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ADVANCED REVIEW

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Environmental records from coral skeletons: A decade of novel insights and innovation

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Abstract

Hundreds of coral paleoclimate records have been developed over the past several decades, significantly extending the instrumental record and improving our understanding of tropical climate variability and change in otherwise data-poor regions. Coral "proxy" records measure the change in skeletal geochemistry or growth as a function of ocean conditions at the time of calcification. Over the past decade (since 2010), new syntheses have identified coherent patterns of warming and variability that are unique within the paleo record (albeit not yet unprecedented). In turn, ocean warming and acidification have had a detrimental impact on coral growth, with reduced extension and increased stress banding. Methodological advances have constrained uncertainties and improved our understanding of the processes by which climate information is archived in coral skeletons. Models that describe these processes have been developed to facilitate proxy-model comparisons, identify sources of uncertainties, and provide a benchmark upon which forced changes may be detected within a highly variable climate system. Finally, several innovative new proxies have expanded the climate and environmental information that may be obtained from corals, including: seawater pH, aragonite saturation, anthropogenic nitrogen, runoff, and trade winds. Further extending established and novel proxies should remain a priority, along with seawater monitoring and density measurements with which to screen and calibrate these records. As this critical climate archive is increasingly threatened by warming and ocean acidification, the community must work closely together to collect this invaluable climate data in an ecologically and culturally sensitive manner, before it is too late.

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KEYWORDS

climate change, climate variability, coral paleoclimate, geochemistry, proxy system models

1 | INTRODUCTION

The tropical oceans are a critical heat engine of the global climate system and drive interannual to decadal changes in global climate through complex feedbacks with atmospheric and oceanic circulation. Understanding how the tropical oceans will be affected by climate change is therefore critical for accurate projections of near-term and future climate on regional to global scales. However, sparse historical data coverage and large internal climate variability make it difficult to assess the magnitude and pattern change, thus limiting the detection and attribution of forced changes (both natural and anthropogenic). Paleoclimate "proxy" records from the skeleton of reef-building corals (herein hermatypic, scleractinian corals) have greatly extended the limited instrumental record, providing improved constraints on internal climate variability and the response of tropical–subtropical (~30°N–30°S) oceans to natural and anthropogenic forcings over the past few hundred thousand years. These coral proxy records leverage changes in the growth or the geochemistry of the coral exoskeleton that reflect the oceanic conditions at the time of growth. This exoskeleton forms incrementally with time as the live coral polyp builds new skeletal material and extends vertically within the walls of individual skeletal units (corallites) in the top few millimeters of the colony (the tissue layer) (Veron, 1986). A few factors make reef-building corals a particularly powerful archive of past climate variability: (1) annual density banding patterns (Knutson et al., 1972), relatively rapid growth (~0.3–2 cm/year, depending on the species), and fine-scale milling techniques permit annual or even sub-annual reconstructions of past climate (hereafter "high-resolution"); (2) annual density banding patterns, combined with advances in radiometric dating techniques (see Section 3.6) permit chronological uncertainties on the order of only a few years or less for well-dated chronologies; and (3) well-preserved colonies of living (modern) and sub-fossil (hereafter "fossil," Figure 1) samples fill critical gaps in both the spatial and temporal coverage of climate information from the global tropics (Lough, 2010). Several reviews have discussed the rich history of coral paleoclimate studies, including an in-depth discussion of the commonly utilized proxies for paleo-temperature ($\delta^{18}O$, Sr/Ca) and coral growth (density, extension, and calcification) (Barnes & Lough, 1996; Corrège, 2006; Felis & Pätzold, 2003; Gagan et al., 2000; Grottoli & Eakin, 2007; Jones et al., 2009; Lough, 2004, 2008, 2010; Lough & Cantin, 2014; Lough & Cooper, 2011; Sadler et al., 2014; Williams, 2020), as well as novel geochemical proxies (Saha et al., 2016).

FIGURE 1 Drilling a massive *Porites* sp. fossil coral colony. Photo credit: Hussein Sayani

Building on these reviews, this article highlights examples of new insights that have been gained over the past decade (since Lough, 2010, i.e., 2010–2021) from new records and syntheses (Section 2), comprehensive analysis of uncertainties and methodological improvements (Section 3), innovative new proxies (Section 4), and advances in proxy data—climate model synthesis (Section 5). The review ends with a reflection of outstanding challenges and opportunities over the coming decades of innovation (Section 6). To complement recent reviews of paleoclimate studies across a diversity of long-lived reef-building (Sadler et al., 2014) and proteinaceous (Williams, 2020) coral genera, this review will focus primarily on *Porites* spp. corals, which remain the most extensively utilized genera for paleoclimate studies. Given the rapid expansion of coral paleoclimate studies (Figure 2), this review does not attempt to summarize each significant finding, but rather highlight promising new directions and overarching themes of the field.

2 | INSIGHTS INTO TROPICAL-SUBTROPICAL CLIMATE VARIABILITY AND CHANGE

This section highlights new insights on two major open questions, as examples of areas where considerable progress has been made by the coral paleoclimate community: (1) How has tropical–subtropical Indo-Pacific climate variability changed in response to natural and anthropogenic forcings over the Holocene? (2) How have ocean warming and acidification impacted the growth of reef-building corals?

2.1 | Indo-Pacific climate variability over the Holocene

The growing network of fossil coral cores from across the tropical–subtropical Pacific has provided additional constraints on the timing and magnitude of the early- to mid-Holocene (~10-5 thousand years ago, hereafter ka) reduction in El Niño–Southern Oscillation (ENSO) variance in response to orbital forcing. High-resolution marine carbonate records (i.e., corals and mollusks) from the western Pacific and the eastern Pacific (EP) suggest an early-mid Holocene reduction in ENSO variance (frequency and/or intensity) (Driscoll et al., 2014; Duprey et al., 2012; McGregor & Gagan, 2004; Tudhope et al., 2001), followed by intensification of ENSO after 4 ka (Carré et al., 2005, 2014). However, coral records from the Central Pacific (CP; Grothe et al., 2020; McGregor et al., 2013) and a multiproxy network of coral and mollusk records (Emile-Geay et al., 2016) suggest a mid-Holocene reduction in ENSO frequency centered around 3–5 ka, out of phase with orbital insolation changes. Depending on the temporal coverage of records, the change may not even be detectable within the highly variable system (Cobb et al., 2013). ENSO's evolution across the Holocene remains debated (paleoENSO workshop 2019), despite large changes in the zonal temperature gradient in response to orbital forcing (Rein et al., 2005; Stott et al., 2004), and broad agreement among climate models for a weakened mid-Holocene ENSO (e.g., see recent synthesis by Tian et al., 2017). Nevertheless, as the network of high-resolution paleoclimate data over the central-eastern Pacific Ocean has grown, so has the confidence in an early-mid Holocene reduction in ENSO strength. The precise timing and magnitude of this forced change will be further constrained as additional records become available.

Such discrepancies among paleoclimate archives are further amplified during periods of comparatively weaker climate forcing over the last 2000 years (the Common Era, CE), with relatively low coherency during many intervals (Dätwyler et al., 2019), particularly on decadal to centennial timescales (Emile-Geay et al., 2013; Henley, 2017; Loope, Thompson, Cole, & Overpeck, 2020; Newman et al., 2016). This is another area in which considerable progress has been made with new coral reconstructions and syntheses of existing records. Located in the center(s) of action for major modes of coupled ocean–atmosphere climate variability (e.g., ENSO and the Indian Ocean Dipole, IOD), coral records provide critical information about these modes without relying on stationary atmospheric teleconnections (a long-standing challenge for terrestrial proxies). For example, a compilation of available $\delta^{18}O$ (temperature and seawater $\delta^{18}O$—hereafter $\delta^{18}O_{sw}$) and Sr/Ca (temperature) records with coverage over the CE (PAGES 2k working groups: temperature, PAGES 2k Consortium, 2013; PAGES2k Consortium, 2017; Oceans 2k, Tierney et al., 2015; Iso2k, Konecky et al., 2020; and Hydro2k, PAGES 2k Consortium, 2019) have identified coherent signals of temperature (Figure 3) and hydroclimate change in response to volcanic (McGregor et al., 2015; PAGES 2k Consortium, 2019; Tierney et al., 2015) and anthropogenic aerosol and greenhouse gas forcing (PAGES 2k Consortium, 2019; Tierney et al., 2015; The PAGES 2k Consortium et al., 2016). These coherent trends emerge despite noise within individual proxies (e.g., Loope, Thompson, Cole, & Overpeck, 2020), regional differences in the timing and/or magnitude of change as a result of regional

