the calibration dataset (20°C for temperature and 4 for $\Omega_{calcite}$). In contrast, species with a shallower temperature slope (*L. wuellerstorfi*, *Uvigerina* spp., and *C. mundulus*) are characterized by a stronger $\Omega_{calcite}$ influence. In the case of Sr/Ca and B/Ca, $\Omega_{calcite}$ can explain the greatest portion of the variance in these elements in all cases except B/Ca and Sr/Ca in *O. umbonatus*, which cannot be predicted from any combination of temperature and seawater carbonate based on the data currently available. This finding also emerges when limiting the analysis to samples from locations with temperature <5°C, which deviate from the general Sr-B/Ca–temperature but not the Sr-B/Ca-$\Omega_{calcite}$ trend (Figures 2D and 2G), suggesting that $\Omega_{calcite}$ is indeed mechanistically responsible for the majority of the observed variance in Sr and B; this demonstrates that in these instances, our calibration approach correctly attributes variability to $\Omega_{calcite}$ bearing in mind the $\Omega_{calcite}$-T covariance in the dataset. This is in good agreement with virtually all of the studies that reported the datasets analyzed here (Rosenthal et al., 1997; Martin et al., 2002; Lear et al., 2002; Rathmann et al., 2004; Lear and Rosenthal, 2006; Elderfield et al., 2006; Marchitto et al., 2007a; Yu and Elderfield, 2007; Yu and Elderfield, 2008; Bryan and Marchitto, 2008; Healey et al., 2008; Raitzsch et al., 2008, 2011; Lear et al., 2010; Brown et al., 2011; Rae et al., 2011; Tisserand et al., 2013; Yu et al., 2014; Kubota et al., 2015; Lo Giudice Cappelli et al., 2015; Gussone et al., 2016; Stirpe et al., 2021; Lawson et al., 2024), and is encouraging in that, while we show that a multivariate approach is desirable and yields substantially different sensitivities in many cases (described in more detail below), no element/Ca response has been incorrectly apportioned to an underlying independent variable as a result of covariance in the modern ocean (Fig. S2). In addition, our analysis enables us to provide recommendations when designing paleoenvironmental reconstructions based on benthic foraminiferal elemental test chemistry, discussed in more detail below.

We find that the predictive power of Mg/Ca measured in the species considered here principally depends on the sensitivity of the Mg/Ca-temperature relationship (Fig. 3). Unexplained variance in the data is greatest in the two species characterized by a significant Mg/Ca-$\Omega^{-2}_{calcite}$ sensitivity (*L. wuellerstorfi and C. mundulus;* Fig. S3B and K) as well as *Uvigerina* spp., which has the lowest Mg/Ca-temperature sensitivity (evident in the latter case in that the range of observed Mg/Ca between 0-2°C is equivalent to that observed between 0-20°C; Fig. S3D). To quantify the degree to which this is likely to impact temperature reconstructions, we calculated the inverse prediction interval (IPI) for the key controlling seawater parameter (temperature in the case of Mg/Ca). The IPI gives the 95% confidence interval of the residual rotated onto the x-axis (McClelland et al., 2021) and thus provides an estimate of the uncertainty associated with the approach based on the unexplained variance in the dataset. We did this by first calculating temperature from Mg/Ca for all samples in the database (Fig. 6) using the multiple linear regression models presented here (Tab. 2). Then, we calculated the IPI of the predicted versus observed temperature. For example, the IPI of the *L. wuellerstorfi* Mg/Ca-derived temperatures is ±12.1°C, that is, 95% of the predicted temperatures fall within this range of the *in situ* world ocean atlas temperature (Fig. 6A). *C. mundulus* and *Uvigerina* spp. also have relatively high IPI, of 13.4 and 13.7°C, respectively (Fig. 6D, J). Given that these temperature ranges are similar in magnitude to the entirety of the Neogene change in deep ocean temperature (Cramer et al., 2011; Meckler et al., 2022; Evans et al., 2024), it may be preferable to focus attention on species with less unexplained variance in the calibration.

Of the species examined here, *O. umbonatus* and *C. pachyderma* are characterized by substantially lower IPI of 4.8 and 5.6°C, largely resulting from their greater Mg/Ca-T sensitivities (Fig. 6G and M). Coupled with their insensitivity of Mg/Ca to seawater carbonate chemistry, these species thus represent good targets for temperature reconstruction.

We note that the IPI represents a best-case uncertainty estimate compared to paleo applications because *in situ* $\Omega^{-2}_{calcite}$ measurements are used to account for this term in core-top samples, and it is unlikely that $\Omega^{-2}_{calcite}$ can be determined with a similar degree of accuracy in the geological past. On the other hand, it may be possible (or likely) that the unexplained variance we find in the core-top dataset might not characterize geological records featured downcore, because downcore samples may average over longer time intervals than core-top samples. We refer the reader to a more detailed discussion of this topic in McClelland et al. (2021), but note that determining whether this is the case is necessary before choosing the calibration uncertainties versus IPI values when propagating uncertainty. For example, Elderfield et al. (2012) and Woodard et al. (2014) observed: 1) a far smaller degree of variance downcore across multiple glacial-interglacial cycles (G-IG) than the IPI values suggest we should expect; 2) and coherent G-IG Mg/Ca-derived temperature changes. This is encouraging and suggests that core-top variance may overestimate uncertainty downcore, particularly when normalizing paleo records to modern deep ocean temperature.