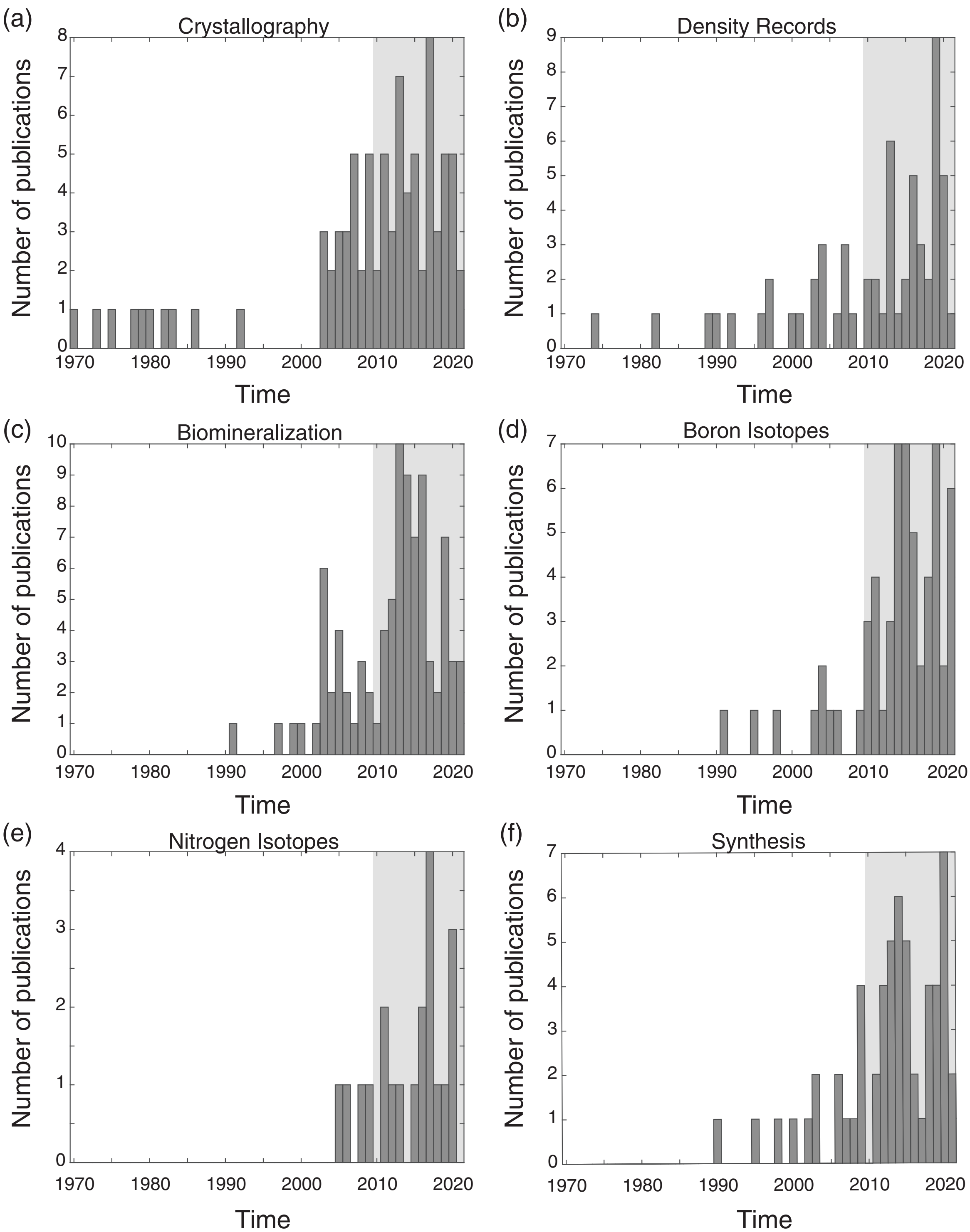

FIGURE 2 Frequency distribution of the number of publications per year since 1970 for a subset of the methodologies reviewed here: (a) crystallography (e.g., raman, aragonite unit cell structure), (b) skeletal density records (e.g., X-ray or CT densitometry), (c) biomineralization (e.g., histology, ion transport, organic matter, biochemistry, genomics, proteomics, or microstructure), (d) boron isotopes (e.g., pH, acidification, and/or calcifying fluid), (e) nitrogen isotope records (skeletal bound organic $\delta^{15}N$), and (f) coral paleoclimate synthesis (e.g., PAGES 2k, multisite networks, etc.). All subpanels were obtained by searching the Elsevier Scopus database with keywords for each subfield; each list was carefully curated to remove publications that were outside the scope of this review (e.g., studies on azooxanthellate or non-Scleractinian coral species). International Coral Reef Society Proceedings and other conference proceedings are not included in the Scopus database; therefore, these panels are used to demonstrate the overall acceleration of research in these subfields since 2010 (light-gray shaded region), rather than the absolute number of publications in each area

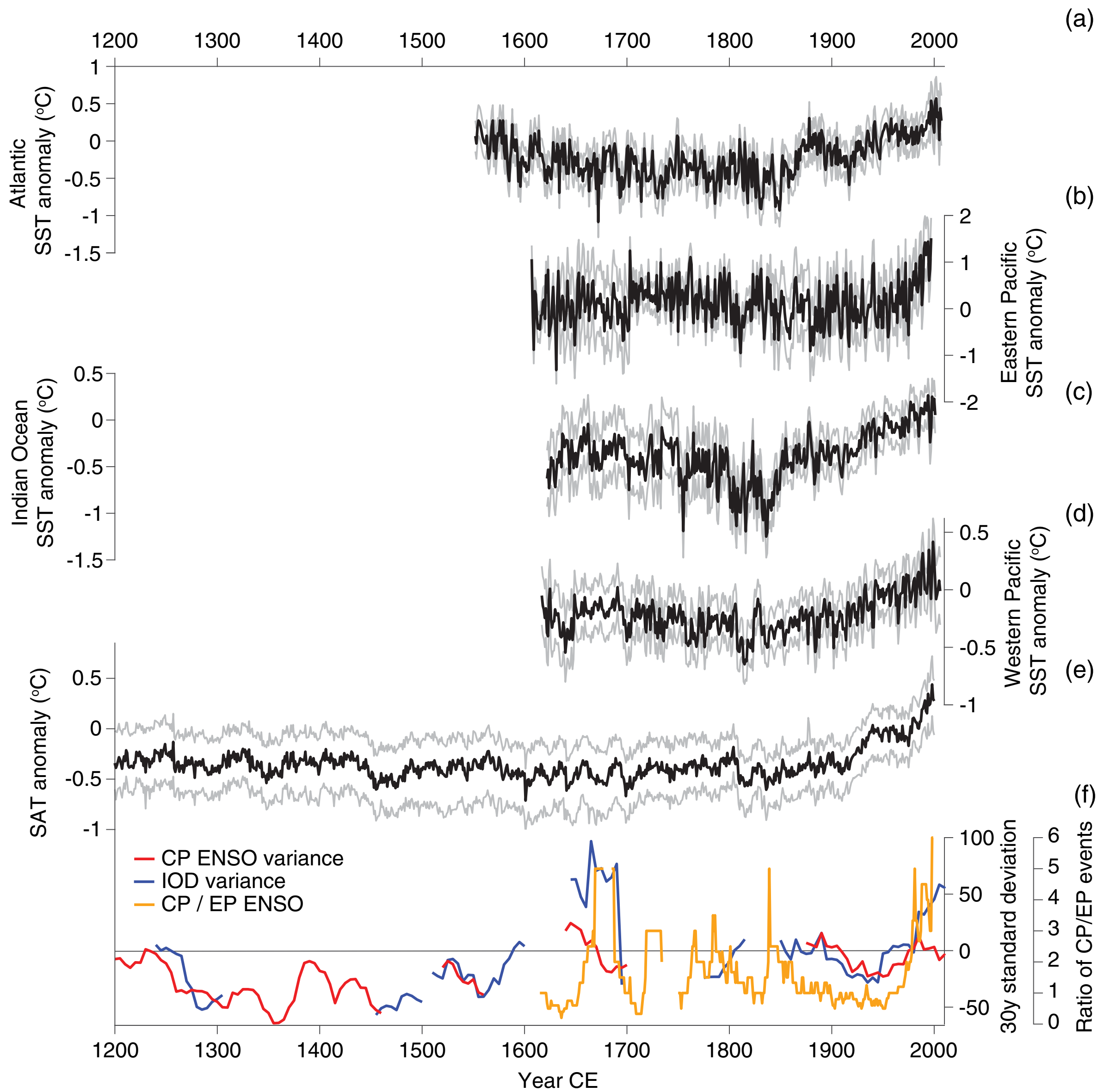

FIGURE 3 Reconstructions of sea surface temperature anomalies (relative to the 1961–1990 reference period) in the (a) western Atlantic Ocean, (b) eastern Pacific Ocean, (c) Indian Ocean, and (d) western Pacific from annual and sub-annually resolved coral records (Tierney et al., 2015), where black denotes the best reconstruction and gray indicates the root mean square error (RMSE). (e) Reconstructed surface air temperature anomalies from the PAGES 2k temperature network (PAGES2k Consortium, 2017). (f) The running 30-year standard deviations of coral-based ENSO (red, Cobb, Charles, Cheng, & Edwards, 2003; Cobb et al., 2013; Grothe et al., 2020) and Indian Ocean Dipole (blue) reconstructions (Abram et al., 2020; axis 1) and the ratio of central Pacific-type to eastern Pacific-type El Niño events (Freund et al., 2019; yellow, axis 2)