Mg/Li has been suggested as an alternative paleothermometer in foraminifera and other marine calcifying organisms (e.g., Bryan and Marchitto, 2008; Lear et al., 2010; Marchitto et al., 2018; Raddatz et al., 2013), with the rationale that normalizing to Li potentially removes some of the vital effect-driven variance in Mg/Ca that results from (e.g.) carbonate chemistry, [Ca^{2+}], or Ca^{2+} utilization at the calcification site. Our analysis confirms the conclusions reached in the original publications that regressions based on Mg/Li rather than Mg/Ca under similar temperature ranges are characterized by substantially improved IPIs for both *Uvigerina* spp. and *C. pachyderma* (Fig. 5G, H), an improvement of a factor of 0.5 and 0.7, respectively. This suggests that Mg/Li temperature reconstructions based on these two species may be less error-prone compared to Mg/Ca despite the fact that Li is present at a much lower concentration in foraminiferal calcite and is therefore analytically more challenging to measure. However, in deeper time this approach may suffer from the limited information available regarding past changes in seawater [Li^+] (Weldeghebriel and Lowenstein, 2023) compared to Mg/Ca (e.g., Coggon et al., 2010; Gothmann et al., 2015; Evans et al., 2018).

In addition to the above analysis, we present Mg/Ca multivariate regression models that combine: 1) data from all the species considered here (Fig. 7A); and 2) data from *C. mundulus* and *C. pachyderma* combined to generate a generic *Cibicidoides* spp. calibration (Fig. 7B). The former may be useful when working with extinct species, whereas the latter may be preferable where insufficient specimens exist to differentiate between *Cibicidoides* species. The multispecies regression is characterized by an IPI of 12.9 °C, generally worse than the species-specific approaches discussed above (Fig. 6). Combining both *Cibicidoides* species results in a regression in which both the temperature and $\Omega^{-2}_{calcite}$ coefficients are significant (Tab. 2), and in common with the individual species for which this is the case, an IPI around double (10.8 °C; Fig. 7B) that of species that lack a carbonate chemistry sensitivity (*C. pachyderma* and *O. umbonatus*). Whenever possible, more precise and accurate temperature reconstructions can be achieved by utilizing *C. pachyderma* alone (cf. Fig. 7B and 5M).

We investigated the IPI of Sr/Ca-derived $\Omega_{calcite}$ using the same approach described above to explore the magnitude of the unexplained variance in the regression models. The IPI ranges from 0.60 to 1.3 (Fig. 6B, E, H, K, N), approximately equivalent to [CO_3^{2-}] of 55-120 µmol/kg, if [Ca^{2+}]$_{sw}$ is equal to modern. Combining both

Cibicidoides species together yields an overall model with similar statistics to those described above (R^2 = 0.81, RMSE = 0.058 mmol/mol per unit, $\Omega_{calcite}$ slope = 0.10), although a marginally worse $\Omega_{calcite}$ IPI (1.1; Fig. 7C), driven by the fact that *C. pachyderma* has a significant Sr/Ca-temperature sensitivity, while *C. mundulus* does not (Figs. 3E, S6J, K, M, N). As per the application of Mg/Ca data from these foraminifera, it is clearly desirable to work with single species where possible.

Seawater carbonate chemistry reconstructions based on B/Ca are characterized by substantially lower degrees of unexplained variance compared to Sr/Ca, with an overall trade-off between ease of making accurate measurements and the utility of the resulting data. The B/Ca-$\Omega_{calcite}$ IPI for *L. wuellerstorfi* and *C. pachyderma* are 0.37 and 0.60, respectively (Fig. 6C and L), which translates into an ~20-60% improvement in the uncertainty with which $\Omega_{calcite}$ can be determined compared to using Sr/Ca in the same species. We find a slightly worse *Uvigerina* spp. B/Ca- $\Omega_{calcite}$ IPI (0.91) and no predictive power of *O. umbonatus* B/Ca in reconstructing $\Omega_{calcite}$ (Fig. 6F and I), but stress that this may reflect the limited data available for these species, or variability in $\Omega_{calcite}$ in their infaunal pore-water habitats compared to overlying bottom waters (see Rae et al., 2011).

To produce the most accurate reconstructions, the above analysis indicates that *O. umbonatus* is a good choice for Mg/Ca palaeothermometry, because it is characterized by the lowest IPI and no resolvable sensitivity to $\Omega^{-2}_{calcite}$. This species also has one of the lowest Sr/Ca-derived $\Omega_{calcite}$ IPI, although we find no significant relationship between B/Ca and $\Omega_{calcite}$ based on the available data. Given that B/Ca-derived $\Omega_{calcite}$ reconstructions are generally more precise than those based on Sr/Ca (Fig. 6), then the best way to derive information about temperature and seawater carbonate chemistry would be to combine *O. umbonatus* Mg/Ca with *L. wuellerstorfi* B/Ca (if there are sufficient specimens of these species). This strategy will produce temperature and $\Omega_{calcite}$ reconstructions with the lowest uncertainty propagated based on the unexplained variance in the regression models, although this should again be viewed with the caveat that core-top variance may not necessarily be present in downcore reconstructions, as discussed above.

While we focus on unexplained variance in the regression models in the above discussion, we also report uncertainty based only on the multivariate least squares linear models, often termed 'calibration uncertainty' when applied to fossil datasets. Following Gray & Evans (2019), we account for covariance between the model intercept and temperature coefficient by bootstrapping the regression. We then derive 67% and 95% confidence intervals for our regression models using a Monte Carlo approach, sampling all coefficients within uncertainty 10,000 times and calculating the temperature difference from the central estimate for a range of test Mg/Ca covering the majority of the data analyzed here (Fig. S11). At the extreme ends of the investigated Mg/Ca range, the calibration uncertainty exceeds the IPIs described above, but is generally <3 °C (95% CI) over the typical range of Mg/Ca values in the case of all species without Mg/Ca sensitivity to seawater carbonate chemistry. In contrast, those that do have this sensitivity (*L.* wuellerstorfi, *Uvigerina* spp., *and C. mundulus*) are characterized by 95% confidence intervals derived from calibration uncertainty alone of >10°C at the upper end of the range of test Mg/Ca for these species, driven by a combination of the addition of an $\Omega^{-2}_{calcite}$ coefficient term to the calibration and the fact that these species are characterized by the shallowest Mg/Ca-temperature slopes (Fig. 3). Coupled with the fact that all the aforementioned confidence intervals assume that $\Omega_{calcite}$ is perfectly known, this suggests that temperature reconstructions based on Mg/Ca of these two species are likely to be associated with relatively high uncertainty even if seawater carbonate chemistry can be accounted for.

Here, we formulate regression models to a different carbonate system parameter compared to most previous studies (Ω and Ω^{-2} versus $\Delta[CO_3^{2-}]$), to facilitate the applicability of these models to deep time (pre-Pleistocene) intervals when $[Ca^{2+}]_{sw}$ was different than today. As such, comparison between the slopes of our multivariate models and those that have been published for Sr/Ca and B/Ca is not possible. However, we can highlight the difference in Mg/Ca-temperature slope between this and previous analyses. Compared to regression analyses that only consider temperature as the independent variable (e.g., Rosenthal et al., 1997; Martin et al., 2002; Rathmann et al., 2004; Rosenthal et al., 2006), the temperature coefficients of the models reported here (Tab. 2) are substantially lower (2.3-7.6 %/°C versus ~10 %/°C) for all species, as a result of the broad positive relationship between temperature and [CO_3^{2-}] in the ocean, and the positive relationship between Mg/Ca and both of these factors. More recent studies that recognize this covariance have broadly reported reduced temperature sensitivities (Lear et al., 2010), although those reported here are nonetheless lower than some previous multivariate calibrations (Yu and Elderfield, 2008) that do not consider the effect of both temperature and carbonate chemistry (Raitzsch et al., 2008), or samples from a narrow range of temperature (Healey et al., 2008). Overall, the multivariate models presented here would result in a substantially larger magnitude of reconstructed temperature change for a given measured Mg/Ca change compared to most previous calibrations, all else being equal (i.e., no covarying change in [CO_3^{2-}]).

4.2. Element/Ca ratios in benthic foraminifera: a biomineralization and ecological perspective

All species included in this study belong to the order Rotaliida (Lankester, 1885). Even so, they exhibit different Mg/Ca sensitivities to temperature, with *L. wuellerstorfi* and *Uvigerina* spp. characterized by lower sensitivities than *O. umbonatus, C. mundulus,* and *C. pachyderma*. In contrast, the sensitivity of Sr/Ca to $\Omega_{calcite}$ is similar for every species investigated except for *O. umbonatus,* while the response of B/Ca to $\Omega_{calcite}$ is more heterogeneous (Fig. 3). Although we might expect biomineralization mechanisms to be broadly similar among species within the same order (cf. de Nooijer et al., 2023), our data indicate that the relative importance of different ion transport processes and/or ecological preferences might play a role in the species element/Ca sensitivity to the environmental parameters considered here.

The exact nature of the biological influence on the chemical composition of foraminifera is an active area of research (e.g., Branson et al., 2025). However, several mechanisms have been hypothesized to influence the incorporation of elements other than Ca within the foraminiferal test. For example, the presence of internal reservoirs used during calcification in perforate foraminifera (ter Kuile and Erez, 1988) is likely to be an important feature because it implies a fractionation step between the extraction of elements from seawater and delivery to the calcification site (cf. Elderfield et al., 1996), which may be influenced by biological processes. In particular, the presence of an inorganic carbon pool might influence the incorporation of B, because the incorporation of this element has been suggested to be driven by the growth-rate dependent attachment/detachment rates of borate ($B(OH)_4^-$) and boric acid ($B(OH)_3^-$) to the growing crystal surface, the former of which is de-hydroxylated to $BO_3^{3-}$and substituted for HCO_3^- or CO_3^{2-} in the calcite lattice (e.g., Hemming and Hanson, 1992; Branson et al., 2015). Similarly, the presence of an internal Ca pool might influence the concentration of cations, like Mg, Sr, and Li at the calcification site if this store is a solid phase (e.g., Erez, 2003). Additional biomineralization-related processes that have been proposed as potential 'vital effects' include variable precipitation rates (e.g., Erez, 2003), Rayleigh fractionation (Elderfield et al., 1996; Evans et al., 2018), the effect that symbionts have on the foraminifer's microenvironment (e.g., Sadekov et al., 2005; van Dijk et al., 2019), transmembrane transport in combination with the passive transport of other cations (Nehrke et al., 2013), the involvement of organic linings during chamber formation (e.g., Bentov and Erez, 2006, Erez, 2003), diffusion of boric acid along with CO_2 to the calcifying space (Gagnon et al., 2021), the possible involvement of an amorphous calcium carbonate phase during calcification (Bentov and Erez, 2006; Evans et al., 2020), and the ability of foraminifera to control the fluid composition in the extracellular calcification space (e.g., Bentov and Erez, 2006) and/or to modify pH during calcite precipitation (Evans et al., 2015). Banding could also arise during calcite precipitation due to chemical oscillatory zoning (Branson et al., 2015).