climate dynamics (Neukom et al., 2019), and differences in the proxy system itself (e.g., skill in reconstructing ENSO phases, Hereid et al., 2013, and/or the relative role of temperature and $\delta^{18}O_{sw}$ in $\delta^{18}O_{coral}$, Konecky et al., 2020; Russon et al., 2013—see Section 5.1). However, despite the community focus on the Medieval Climate Anomaly (~800–1200 CE) and Little Ice Age (~1300–1850 CE) for understanding the climate system response to natural (solar and volcanic) forcing, reconstructions display little regional coherence (Neukom et al., 2019) and no consistent response of major modes of climate variability between these periods (e.g., ENSO: Dee et al., 2020; Emile-Geay et al., 2013). These compilations emphasize the utility of multiproxy paleoclimate data syntheses, as well as the unprecedented nature of 20th-century warming and its global coherence, relative to the pre-industrial CE.

Additional data coverage across key intervals and well-calibrated, replicated modern records are critical for detecting forced changes within an inherently variable climate system (see Sections 5.1 and 5.2). At sites where long, replicated records exist with coverage across the CE, coherent changes in variability across the Indian and Pacific Oceans has begun to emerge from high background variability (Cobb et al., 2013), with significantly stronger (albeit not yet unprecedented) variability associated with ENSO and IOD in recent decades (Abram et al., 2020; Grothe et al., 2020) (Figure 3). The frequency of CP-type and the magnitude of EP-type ENSO events are also both anomalously high over the last few decades (relative to the last 400 years, Freund et al., 2019) (Figure 3). Ongoing record development and innovative syntheses (Figure 2f) will certainly bring additional constraints on the climate-system sensitivity to internal and external forcing in the coming years.

2.2 | Thermal stress and bleaching

The skeletons of reef-building corals provide essential records of coral growth and reef accretion that can be used to assess the impacts of changing ocean conditions (namely, warming and acidification) on reef health. Advances in methods for quantitative densitometry by X-ray radiography (Anderson et al., 2017; Carricart-Ganivet & Barnes, 2007; Helmle et al., 2002) and computerized tomography (CT, DeCarlo, 2017; DeCarlo, Cohen, et al., 2015; Helmle et al., 2000) permit wholistic assessment of coral growth: skeletal density (g/cm^3), linear extension (cm/year), and calcification (g/cm^2/year, the product of skeletal density and extension). Although such studies have been conducted by gamma densitometry (Lough & Barnes, 1990) for decades (as reviewed by Barnes & Lough, 1996; Lough, 2008, 2010; Lough & Cantin, 2014; Lough & Cooper, 2011), these new approaches permit comparably rapid assessment of multiple tracks along a slab and within 3D coral cores (Figure 2b). Application of these techniques have: (1) determined the effect of warming and ocean acidification (OA) on coral growth (e.g., Cantin et al., 2010; Cooper et al., 2012; Helmle et al., 2011; Mollica et al., 2018; Rippe et al., 2018) and bioerosion (from boring bivalve, worms, and sponges, DeCarlo, Cohen, et al., 2015); (2) identified historical bleaching-related growth anomalies (Barkley et al., 2018; Barkley & Cohen, 2016; Cantin & Lough, 2014; Carilli et al., 2010, 2012; DeCarlo et al., 2019); (3) estimated bleaching susceptibility (e.g., percentage of the coral community bleached, Barkley & Cohen, 2016; Mollica et al., 2018); and (4) assessed reef recovery following disturbance (Cantin & Lough, 2014).

Within individual cores, bleaching events may be identified from an abrupt reduction in linear extension rate (Carilli et al., 2012, 2014), a high-density anomaly ("stress band," after Hudson et al., 1976: Barkley et al., 2018; Barkley & Cohen, 2016; Cantin & Lough, 2014; DeCarlo et al., 2019), and/or a partial mortality scar where part of the coral died and then re-grew following stress (Cantin & Lough, 2014; Carilli et al., 2012; DeCarlo & Cohen, 2017). Studies to date emphasize the unprecedented nature of recent global-scale bleaching events (e.g., Barkley et al., 2018; Cantin et al., 2010; Carilli et al., 2010; DeCarlo & Cohen, 2017), and the role of local human stressors (Carilli et al., 2010) and historical temperature variability (Barkley et al., 2018; Carilli et al., 2012; DeCarlo et al., 2019) in shaping a reef's susceptibility to thermal stress. These results are consistent with observational studies, which demonstrate lower susceptibility to bleaching in areas with high temperature variability (e.g., Donner, 2011; Safaie et al., 2018; Sully et al., 2019; Thompson & van Woesik, 2009). Site-specific responses (even across individual reefs; Barkley & Cohen, 2016; Cantin & Lough, 2014; Castillo et al., 2012; D'Olivo et al., 2013) highlight the need for replicated cores to quantify the community bleaching response, and to separate local- and global-scale drivers of growth variability. Such replication is also critical to ensure that sampling-related artifacts (e.g., the impact of off-axis growth on estimates of linear extension, see Section 3.3) do not lead to incorrect and misleading conclusions (as in Kamenos & Hennige, 2018; see response by Hoegh-Guldberg et al., 2019). In summary, building on a rich history of coral growth studies, the continued expansion and synthesis of coral growth data has improved our understanding of the impact of local and global disturbances on ecosystem health, the differences in susceptibility among reefs, and the trajectory of reef recovery following disturbance.

3 | CONSTRAINING UNCERTAINTIES AND IMPROVING INTERPRETATION

As reviewed here and in previous compilations (e.g., Gagan et al., 2000; Lough, 2010), much of what we know about past ocean change and its effect on coral communities relies on the interpretation of the fossil reef framework (e.g., Dullo, 2005; Toth et al., 2012) or individual coral colonies across time (e.g., De'ath et al., 2012; Lough, 2010). There is a critical need to understand the physical, chemical, and biological processes by which environmental conditions are recorded in the skeletons of reef-building corals to improve the interpretation of coral paleoclimate proxies. Despite major advances in understanding and modeling these processes with proxy system models (PSMs, Evans et al., 2013; Section 5.2), the potential impact of coral biology and physiology on commonly utilized geochemical proxies (i.e., $\delta^{18}O_{coral}$, Sr/Ca, Li/Mg, etc.) has remained poorly understood and under-studied until relatively recently. Furthermore, although there has been a rapid increase in publications on biomineralization processes in recent decades (Tambutté et al., 2011), a disconnect remains between the model species most commonly studied in experimental settings (*Acropora cervicornis*, *Galaxea fascicularis*, *Pocillopora damicornis*, *Favia stelligera*, and *Stylophora pistillata*; Tambutté et al., 2011) and those utilized for paleoclimate reconstructions (namely, massive *Porites* spp., *Diploastrea heliopora*, *Diploria labyrinthiformis*, *Pseudodiploria strigosa*, *Dipsastraea* (*Favia*) *speciosa*, *Orbicella faveolata*, *Pavona clavus*, *Siderastrea siderea*, and *Siderastrea radians*, as reviewed by Sadler et al., 2014). Nevertheless, a few species of branching corals used in biomineralization studies have shown promise for paleoenvironmental applications (*Acropora palmata*, *Acropora nobilis*, *Isopora* spp., *Montipora capitata*, *Pocillopora damicornis*, *Porites cylindrica*, as reviewed by Sadler et al., 2014).