Here, we show that the Mg/Ca of different species is affected differently by oxidative versus reductive cleaning (*L. wuellerstorfi*, *Uvigerina* spp., and *O. umbonatus*), while for *C. mundulus*, there is no significant difference in test Mg/Ca when an oxidative versus reductive cleaning protocol is applied. While this may simply reflect differential cleaning between studies focused on different regions, it may alternatively be because different species are characterized by different degrees of intratest elemental heterogeneity. For example, Glock et al. (2019) reported a different distribution of nitrogen, sulfur, and iodine between cleaned (following Glock et al., 2016) and uncleaned specimens. Importantly, in this study the inside of the test wall was affected by the cleaning procedure even if the specimens were cleaned without breaking the test. This has important implications because if the test is characterized by a microporous texture, the reagents used during the oxidative cleaning can penetrate deep within the test and remove parts of the organic phase (Glock et al., 2019), potentially affecting the elements associated with it, to different degrees in different species. Whether or not this applies to the proxy systems in the species considered in this study requires intratest chemical heterogeneity to be comprehensively documented in each species.

Ecological preferences, like microhabitats, can also impact a species' chemical signature. For example, epifaunal species like *L. wuellerstorfi* and *C. mundulus* (e.g., Lutze and Thiel, 1989; Elderfield et al., 2006; Raitzsch et al., 2008; Rae et al., 2011) are exposed to bottom water conditions. In contrast, shallow to deep infaunal species, such as *O. umbonatus* and *Uvigerina* spp. (e.g., Brow et al., 2011; Rathmann and Kuhnert, 2008; Stirpe et al., 2021), are affected by porewater chemistry (e.g., Jorissen, 1999). Infaunal benthic foraminiferal species are characterized by lower apparent partition coefficients for Cd, Sr, and B compared to epifaunal species (e.g., Tachikawa and Elderfield, 2002; Yu et al., 2014). In addition, pore waters often are characterized by altered or somewhat buffered saturation state compared to bottom water due to organic matter remineralization and $CaCO_3$ dissolution in the upper ~10 cm of sediment (e.g., Zeebe 2007; Cetiner et al., 2025). Species that calcify from a pore water-derived fluid have been suggested to have a weak or absent carbonate saturation effect for this reason (e.g., Elderfield et al., 2006, Raitzsch et al., 2008; Brown et al., 2011). This is in overall agreement with our observations, namely, that *L. wuellerstorfi* and *C. mundulus* (epifaunal species) are characterized by a similar Mg/Ca sensitivity, within uncertainties, to $\Omega^{-2}_{calcite}$ (Fig. 3A), whereas no resolvable sensitivity exists for the infaunal species *O. umbonatus*. However, this is not the same for *Uvigerina* spp., which exhibits a negative sensitivity to $\Omega^{-2}_{calcite}$. This may be a result of variability in porewater chemistry and related differences in biomineralization strategy, e.g., as an adaptation to undersaturated conditions. This is additionally supported by the much lower B/Ca-$\Omega_{calcite}$ sensitivities of the infaunal species (Fig. 3C), although not all species fit this pattern, with *C. pachyderma,* which is also an epifaunal species (e.g., Rathburn et al., 1996; McCorkle et al., 1997) characterized by a Mg/Ca-$\Omega^{-2}_{\mathrm{calcite}}$ sensitivity similar to the infaunal species (Fig. 3A). In addition, while microhabitat similarities can partially explain the observed Mg/Ca and B/Ca sensitivities to $\Omega_{\mathrm{calcite}}$, we observe similar Sr/Ca-$\Omega_{\mathrm{calcite}}$ slopes among all species considered here. Why Mg/Ca and B/Ca should be buffered in infaunal species while Sr/Ca is not is mechanistically problematic and potentially suggests that the grouping of sensitivities between infaunal/epifaunal species discussed above may be coincidental, and perhaps better ascribed to (e.g.) biologically-driven differences in calcification site carbonate chemistry among species that inhabit different niches, rather than the direct effect of bottom/pore water chemistry.

Interestingly, *C. pachyderma* juveniles were observed up to 4.6 cm deep in the sediment, which suggests that this species changes microhabitat during different ontogenetic stages (Rathburn and Corliss, 1994). This could explain the lack of $\Omega^{-2}_{\mathrm{calcite}}$ influence on *C. pachyderma* Mg/Ca (Table 2) as observed for *O. umbonatus* and *Uvigerina* spp.. Microhabitat changes during a species life cycle have also been invoked to explain the Mg/Ca offset between *C. mundulus* and *L. wuellerstorfi*, with the former migrating within the sediment during ontogenesis (Rathburn and Corliss, 1994; Raitzsch et al., 2008). However, it should also be borne in mind that benthic foraminiferal distributions in sediment can vary geographically and temporally (e.g., Kitazato, 1994; Jorissen, 1999). For example, *L. wuellerstorfi* is commonly described as epifaunal, although the presence of this species below 1 cm was also reported (e.g., Rathburn and Corliss, 1994), possibly as a consequence of bioturbation in deep-sea sediments (e.g., Jorissen, 1999).

Overall, we conclude that while microhabitat preferences broadly align with test geochemical relationships, this factor alone cannot explain differential inter-species element/Ca sensitivity to environmental parameters. Further studies are necessary to better understand different species' ecological preferences and their relationship with element/Ca incorporation in foraminiferal tests.

4.3. `ElCaRBenthic`: Calibration implementation, uncertainty propagation, and downcore application examples

To apply the calibrations described above (Sec. 3.2 and 4.1), we provide `ElCaRBenthic` (https://www.github.com/dbjevans/ElCaRBenthic), a Matlab script for the calculation of temperature, $\Omega_{calcite}$, and [CO_3^{2-}] from benthic foraminiferal Mg/Ca, Sr/Ca, B/Ca, or Mg/Li data. Following *MgCaRB* (for planktonic foraminifera; Gray & Evans, 2019), the program provides a convenient implementation of the above multivariate regression models. In addition, *ElCaRBenthic* can account for nonthermal controls on Mg/Ca and non-carbonate chemistry controls on Sr/Ca (where relevant), and it fully propagates uncertainty associated with data, calibration, and all relevant input datasets (seawater chemistry, $\Omega_{calcite}$ in the case of Mg/Ca and temperature in the case of Sr/Ca, the relationship between seawater and test chemistry). The calibration inverse prediction intervals (IPI) are also returned. While we focus on $\Omega_{calcite}$ and $\Omega^{-2}_{calcite}$ in the regression models, given that this is easier to implement over a range of timescales, *ElCaRBenthic* also converts $\Omega_{calcite}$ to [CO_3^{2-}] using optional temperature and depth inputs (or using Mg/Ca-derived temperature). Where a given system is sensitive to more than one factor (e.g., Mg/Ca in the case of *L. wuellerstorfi*, Sr/Ca in the case of *C. pachyderma*; Fig. 3), more than one trace element dataset can be input at the same time to simultaneously solve for both dependent variables. The script derives the multivariate calibrations discussed above from the database file provided here each time it is run, such that it can easily be applied to new datasets or to an updated version of our compilation database in future.

To achieve this, several reference datasets are required to correct foraminiferal test chemistry datasets for changes in the minor and major ion composition of seawater for application in deep time (>1 Ma). Specifically, we use a compilation of Mg/Ca_{sw} datasets (Dickson, 2004; Coggon et al., 2010; Brennan et al., 2013; Rausch et al., 2013; Gothmann et al., 2015; Evans et al., 2016, 2018; Zhou et al., 2020) with uncertainty derived from the 2.5th and 97.5th percentiles of 10^3 bootstrapped LOWESS fits to the data, resampled within uncertainty. The seawater [Li^+] and [Ca^{2+}] datasets required to correct Mg/Li (via Li/Ca) are, to our knowledge, only available in the former case from modeling the composition of fluid inclusions measured in marine evaporitic sequences (Weldeghebriel and Lowenstein, 2023). As such, these $[Li^+]_{sw}$ data were combined with fluid inclusion and foraminiferal $[Ca^{2+}]_{sw}$ reconstructions (Brennan et al., 2013; Zhou et al., 2021), resampled within uncertainty, and fit using a LOWESS function 10^3 times, with the propagated uncertainty taken from the 2.5th and 97.5th percentiles of the resulting dataset.

In addition to knowledge of how the composition of seawater has changed through geological time, correcting foraminiferal test chemistry data requires that the shape of the relationship between seawater and test elemental ratios is known (exponent H in Eq. 5). This has been argued to be nonlinear in the case of Mg/Ca (Segev and Erez, 2006; Hasiuk and Lohmann, 2010; Evans and Müller, 2012; Evans et al., 2015a), although linear (i.e., a constant apparent distribution coefficient) relationships have been applied (e.g., Lear et al., 2000) and even the absence of such a relationship has been argued for (Lear et al. 2015). Given that no consensus and/or insufficient data exist to constrain this aspect of deep ocean benthic foraminifera, we leave *H* and associated uncertainty as a required *ElCaRBenthic* input field when processing samples older than 800 ka, where:

$$\text{Mg/Ca}_{\text{corrected}} = \text{Mg/Ca}_{\text{measured}} \times 5.2^{H} / \text{Mg/Ca}_{\text{sw}}^{H} \qquad \text{(Eq. 5)}$$

Mg/Ca_{sw} is the value at a time interval of interest, and 5.2 is the modern ratio. In the examples below, we follow the recommendation of Evans et al. (2016) regarding the value of *H* for the species utilized here, but note that this analysis likely requires revision in light of the multivariate calibration models presented here.

Foraminiferal Li/Ca are corrected for changes in Li/Ca_{sw} using a constant distribution coefficient, because the limited amount of data from foraminifera cultured in seawater with varying Li/Ca indicates that foraminiferal test and seawater Li/Ca are linearly related (Hauzer et al., 2024):

$$\text{Li/Ca}_{\text{corrected}} = \text{Li/Ca}_{\text{measured}} \times 2.6 / \text{Li/Ca}_{\text{sw}} \qquad \text{(Eq. 6)}$$

where Li/Ca_{sw} is that at a time interval of interest and 2.6 is the modern ratio (in mmol/mol). We do not include a correction for past changes in Sr/Ca_{sw} because the (high quality) available data suggest that $[\text{Sr}^{2+}]_{\text{sw}}$ and $[\text{Ca}^{2+}]_{\text{sw}}$ have covaried over the course of the Cenozoic (Gothmann et al., 2015), but note that this could be accounted for by correcting the data along similar lines to our processing of Li/Ca (Eq. 6) if desired. Likewise, no attempt has been made to correct B/Ca data for past changes in seawater chemistry given that the secular evolution of the total boron seawater concentration is very poorly constrained (Lemarchand et al., 2002).