The role of changing environmental conditions on coral growth variations (density, extension, and calcification) in paleo-relevant species has been extensively studied (collectively known as "growth," "kinetic," "metabolic," or "vital" effects, e.g., DeLong et al., 2011; Kuffner et al., 2012; Lough & Cooper, 2011; McConnaughey, 1989; Reed et al., 2018, 2021; Sinclair, 2005; Weber & Woodhead, 1972), particularly following thermal stress and bleaching (Clarke et al., 2017, 2019; D'Olivo & McCulloch, 2017; Hetzinger et al., 2016). Inter-colony and inter-site variations in the Sr/Ca-temperature relationship (Alpert et al., 2016; Sayani et al., 2019) have spawned questions regarding the utility of coral Sr/Ca as a paleothermometer, as well as exploration of alternative paleothermometers such as Li/Mg (Hathorne, Felis, et al., 2013), Δ^{26}Mg (Saenger & Wang, 2014), Rayleigh-based, multi-element (Gaetani et al., 2011; Sinclair 2015), and Sr–U (Alpert et al., 2017; DeCarlo et al., 2016). Each proposed paleothermometer leverages the differential impact of Rayleigh fractionation (Section 3.1, Figure 4) on trace elemental concentrations within the calcifying fluid (hereafter CF) to isolate the climate signal from non-climatic noise. However, these new paleothermometers have uncertainties and limitations (e.g., Sr–U is limited to annual resolution), and these uncertainties have yet to be well constrained with replicated, long reconstructions across species and sites. On the other hand, a growing number of studies have demonstrated reproducibility of δ^{18}O, Sr/Ca, and luminescence across colonies, sites, and even different species and methods (e.g., Allison & Finch, 2009; Cobb, Charles, Cheng, & Edwards, 2003; Cobb, Charles, Cheng, Kastner, & Edwards, 2003; DeLong et al., 2011, 2016; D'Olivo et al., 2018; Grothe et al., 2020; Grove et al., 2012; Grove, Kasper, et al., 2013; Grove, Zinke, et al., 2013; Hendy, 2002; Jimenez et al., 2018; Linsley et al., 2004; Rodriguez-Ramirez et al., 2014; Stephans, 2004), reproducibility which can be further constrained with crossdating approaches and optimal sampling methods (DeLong et al., 2013, 2014; Flannery et al., 2018; Grothe et al., 2020; Sayani et al., 2019). Nevertheless, this debate has motivated studies on the incorporation of geochemical proxies into the coral skeleton during the calcification process. Studies of biomineralization processes using boron isotope systematics (Section 4.1) and mineralogical techniques (Section 4.2) have also improved the interpretation of coral paleoclimate reconstructions, as variability in coral calcification may confound the original climate signal of interest in complex and likely indeterminate ways. This section summarizes advances that have helped reduce uncertainties in coral paleoclimate proxies.

3.1 | Coral growth and biomineralization

Innovations in boron isotope geochemistry, coral densitometry, and mineralogy and crystallography (hereafter "biomineralization tools") have transformed our understanding of the impact of biomineralization and coral physiology on coral paleoclimate records (Figure 2a–d). Particularly when combined, these techniques permit rigorous assessment of the role of CF chemistry, calcification rate, and even aragonite crystal structure (e.g., unit cell parameters) on the incorporation of isotopes and trace elements into the aragonite skeleton (e.g., DeCarlo et al., 2017; Farfan, Apprill, et al., 2018; Farfan, Cordes, et al., 2018), and thus the fidelity of these geochemical proxies. Ultimately, coral biomineralization is modulated by changes in coral physiology, including photosynthesis by zooxanthellae, coral metabolism and dissolved inorganic carbon (DIC) production, energy availability, and the overall health of the coral holobiont (polyp, symbionts, and microbiome) (see Drake et al., 2020; Tambutté et al., 2011, for review of coral biomineralization). For example, these processes are likely responsible for the breakdown in the relationship among many trace elemental proxies and temperature following thermal stress and bleaching (Clarke et al., 2017, 2019; D'Olivo & McCulloch, 2017; Hetzinger et al., 2016), during which time coral extension and CF chemistry are likely disrupted

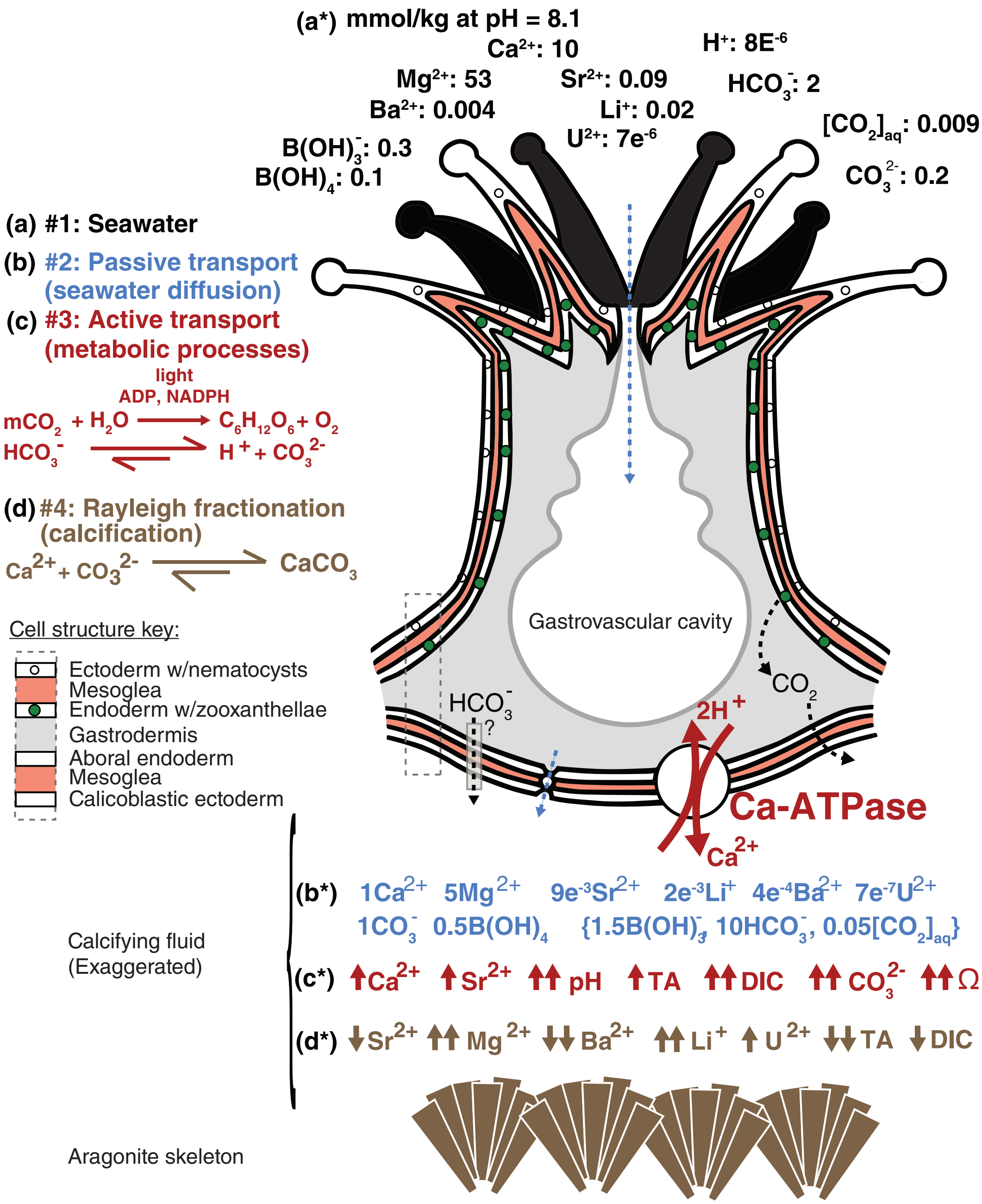

FIGURE 4 Overview of the four main factors impacting the geochemistry of the coral calcifying fluid (CF): (a) seawater chemistry (black); (b) passive transport of ions via diffusion and invaginated vacuoles (blue); (c) active transport via transcellular pathways such as the Ca-ATPase pump, linked to metabolic DIC (mCO_2) and ATP production by respiration and zooxanthellae photosynthesis, respectively (red); and (d) Rayleigh fractionation during calcification (tan). For major cations and anions discussed in the text, the notation is as follows: (a*) concentration in seawater at a pH of 8.1 (in mmol/kg, rounded to one significant figure; values approximate typical open ocean stoichiometry, e.g., Millero, 1974); (b*) as in (a*), due to 1:1 passive transport of ions, but now expressed as stoichiometric ratios with respect to 1 mole of $CaCO_3$ (ions in curly brackets are thought to play a minor role in coral carbonate reactions); (c*) the relative impact of Ca-ATPase pump on the CF geochemistry, where known (Marchitto et al., 2018; McCulloch et al., 2017); (d*) impact of calcification on the concentration of major cations whose substitution for Ca^{2+} is used for paleo proxy(ies), based on the partitioning of each between the fluid and aragonite phases (DeCarlo, Gaetani, et al., 2015; Gonneea et al., 2017; Hathorne, Felis, et al., 2013; Holcomb et al., 2016; Marchitto et al., 2018; Z. Wang et al., 2013). While the stoichiometry of major ions in seawater varies regionally (see Sections 4.4 and 6.1), the relative change in calcifying fluid geochemistry by active and passive transport should respond proportionally to the processes depicted here. DIC, dissolved inorganic carbon; TA, total alkalinity. Diagram not to scale. Polyp artwork by E.V. Reed

(DeCarlo et al., 2017; DeCarlo & Cohen, 2017). Therefore, more routine application of these biomineralization tools alongside geochemical measurements will improve our understanding of non-climatic noise and ultimately improve climate reconstructions from reef-building corals.

Studies to date suggest that there are three main processes (Figure 4b–d) that modulate the geochemistry of the semi-isolated CF from which the aragonite skeleton precipitates during biomineralization (Allemand et al., 2011; Cohen & McConnaughey, 2003; McCulloch et al., 2017). These processes dictate the rate of coral calcification, the geochemistry and crystallography of the aragonite skeleton, and even a coral's sensitivity to changing ocean conditions. In the first process (Figure 4b), paracellular (between cell) diffusion, leakage from the exoskeleton, and/or invaginated vacuoles in the calicoblastic ectoderm (or calicodermis) passively transport seawater to the CF, located between the exoskeleton and the lowermost calicoblastic ectoderm of the coral living tissue (Figure 4). This passive transport mechanism imparts a chemical signature that reflects that of local seawater or the electrochemical gradient relative to the CF (depending on the permeability of the cell junctions, Figure 4b*). In the second process, specific transcellular (through cell) metabolic pathways (Figure 4c) actively transport select ions against the electrochemical gradient, which thereby become concentrated in the CF relative to local seawater (Figure 4c*). Finally, calcification of the aragonite skeleton during biomineralization modifies the geochemistry of the CF via Rayleigh-like fractionation processes (Figure 4d). This fractionation occurs due to the differential partitioning of ions between the CF and the aragonite skeleton during calcification (e.g., DeCarlo, Gaetani, et al., 2015; Gonneea et al., 2017; Holcomb et al., 2016; Marchitto et al., 2018; Wang et al., 2013), whereby certain cations (e.g., Sr, Ba) are preferentially incorporated into the aragonite lattice over others (e.g., Mg, U, Li, Figure 4d*). Due to the semi-isolated nature of this fluid, the impacts of Rayleigh fractionation are thought to be most severe during periods of rapid calcification.

Supersaturation of the CF is essential for rapid growth in these "supercalcifiers," and is tightly regulated during biomineralization by active transcellular ion transport (via the Ca-ATPase pump or other similar pathways that raise the alkalinity of the CF). These active pathways selectively transport calcium, two sodium, or two potassium ions into the CF, while simultaneously removing two hydrogen ions (Ip et al., 1991). By raising the pH of this semi-isolated fluid, this process shifts the balance of DIC to favor the carbonate ion (CO_3^{-}, Figure 4c), further increasing the saturation state (Figure 4c*). These active transport pathways are thought to be most active during the day and times of high energy availability (Cohen & McConnaughey, 2003), as it is fueled by metabolic energy and activated by light (Al-Horani et al., 2003). However, evidence for Ca-ATPase activity during winter months suggests that this process may not be energy limited but instead triggered by low DIC production when cold temperatures and low light limit photosynthetic activity (D'Olivo & McCulloch, 2017; McCulloch et al., 2017; Ross et al., 2017, 2019). This is supported by a strong inverse relationship between DIC_{cf} and pH_{cf} in Australian corals (McCulloch et al., 2017). However, energy availability may become limiting under frequent, extreme, or prolonged thermal stress, particularly in suboptimal and marginal environments. More work is therefore needed to explore the mechanistic links among photosynthetic activity by zooxanthellae, metabolic DIC within the calicoblastic ectoderm, and the transport of metabolic DIC to the CF by active and passive pathways (e.g., Furla et al., 2000; Zoccola et al., 2015). Nevertheless, work to date suggests that the transport stoichiometry of Sr and Ca by the Ca-ATPase pump is likely near 1:1; if this holds over additional studies, variations in Ca-ATPase efficiency are unlikely to contribute non-climatic noise to the Sr/Ca paleothermometer (Allison et al., 2011; Marchitto et al., 2018).

3.2 | Screening for diagenesis

The primary aragonite skeleton and its geochemistry can be reworked by either submarine or subaerial diagenesis. Diagenetic alterations may occur by the precipitation of secondary cement, by the dissolution of the primary aragonite, or by the recrystallization of metastable aragonite to calcite. Secondary cement is commonly observed in submarine environments, even in relatively young corals (as little as 30 years old; Hendy et al., 2007; Sayani et al., 2011), while dissolution with or without recrystallization is common in subaerial environments (e.g., McGregor & Gagan, 2003; Sayani et al., 2011). Although the geochemical signatures of these diagenetic alterations are reasonably well known (Allison et al., 2007; MacIntyre, 1977; McGregor & Gagan, 2003; Nothdurft & Webb, 2009; Obert et al., 2016; Sayani et al., 2011), their impact depends on the extent of the alteration, the geochemistry of the fluid, and whether the reactions occur rapidly and thus exhibit open-system behavior (with insufficient time for isotopes and trace metals to be redistributed during dissolution and recrystallization; James, 1972).

Several standard methods can be used to identify the nature and extent of post-depositional alteration, namely: analysis of petrographic thin sections, (MacIntyre & Towe, 1976), scanning electron microscopy (Bar-Matthews et al., 1993;

James, 1972), and X-ray diffraction (Guilderson et al., 2001; Müller et al., 2001), particularly when utilized in combination (Quinn & Taylor, 2006; Tudhope et al., 2001). However, such alterations may be difficult to avoid with traditional bulk sampling methods and may therefore impact the length (and/or quality) of the resulting paleoclimate reconstructions. Furthermore, these techniques are typically applied at discrete, discontinuous intervals within the coral core and may miss subtle diagenetic alterations, particularly since they are not typically measured on the same samples used for geochemical analysis (although adjacent slices may be used to minimize the distance between the diagenetic assessments and geochemical analyses, Asami et al., 2009). Recent advancements in 2D X-ray diffraction enable rapid, non-destructive identification of secondary calcite at relatively high resolution (4 mm) (Smodej et al., 2015), which may be leveraged to detect and avoid areas of diagenesis before geochemical sampling.

Pristine portions of the aragonite skeleton may be targeted using secondary ion-probe mass spectrometry (SIMS; Allison et al., 2007; Sayani et al., 2011) or LA-ICP-MS (Eggins et al., 2005; Hathorne et al., 2011). These high-resolution geochemical methods have improved our ability to detect and even avoid areas of post-depositional alteration of the coral skeleton. However, such analyses may be confounded by micro-scale variations in skeletal geochemistry that are still not well understood (e.g., Allison & Finch, 2009; Holcomb et al., 2009). Nevertheless, these approaches offer great potential for developing robust reconstructions from altered colonies (extending the spatial and temporal coverage of high-resolution coral records), particularly when combined with continued advances in our understanding of biomineralization and micro-scale variations in the coral skeleton.

3.3 | Subsampling complex skeletal architecture

Advances in 3D visualization tools (e.g., CT scanning), expansion to additional massive coral species, and a focus on replication have led to key method refinements for subsampling the coral skeleton for geochemical measurements. The massive corals targeted for paleoclimate reconstruction are characterized by complex skeletal architecture, growth direction, and corallite orientation that varies among species (DeLong et al., 2013; Reed et al., 2021; Veron, 2000). The impact of major features of growth and skeletal architecture that are visible on X-ray images have long been recognized, particularly: extension rate (Allison & Finch, 2004; Darke & Barnes, 1993; de Villiers et al., 1994, 1995; Goodkin et al., 2007; Grove, Kasper, et al., 2013; Grove, Zinke, et al., 2013; McConnaughey, 1989), growth troughs (Alibert & McCulloch, 1997; Cohen & Hart, 1997; Felis et al., 2000), and biosmoothing within the tissue layer (Barnes et al., 1995; Barnes & Lough, 1993; Gagan et al., 2012; Nothdurft & Webb, 2007; Taylor et al., 1993). In recognition of the potential for growth-related offsets from equilibrium at low linear extension rates (e.g., below ~5–6 mm/year for *Porites* and *Pavona* sp., de Villiers et al., 1994; Felis et al., 2003; McConnaughey, 1989, or below 2 mm/year for *Siderastrea siderea*, Kuffner et al., 2017), corals are routinely cored along a "primary" (typically either horizontal or vertical) growth axis of the coral colony and subsampled perpendicular to the annual density bands along the apex of individual diverging corallite fans (or growth lobes). Although the vast majority of studies utilize the vertical growth axis, robust $\delta^{18}O$ and Sr/Ca records have also been developed along the horizontal growth axis of lagoonal microatolls, whose vertical growth is constrained by sea level (McGregor, Fischer, et al., 2011; Woodroffe & Gagan, 2000; Wu et al., 2013).