Example application 1: late Pleistocene deep ocean carbonate chemistry. To demonstrate the utility of B/Ca and Sr/Ca for carbonate chemistry reconstruction, we applied our *L. wuellerstorfi* B/Ca and Sr/Ca calibrations to site VM28-122 (3620 m, Caribbean Basin, e.g., Yu et al., 2010; see Sec. 2.3 for further details and data sources). We derive $\Omega_{calcite}$ directly from the above calibrations, as well as $[CO_3^{2-}]$ calculated from $\Omega_{calcite}$ using the depth of the core site and assuming T = 3°C in the absence, to our knowledge, of published Mg/Ca data for this site (Figure 8). We reconstructed glacial-interglacial $\Omega_{calcite}$ changes of ~0.5-0.75 units and B/Ca-derived $[CO_3^{2-}]$ ~40 µmol/kg higher during the last two glacials compared to the Holocene. This latter reconstruction agrees with Yu et al. (2013) to better than 10 µmol/kg throughout the duration of the record. While this reflects that our *L. wuellerstorfi* B/Ca calibration does not differ substantially from previous approaches, we fully propagate all sources of uncertainty, demonstrating significant G-IG $[CO_3^{2-}]$ change when considering calibration uncertainty alone, although with an IPI of the same order of magnitude as the late Pleistocene variability. Moreover, our new Sr/Ca-derived $\Omega_{calcite}$ and $[CO_3^{2-}]$ reconstructions are in good agreement with those based on B/Ca (Fig. 8). While several previous studies have noted the downcore correlation between B/Ca and Sr/Ca (Yu et al., 2013; Lo Giudice Cappelli et al., 2015), and Sr/Ca-derived $\Delta[CO_3^{2-}]$ have been reported based on a regression of down core Sr/Ca against B/Ca-derived $\Delta[CO_3^{2-}]$ (Lawson et al., 2024), our analysis may represent the first truly independent Sr/Ca-based reconstruction; that is, the Sr/Ca-derived reconstructions (Fig. 8) are based on independent core-top data rather than an ad hoc downcore correlation. The B/Ca and Sr/Ca datasets show an good degree of coherence over the last two G-IG cycles, further demonstrating the utility of benthic foraminiferal Sr/Ca data for the purposes of carbonate chemistry reconstruction, especially given that it is more routinely and more easily measured, as

as noted by Lawson et al. (2024). However, as discussed in Sec. 4.1, Sr/Ca based carbonate chemistry reconstructions are a factor of ~2 times more uncertain than those based on B/Ca. In addition, we observe substantial offsets in certain intervals;

for example, $\Omega_{calcite}$ during the last interglacial period was ~0.3 units lower based on Sr/Ca, outside of the combined calibration uncertainty of the two approaches. This highlights that calibration uncertainty alone cannot account for all sources of uncertainty when applying these systems downcore (in contrast to the IPI intervals in this case) and warrants caution when interpreting the details of reconstructions such as these at this scale.

Example application 2: Neogene temperature and carbonate chemistry changes. Using ODP Site 806 as an example, we used data (see Sec. 2.3) reported by Lear et al. (2003; 2015) and Lear & Rosenthal (2006) to assess Mg/Ca and Sr/Ca-derived temperature and $\Omega_{calcite}$ reconstructions across the last 15 Myr from *L. wuellerstorfi, O. umbonatus,* and *C. mundulus* using the multivariate calibration models presented above. This enabled us to compare results from species that are and are not characterized by a Mg/Ca sensitivity to $\Omega_{calcite}$, including the use of Sr/Ca to reconstruct and correct for the $\Omega_{calcite}$ influence on Mg/Ca-based temperature reconstructions across multi-million-year timescales.

Calculating temperature from Mg/Ca without accounting for the possible effects of changing $\Omega_{calcite}$ (i.e., assuming $\Omega_{calcite} = 1 \pm 0.5$ throughout the duration of these records) results in reconstructions that deviate from each other by up to 8°C in the late Neogene (<4 Ma) and by >15°C before then (Fig. 9A). Although all reconstructions agreed within uncertainty, our results demonstrate the substantial influence of nonthermal factors on Mg/Ca. In particular, *L. wuellerstorfi* yielded an unreasonable degree of cooling in the last 5 Myr. At the same time, temperatures based on *C. mundulus* Mg/Ca were 5-10 °C higher between 5-10 Ma compared to the temperatures obtained using *O. umbonatus*, the only species in the comparison that is not characterized by a Mg/Ca-$\Omega_{calcite}$ sensitivity. Reconstructing $\Omega_{calcite}$ using the species-specific Sr/Ca calibrations presented here (Fig. 9C) results in somewhat different $\Omega_{calcite}$ reconstructions, albeit within uncertainty, with the *O. umbonatus* and *C. mundulus* records in broadly good agreement, while the reconstruction based on *L. wuellerstorfi* Sr/Ca would imply that Site 806 was undersaturated with respect to calcite prior to 4 Ma. This disagreement may reflect habitat differences among the species analyzed, or could highlight the overall limitations of the approach given that a portion of the inferred change in $\Omega_{calcite}$ based on *L. wuellerstorfi* is partially driven by the unreasonably large reconstructed temperature change. We also stress that these reconstructions are within uncertainty of each other at the level of the calibration IPI.