The impact of micro-scale variations on geochemical reconstructions is now widely recognized across a wide range of proxies (e.g., Allison et al., 1996, 2001; Allison & Finch, 2009; Allison & Tudhope, 1992; Chalk et al., 2021; Cohen et al., 2001; Holcomb et al., 2009; Meibom et al., 2006, 2008; Rollion-Bard et al., 2003; Watanabe et al., 2007). Differences in geochemical signals between skeleton deposited during the day (fibrous skeleton, also known as fasciculi or thickening deposits) and during the night (centers of calcification, also known as early mineralization zone or rapid accretion deposits) suggest that micro-scale (or even millimeter scale, depending on the species) variations may impact the fidelity of coral paleoclimate reconstructions (Allison et al., 2011; Allison & Finch, 2004; Brahmi et al., 2012; Cohen & McConnaughey, 2003; Giry et al., 2010; Leder et al., 1996). Subsampling techniques typically smooth across these disparate skeletal features, particularly for species with small corallites and fast linear extension rates relative to tissue thickness (Nothdurft & Webb, 2007, e.g., massive *Porites* sp.), producing robust estimates of the underlying climate signal. Nevertheless, considerable improvements in community standards for subsampling and analyzing coral cores collected from massive coral colonies have been developed. These advances have been motivated by: (1) the expansion of traditional techniques to species with larger corallites, distinct centimeter-scale structures, and/or reduced extension rate relative to tissue thickness (and thus greater degree of biosmoothing, Gagan et al., 2012; Nothdurft & Webb, 2007; see Sadler et al., 2014 for a review), (2) expanded application of ultra-high-resolution geochemical analysis (e.g., ion microprobe, SIMS and LA-ICP-MS, Allison et al., 2011; Allison & Finch, 2010; Cohen et al., 2009; Grottoli et al., 2013; Holcomb et al., 2009; Sayani et al., 2011; Sinclair, 2005), and (3) discrepancies among transects from different skeletal elements (Alibert & McCulloch, 1997; Chalk et al., 2021; DeLong et al., 2016; Giry et al., 2010; Leder et al., 1996) or with different corallite orientation (DeLong et al., 2013).

For example, in a seminal study of sampling methods and among-core reproducibility in *Porites lutea* colonies from New Caledonia, DeLong et al. (2013) demonstrated that suboptimal sampling relative to the 3D corallite growth orientation can lead to geochemical artifacts in the Sr/Ca paleothermometer of up to $+2.30°C$ or $-2.45°C$ along paths where the corallite structure was angled or disorganized, respectively. Angled corallites relative to the sampling plane occurs where the primary growth axis is slightly offset from the core and/or slab axis, resulting in corallites that angle into the sampling plane (at angles of up to 90°). This type of suboptimal sampling transect is therefore relatively common, particularly in long cores of lobate species whose growth direction varies through time (e.g., following thermal stress and bleaching or near boreholes). These 3D variations in corallite angle relative to the sampling plane can also lead to biased estimates of extension rate and higher sampling density during the summer months, as the extension rate measured between density bands represents apparent (and anomalously high relative to the true) extension in cases of suboptimal sampling (DeLong et al., 2013). Furthermore, the linear extension may be unaffected by disorganized corallites (DeLong et al., 2013; Reed et al., 2021), leading to inaccurate transect quality assessments based on extension rate variability alone. Indeed, recent work pairing wholistic measures of growth (i.e., density, extension, and calcification) alongside geochemistry demonstrate that density is a more reliable metric than extension rate for identifying the impact of changing saturation state (Mollica et al., 2018) or architecture-related artifacts on coral paleoclimate records (Reed et al., 2018, 2021). Removing data from suboptimal sampling transects may therefore improve the quality of the reconstruction (Reed et al., 2021), emphasizing the importance of paired skeletal density and geochemistry data.

3.4 | Replication and reproducibility

Crossdating of growth increment widths of tree cellulose or carbonate skeletons (corals and bivalve species *Arctica islandica* and *Panopea abrupta*) has been the "gold standard" in the paleoclimate community for decades (Douglass, 1941; Fritts, 1976; Lough & Barnes, 1997; Strom et al., 2004), generating reconstructions virtually free of chronological uncertainties. Despite the proven utility of these methods for growth and luminescence chronologies across vastly different marine archives and environments (e.g., Black et al., 2016, 2019; Cooper et al., 2008; Lough, 2011; Smoliński et al., 2020) and major advances in tools to generate chronologies, applications are often limited by the number of cores available from an individual site or region. Although replication has always been a target of coral paleoclimate studies, a few challenges make it a bit more of an elusive goal than in other annually-resolved archives.

First and foremost, the impact of warming and acidification on the health of the world's reefs has made the preservation of the long-lived, slow-growing ("massive") coral colonies an utmost priority of the coral paleoclimate community. Core holes are routinely filled with cement plugs to protect the coral from bioerosion and to provide a surface upon which the coral can regrow—regrowth that can occur in less than a few years time. Nevertheless, the coral paleoclimate community makes every effort it can to limit these disturbances, as ultimately our work is motivated by the need to understand the impacts of our changing oceans on reef ecosystems.

Other challenges ultimately derive from the time- and resource-intensive nature of finding and developing these records, and it is in these areas where considerable progress has been made. While replication and cross-dating of growth records have been industry standard for some time (e.g., Barnes et al., 2003; Carricart-Ganivet & Barnes, 2007; Helmle et al., 2011; Lough & Barnes, 1997), replication of geochemical records has been more limited by the slow and costly nature of these analyses. Recent advances in instrumentation, methodologies, cleaning techniques, and interlaboratory calibration (particularly for trace elemental proxies, e.g., Fernandez et al., 2011; Hathorne, Gagnon, et al., 2013; Nagtegaal et al., 2012; Schrag, 1999) have greatly improved precision while reducing the time and cost associated with record development. Fortunately, with increased replication of the Sr/Ca and $\delta^{18}O$ paleothermometers, several studies have demonstrated that two records from the same location are typically sufficient to constrain chronological and other among-colony uncertainties (with limited return on investment for further replication, e.g., DeLong et al., 2007, 2013, 2016; Flannery et al., 2017, 2018). Nevertheless, additional replication may be beneficial where suboptimal transect qualities are present (e.g., DeLong et al., 2013; Reed et al., 2021).

There is a growing number of highly replicated and even crossdated temperature, salinity, and growth reconstructions from subannually resolved corals (e.g., Carilli et al., 2012; Cobb et al., 2013; Dassié et al., 2014; Dassié &

Linsley, 2015; DeLong et al., 2011, 2012, 2013, 2014; Flannery et al., 2017, 2018; Grothe et al., 2020; Hendy, 2002; Linsley et al., 1999, p. 199; Pfeiffer et al., 2009; Sayani et al., 2019; Wu et al., 2013, 2014; Zinke et al., 2014; Zinke, Hoell, et al., 2015; Zinke, Loveday, et al., 2015). Years of laborious exploration of remote areas have further extended the temporal coverage and replication of pre-industrial climate information from sub-fossil coral colonies (e.g., Abram et al., 2020; Cobb et al., 2013; DeLong et al., 2010; Felis et al., 2014; Grothe et al., 2020; Leupold et al., 2021; McGregor et al., 2013; Sayani et al., 2019; Woodroffe et al., 2012). Several studies have also leveraged the spatial coherence and decorrelation length scale characteristic of major modes of oceanic variability to develop regional composites and syntheses of the rapidly expanding network of published records (e.g., Dassié et al., 2018; Gorman et al., 2012; Konecky et al., 2020; Linsley et al., 2015; Tierney et al., 2015).

Replication and crossdating are essential for reducing the errors of reconstruction (DeLong et al., 2013), constraining estimates of chronological errors (i.e., missing or doubly counting growth bands, Comboul et al., 2014; DeLong et al., 2013), and reducing the impact of chronological uncertainties and non-climatic noise on interannual to decadal coherence among records (Black et al., 2019; Comboul et al., 2014; Loope, Thompson, Cole, & Overpeck, 2020). Additional replication may be particularly valuable in undersampled regions (e.g., eastern equatorial Pacific, see Figure 3b) that are likely to have a disproportionate impact on reconstruction statistics (Comboul et al., 2015), and should remain a high priority of the community. Authors are also encouraged to archive their raw data versus depth and age-depth models (Section 3.5) so that new replicated, cross-dated reconstructions can be generated as the network of high-resolution coral geochemical records expands.

3.5 | Geochronology and age-model development

The growing network of fossil corals with which to reconstruct tropical–subtropical climate has propelled advances in both rapid-screening and high-precision techniques for radiometric dating of geologically young marine carbonates. Rapid-screening techniques are essential for identifying the best targets for paleoclimate reconstruction among clusters of wave, cyclone, or tsunami-swept coral boulders, while high-precision techniques are essential for splicing floating chronologies and constraining chronological errors in the resulting reconstructions. Both techniques have leveraged advances in both sample preparation and instrumentation, which have improved the efficiency, cost, and precision of dating fossil coral material.

U/Th dating by multicollector inductively coupled plasma mass spectrometry (MC-ICP-MS) has become the gold standard for high-precision dating of coral sub-fossil material. Methodological advances over the past few decades (i.e., since Edwards et al., 1987; Shen et al., 2008, 2012) have improved the efficiency of U/Th dating of corals by orders of magnitude, with unparalleled uncertainties (e.g., 2σ errors of 0.1% for samples formed within the last 10,000 years) and smaller sample size requirements (Cheng et al., 2013; see reviews by Dutton, 2015; Edwards, 2003; Hellstrom & Pickering, 2015). However, a few critical assumptions of the U–Th geochronometer may add considerable uncertainties under certain conditions.

First, many different processes may lead to non-negligible initial ^{230}Th and substantial variability among reefs in ^{230}Th/^{232}Th ratios (used to correct for this effect from a sample's ^{232}Th). For example, a significant contribution of detrital material, wind-blown dust, deep-water intrusion, or carbonate substrate may elevate initial ^{230}Th (Cobb, Charles, Cheng, Kastner, & Edwards, 2003; Robinson et al., 2004; Shen et al., 2008). Contamination during sample collection and preparation also contributes ^{230}Th, though advances in procedural blanks have reduced this error considerably (to an age uncertainty of $\pm$0.2 years for 1 g of coral sample, Shen et al., 2008). Reef-scale constraints on ^{230}Th/^{232}Th ratios have been obtained using isochron techniques on coeval samples with differing Th/U ratios (Bischoff & Fitzpatrick, 1991; Shen et al., 2008) or by using independent age constraints from band counting or correlations across individually dated segments (Clark et al., 2012; Cobb, Charles, Cheng, Kastner, & Edwards, 2003; McCulloch & Mortimer, 2008; Shen et al., 2008; Yu et al., 2006). Application of local ^{230}Th/^{232}Th ratios rather than the conservative bulk earth value may substantially reduce age uncertainties (particularly in young samples, in which initial ^{230}Th has a proportionally large impact, Clark et al., 2012; Shen et al., 2008); such constraints should therefore remain a high-priority for future work.

The second main uncertainty stems from the potential for open-system behavior (e.g., Obert et al., 2016), which increases with sample age as a function of exposure and the likelihood of diagenetic alteration (though it may also occur in young samples). Models of open-system behavior (e.g., Scholz & Mangini, 2007; Thompson et al., 2003) may be used to correct the U/Th ages of altered samples, but should be utilized only if multiple subsamples or corals from a given site have ^{230}Th–^{234}U–^{238}U values that are consistent with model predictions and if the initial value of ^{234}U/^{238}U of seawater is known (as reviewed by Hibbert et al., 2016). However, the processes behind and therefore impact of open-system alteration are complex and likely site or even sample-specific; therefore, the wide-spread utility of these models remains debated (Hibbert et al., 2016; Obert et al., 2016). Alternatively, samples may be screened for open-system alteration using benchmarks or accepted thresholds of ^{238}U relative to modern corals, initial ^{234}U/^{238}U relative to modern seawater, sufficiently low ^{232}Th concentration, and sufficiently low proportion of secondary calcite (Hibbert et al., 2016). However, these commonly utilized criteria may fail to identify cases of open-system alteration (e.g., Obert et al., 2016); in such cases, combining isotope systems (e.g., ^{230}Th/U and ^{231}Pa/U over the past 250,000 years) has proven useful for the identification of open-system behavior, assessing its spatio-temporal patterns, and improving age constraints (Edwards, 2003; Obert et al., 2019).

Finally, considerable progress has been made on the development and application of rapid-screening techniques to date large quantities of fossil coral samples. Several approaches have considerably increased sample throughput, including U/Th dating by laser ablation multi-collector inductively coupled plasma mass spectrometry (LA MC-ICPMS) (Eggins et al., 2005; McGregor, Hellstrom, et al., 2011; Potter et al., 2005) or inductively coupled plasma-quadruple mass spectrometry (ICP-QMS) (Douville et al., 2010), and direct high-precision ^{14}C dating of carbonate powders via accelerator mass spectrometry (AMS) (Bush et al., 2013; Grothe et al., 2016). Although the LA MC-ICPMS and ^{14}C-AMS techniques have proven successful at accurately dating large quantities of fossil corals (Grothe et al., 2016; McGregor, Hellstrom, et al., 2011), these methods suffer from comparatively large uncertainties and greater susceptibility to diagenetic alteration, relative to high-precision U/Th dating by MC-ICP-MS. For example, U/Th dating by LA MC-ICPMS may produce prohibitive dating uncertainties of up to 15% (2σ) for samples older than 3000 years old, and errors as large as 33% (2σ) or more for younger samples (Eggins et al., 2005; McGregor, Hellstrom, et al., 2011). Furthermore, McGregor, Hellstrom, et al. (2011) found that subtle diagenetic alteration may not be detected using this method, and therefore recommend that it is paired with other screening methods (i.e., thin section, SEM, and XRD analysis). In comparison, rapid ^{14}C dating of mildly altered samples (<2% calcite) produced uncertainties of 100–200 years and 200–300 years (2σ) in last millennium and mid-Holocene aged samples, respectively (Grothe et al., 2016). However, this technique is more sensitive to diagenetic calcite alteration, as ^{14}C is readily exchanged with the atmosphere during calcite precipitation (Burr et al., 1992). Furthermore, additional uncertainties may occur across plateaus in the radiocarbon calibration curve and due to variations in the ocean reservoir age associated with changes in upwelling or ocean circulation on centennial to millennial timescales (Grothe et al., 2016). Taken together, these studies demonstrate considerable advances in radiometric dating of fossil corals, while leaving many opportunities for further advances over the coming years.

3.6 | Calibration and validation

Another source of uncertainty arises from the calibration methods that assess the numerical relationship of the proxy to climate, which can be subsequently inverted to reconstruct the climate signal of interest. Challenges related to proxy calibration are primarily twofold: those related to instrumental or target data and its quality, and those related to the calibration methodology. First, the paucity of local instrumental sea-surface temperature (SST) and salinity (SSS) data for calibration of the coral Sr/Ca and δ^{18}O thermometers can add considerable uncertainty to the resulting temperature and salinity reconstructions from data-poor regions. This problem is exacerbated for proxies recording other components of the coupled ocean–atmosphere climate system that are even less commonly observed (e.g., Mn/Ca-based wind proxy or the Ba/Ca-based runoff proxy, Section 4.4). In data-poor regions, the magnitude and even sign of 20th-century trends and interannual anomalies differ substantially among available observational products (e.g., SSTs in the eastern equatorial Pacific, Deser et al., 2010, or zonal wind anomalies, Thompson et al., 2015). Furthermore, even in the most well-observed regions, the length of reliable observations may limit the validation/verification interval retained to assess the errors of reconstruction (Crowley et al., 1999). Nevertheless, expansion of in situ monitoring near coral collection sites (e.g., Cahyarini et al., 2014; DeLong et al., 2011) and advances in historical (e.g., IAP, Cheng et al., 2020; Delcroix, Delcroix et al., 2011; EN4, Good et al., 2013) and reanalysis (e.g., SODA3, Carton et al., 2018; ERA5, Hersbach et al., 2020; 20th Century Reanalysis, Compo et al., 2011) products have constrained some of these uncertainties. In particular, major efforts have focused on the identification and quantification of error and bias (i.e., systemic errors) in SST and SSS data (e.g., Huang et al., 2017; Kennedy, 2014; Kennedy et al., 2011; Pfeiffer et al., 2017).