Our results emphasize that using species-specific results to correct for the influence of $\Omega_{calcite}$ on Mg/Ca temperature reconstructions results in much better agreement among the three species (Fig. 9B), even though the magnitude of cooling and Pleistocene temperatures remain unrealistic in the case of *L. wuellerstorfi*. Overall, this highlights: 1) the power of interpreting Mg/Ca and Sr/Ca (or B/Ca) data together, without which temperature would have been greatly overestimated using species with an $\Omega_{calcite}$ sensitivity; and 2) the large degree of inherent uncertainty in using *L. wuellerstorfi* Mg/Ca for temperature reconstruction.

5. Conclusions

We compiled published Mg/Ca, Sr/Ca, B/Ca, and Li/Ca core-top data for *C. mundulus, C. pachyderma*, *L. wuellerstorfi*, *N. umbonifera, O. umbonatus*, and *Uvigerina* spp. Multivariate regression models that relate these geochemical datasets to *in situ* environmental parameters demonstrate that temperature can explain much of the variance in the Mg/Ca datasets with species clustering in two main groups: (1) *O. umbonatus* and *C. pachyderma*, with sensitivities of 7.6 and 5.9%/°C respectively (similar to planktonic foraminifera); and (2) *L. wuellerstorfi*, *Uvigerina* spp., and *C. mundulus,* with sensitivities of 2.3-3.6%/°C (similar to inorganic calcite). As previously suggested, we find that $\Omega_{calcite}$ is a significant predictor of *C. mundulus* and *L. wuellerstorfi* Mg/Ca, with the implication that temperature reconstructions using these species are inherently more uncertain irrespective of whether $\Omega_{calcite}$ can be independently constrained. The combination of Mg/Ca with Li/Ca data results in a proxy (Mg/Li; e.g., Bryan & Marchitto, 2008) that is characterized by lower calibration uncertainties despite the possible analytical challenges compared to Mg/Ca (e.g. determination via ICP-OES may not be possible).

Our results also demonstrate that all species, with the exception of *O. umbonatus*, are characterized by the same Sr/Ca-$\Omega_{calcite}$ relationship within uncertainty, suggesting that Sr/Ca data are likely to be a useful means for reconstructing $\Omega_{calcite}$, as recently suggested by Lawson et al. (2024). Only *C. pachyderma* exhibits a significant Sr/Ca-T sensitivity, thus requiring correction before interpreting Sr/Ca data in terms of seawater carbonate chemistry.

B/Ca is tightly correlated with $\Omega_{calcite}$ in *C. mundulus, L. wuellerstorfi*, and *N. umbonifera* without a resolvable temperature influence, whereas the infaunal species are characterized by substantially lower test B concentrations and no significant sensitivity to $\Omega_{calcite}$ in the case of *O. umbonatus* (although limited data are available).

Overall, the most precise and accurate temperature reconstructions can be obtained from *O. umbonatus* Mg/Ca (or *C. pachyderma* Mg/Li), whereas the most precise and accurate $\Omega_{calcite}$ reconstructions can be generated using *L. wuellerstorfi* B/Ca. However, if data from only one species can be generated, and a choice of species is available, combined *C. pachyderma* Mg/Ca and Sr/Ca measurements provide the best compromise of temperature and $\Omega_{calcite}$ data quality, although there is no substitute for *L. wuellerstorfi* B/Ca-derived $\Omega_{calcite}$ reconstructions that is not associated with a substantial (factor ~2) increase in uncertainty. Combining the dataset for all the species analyzed here into genus or multispecies calibrations results in substantially larger uncertainties, emphasizing the importance of single-species analysis whenever possible.

Finally, based on the species-specific multivariate calibrations generated here, we develop a new processing software (ElCaRBenthic) that provides a convenient way of applying our calibrations to fossil samples. The software can account for the thermal and non-thermal controls on Mg/Ca, Sr/Ca, B/Ca, and Mg/Li by accepting up to two datasets simultaneously (e.g., Mg/Ca and Sr/Ca), as well as fully propagating uncertainty and correcting for changes in seawater elemental chemistry throughout the Cenozoic. Applying this tool to two published example datasets demonstrates for the first time the accuracy (i.e. match to B/Ca derived estimates) of Sr/Ca-derived $\Omega_{calcite}$ reconstructions based on core-top calibrations vs. ad hoc down core Sr/Ca calibration. It also highlights the importance of accounting for $\Omega_{calcite}$ in Mg/Ca-based temperature reconstructions, which increases the agreement among records generated using different species.

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Declaration of Competing Interest

The authors declare that they have no competing financial or personal interests that could have affected the work presented in this paper.

Open Research

The dataset used in this research was deposited to the Pangaea data repository and can be found online (Nauter-Alves et al., XXXX; doi:XXXXXXX). The “El/CaRBenthic” Matlab code is available on Github https://github.com/dbjevans/ElCaRBenthic (Evans, 2025), and the code written to perform the data analysis and produce all figures is available at https://zenodo.org/records/XXXXXXXX.

Figure 1. Site locations of the core-top samples included in this study. The map was generated using QGIS software version 3.38. See Table 1 for references. The compiled dataset can be found on Pangaea (Nauter-Alves et al., XXXX; doi:XXXXXXX).

Figure 2. Mg/Ca, Sr/Ca, B/Ca, and Li/Ca data are shown as a function of *in situ* temperature (A, D, G, J), $\Omega_{calcite}$ (C, F, I, L), and dissolved inorganic carbon concentration (DIC) (B, E, H, K) for all

species considered in this study. See Figs. S3, S5, and S7 for equivalent plots with each species displayed in individual panels.

Figure 3. Temperature and $\Omega^{-2}_{calcite}$ / $\Omega_{calcite}$ regression coefficients for the preferred models presented here for (A) Mg/Ca, (B) Sr/Ca, and (C) B/Ca; y axis units are the same as those given on the x axes, per $\Omega^{-2}_{calcite}$ or unit $\Omega_{calcite}$. The vertical gray shaded region in panels A and D shows the range of Mg/Ca-T sensitivities for planktonic foraminifera for which sufficient laboratory culture data exist to characterize this relationship (Gray & Evans, 2019). Other gray bars delineate the position of zero. Error bars show 1SE coefficient uncertainties. (D-F) show equivalent plots based on alternative regression models in which nonsignificant parameters have been removed (e.g., the $\Omega^{-2}_{calcite}$ coefficient in the case of *C. pachyderma* and *O. umbonatus* Mg/Ca, see text for details).

Figure 4. Corrected test Mg/Ca (A, B, C), Sr/Ca (D, E, F), and B/Ca (G, H, I) data shown as a function of *in situ* temperature, $\Omega_{calcite}$, and dissolved inorganic carbon concentration (DIC). Corrected data plotted as a function of temperature are those with the $\Omega_{calcite}$ component subtracted out (e.g., $\Omega^{-2}_{calcite}$-corrected Mg/Ca). Corrected data plotted as a function of $\Omega_{calcite}$ are those with the temperature component subtracted out (e.g., T-corrected Mg/Ca). Corrected data plotted against DIC show the residual variance in the data after the temperature and $\Omega_{calcite}$ components have been removed (e.g., T and $\Omega^{-2}_{calcite}$-corrected Mg/Ca) (see text for details). See Figs. S4,6,8 for equivalent plots with each species displayed in individual panels and significant linear regressions overlain. Note that we plot corrected Mg/Ca as a function of $\Omega_{calcite}$ for consistency, although the regression and correction were applied using $\Omega^{-2}_{calcite.}$

Figure 5. Controls on Mg/Li for the genus and species for which sufficient data are available to assess this (*Uvigerina* spp. and *C. pachyderma*). (A-C) Mg/Li shown as a function of *in situ* temperature, $\Omega_{calcite}$, and DIC. (D-F) As panels A-C, except with the $\Omega_{calcite}$ (D) or temperature (E) component subtracted out. Panel (F) shows the residual variance in the data as a function of DIC. (G-H) *In situ* versus predicted temperature using our preferred regression model, with the dashed confidence intervals showing the inverse prediction interval (IPI, see Fig. 6 caption). (I) The temperature and $\Omega_{calcite}$ coefficients of the least-squares linear regression model.

Figure 6. *In situ* temperature versus predicted temperature based on Mg/Ca (left panels). *In situ* $\Omega_{calcite}$ versus predicted $\Omega_{calcite}$ based on Sr/Ca (central panels) and B/Ca (right panels) using the preferred regression model form (see text for additional details). The inverse prediction interval (the 2SD of residual variance rotated onto the x-axis; McClelland et al., 2021) is shown by dashed lines.

Fig. 7. *In situ* temperature versus temperature predicted based on the (A) multi-species Mg/Ca and (B) *Cibicidoides* spp. Mg/Ca regressions presented here. (C) *In situ* versus predicted $\Omega^{-2}_{calcite}$ based on the *Cibicoides* spp. Sr/Ca model presented here. The inverse prediction interval (the 2SD of residual variance rotated onto the x axis; McClelland et al., 2021) is shown by dashed lines.

Figure 8. Example application of ElCaRBenthic to reconstruct seawater carbonate chemistry using *L. wuellerstorfi* B/Ca and Sr/Ca from VM28-122 (Caribbean, 3.6 km; with a sill depth of 1.8 km, data from Yu et al. 2010a, 2010b, and 2014). The three shaded regions show the 67 % and 95 % calibration uncertainties, as well as the prediction intervals derived from the unexplained variance in the calibration dataset. The regression model is formulated in terms of $\Omega_{calcite}$ (panel A) and is converted into [CO_3^{2-}] (panel B) using the core depth assuming a

constant S = 35 and T = 3 °C, in order to facilitate comparison to a previous calibration approach.

Figure 9. Application example of ElCaRBenthic to reconstruct temperature and seawater carbonate chemistry at ODP Site 806 over the last 15 Myr (western Equatorial Pacific, 2.5 km, data from Lear et al., 2015). (A) Mg/Ca-derived temperature assuming constant $\Omega_{calcite} = 1$ where relevant (*L. wuellerstorfi* and *C. mundulus*). The three shaded regions show the 67% and 95% calibration uncertainties, as well as the prediction intervals derived from the unexplained variance in the calibration dataset. (B) Mg/Ca-derived temperature corrected for changes in $\Omega_{calcite}$ where relevant. (C) Sr/Ca-derived $\Omega_{calcite}$. No correction has been applied for potential changes in Sr/$Ca_{sw,}$ although Sr/Ca_{sw} uncertainty is fully propagated into the reconstructions.

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