Instrumental error estimates have improved calibration methodologies utilized to relate proxy data to the climate signal(s) of interest, with reduced major axis (RMA; Clarke, 1980) or weighted least squares (WLS; York et al., 2004) regression (both of which consider errors in the proxy predictand and the climate predictor) increasingly applied over the traditional ordinary least squares regression (OLS, which only considers errors in the proxy predictand and is sensitive to predictor errors, e.g., Ammann et al., 2010). RMA and WLS differ in the way they handle these errors (see Thirumalai et al., 2011; Wehr & Saleska, 2017; Xu et al., 2015 for reviews of these techniques), with WLS having superior performance in cases (as in proxy calibration) where the errors are correlated (York et al., 2004) and is thus the recommended calibration method. While the limitations of OLS regression for calibrating paleoclimate proxies have been proposed for some time (DeLong et al., 2007; Solow & Huppert, 2004), new within and among site comparisons have highlighted the significant impact these methodological choices have on the resulting calibration equation (Xu et al., 2015). Recent work applying the WLS approach to Sr/Ca and Li/Mg across multiple sites suggests that a universal calibration may be developed, circumventing site-specific vital effects (D'Olivo et al., 2018). New toolboxes (e.g., Thirumalai et al., 2011) have also aided the expansion of these regression techniques to an increasing number of records. Nevertheless, there are still large discrepancies across studies in calibration datasets and methods utilized, discrepancies that likely contribute to the spread of calibration slopes across published studies and compilations (e.g., Corrège, 2006; Gagan et al., 2012). Therefore, assessment and standardization of calibration methodologies should be a priority of the coral paleoclimate community moving forward.

4 | NOVEL METHODS AND PROXIES FROM CORAL ARCHIVES

This section highlights innovative approaches that can have expanded or improved the climate information extracted from coral archives.

4.1 | Boron isotope systematics: pH_{sw} and CF geochemistry

Boron isotope systematics have provided new insights into paleo-pH and the carbonate chemistry of the coral CF (Figure 2d). Three key features of boron systematics permit simultaneous analysis of pH and carbonate ion concentration from paired B/Ca and boron isotope ratios (see DeCarlo, Holcomb, & McCulloch, 2018 for a review). First, boron speciation is strongly dependent on pH, with a greater abundance of the borate ion ($B(OH)_4^-$) under higher pH, and a greater abundance of boric acid ($B(OH)_3$) under lower pH. Second, $\delta^{11}B$ is +27 permil higher in boric acid than borate, indicating that boron isotopes are strongly fractionated between these species. Therefore, as the ocean acidifies, $\delta^{11}B$ becomes more positive as the proportion of boric acid increases. Third, borate can substitute for the carbonate ion in the aragonite skeleton emplaced from the semi-isolated coral CF. Recent inorganic precipitation studies suggest that this most likely occurs via de-protonation and co-precipitation with CO_3^- (McCulloch et al., 2017), rather than via bicarbonate or a mixture of the two (as previously proposed by Allison et al., 2014). However, there are multiple pathways by which this could occur, and the species and transport pathways of DIC to the CF are still active areas of research (Furla et al., 2000; Zoccola et al., 2015). Furthermore, despite recent constraints on the partitioning of B/Ca between the fluid and skeleton (i.e., the partition or distribution coefficient K_D, Gaetani & Cohen, 2006; Kinsman & Holland, 1969)—constraints which are essential for the joint reconstructions of pH and carbonate ion from boron systematics (Holcomb et al., 2016; McCulloch et al., 2017)—differences among the proposed formulations add uncertainties to the resulting reconstructions (DeCarlo, Holcomb, & McCulloch, 2018). Additional uncertainties in boron-based CF reconstructions may stem from changes in the $\delta^{11}B$ and total boron concentration of the CF relative to seawater under certain conditions (e.g., deep-water corals, Gagnon et al. 2021). Additional inorganic precipitation and physiological studies with symbiont-bearing species are therefore critical, as these uncertainties can lead to grossly different conclusions regarding the susceptibility of corals to OA (e.g., Allison et al., 2014; McCulloch et al., 2017).

Although the $\delta^{11}B$ proxy was originally interpreted as a proxy for seawater pH (pH_{sw}) (Vengosh et al., 1991), recent work has demonstrated large changes in the pH of the coral CF (pH_{cf}) in response to seasonal changes in temperature and metabolic DIC availability. When cold temperatures and low light availability cause a drop in metabolic (i.e., respiratory) DIC and aragonite saturation (Ω) during the winter months, corals upregulate pH_{cf} via the Ca-ATPase pump (and/or other alkalinity pumps, see Section 3.1, Figure 4; D'Olivo & McCulloch, 2017; McCulloch et al., 2012, 2017; Ross et al., 2017, 2019; Venn et al., 2011). Some species may also regulate [Ca^{2+}] (DeCarlo, Holcomb, &

McCulloch, 2018), though Ca regulation is not as well understood. Corals thereby maintain a nearly constant Ω_{cf} and calcification despite large temperature-induced changes in calcification kinetics and buffering capacity (Guo, 2019), as well as light-induced changes in photosynthetic activity and metabolic DIC (D'Olivo & McCulloch, 2017; McCulloch et al., 2017; Ross et al., 2017, 2019). Such pH "homeostasis" may therefore allow corals to maintain calcification across large natural acidification gradients or under acidification (Barkley et al., 2015, 2017; Fabricius et al., 2011; Georgiou et al., 2015; Shamberger et al., 2014; Wall et al., 2016, 2019).

While physiological processes dominate pH_{cf} variability on seasonal timescales, long-term trends are primarily driven by changes in pH_{sw} associated with OA (D'Olivo et al., 2019). Relative changes in pH_{cf} across periods may therefore still serve as a robust proxy of paleo-pH, though more work is needed to deconvolve these two important drivers across sites and timescales. Extension of these techniques to suboptimal or marginal environments (e.g., CO_2 seeps, eastern equatorial Pacific, and other naturally low-pH sites, e.g., Wall et al., 2016, 2019) and pre-industrial periods using fossil corals would further constrain boron-based pH_{sw} estimates. Nevertheless, these studies have greatly improved our understanding of the role of coral physiology in the biomineralization processes, and have constrained estimates of pH and coral calcification under changing ocean conditions.

4.2 | Mineralogy and crystallography

Additional key insights into biomineralization processes have been obtained from recent innovative studies on the mineralogy and crystallography of (biogenic and abiogenic) aragonite precipitated under a range of environmental conditions (Figure 2a). For example, X-ray diffraction (XRD) and Raman spectroscopy may provide independent constraints on Ω_{cf} (DeCarlo et al., 2017; Farfan, Cordes, et al., 2018), complementing those obtained from boron systematics. Such independent estimates are critical, as boron-based Ω_{cf} estimates assume that $[Ca]^{2+}$ of the CF remains similar to that of seawater. This assumption may break down after thermal stress and bleaching (Clarke et al., 2017; D'Olivo & McCulloch, 2017) due to a decrease in Ca^{2+} transport into the CF (via Ca channels or Ca-ATPase, Section 3.1, Figure 4). Furthermore, the crystal structure of these biominerals likely dictates coral reef form and function under an acidifying ocean, as it determines the solubility and strength of the coral skeletons (Farfan, Cordes, et al., 2018; Hennige et al., 2015). Finally, such changes in the crystal structure may occur without any detectable changes in morphology (Coronado et al., 2019; Farfan, Cordes, et al., 2018), emphasizing the importance of more routine investigations of crystallography in coral paleoclimate studies.

The potential of Raman spectroscopy for constraining ($[CO_3]^{2-}$ or $[Ca]^{2+}$-related) changes in Ω_{cf} was illustrated in a recent study of synthetic (abiogenic) aragonite minerals. DeCarlo et al. (2017) demonstrate that positional disorder of the carbonate ion (i.e., rotation out of the basal plane) within the aragonite lattice increased with aragonite saturation state (Ω_{ar}) of the solution. In disordered crystals, the length of the C—O bond increases, impacting both the strength and vibrational frequency of the molecular bonds. In turn, these changes increase the width of the bond's frequency peak (ν_1, between 1080 and 1100 cm^{-1}) in the Raman spectrum, measured as the peak width at half maximum intensity (or "full width at half maximum," FWHM, DeCarlo et al., 2017). Similarly, using quantitative estimates of unit cell parameters (*a*-, *b*-, and *c*-axis length and cell volume) from fitting whole-pattern Rietveld refinements to XRD patterns, Farfan, Cordes, et al. (2018) demonstrate a relationship between Ω_{ar} and unit cell volume due to anisotropic lengthening along the *b*-axis (a relationship which may be nonlinear, Coronado et al., 2019). If these relationships hold across additional biogenic aragonite samples and a variety of environmental conditions, estimates of unit cell volume and FWHM may therefore be used to reconstruct Ω_{ar} of seawater or the semi-isolated CF (Ω_{cf}, in the case of reef-building corals) from which the crystals precipitate. Disagreements between Raman (DeCarlo et al., 2017) and boron-derived (D'Olivo & McCulloch, 2017) estimates of Ω_{cf} following thermal stress and bleaching emphasize the critical importance of such independent (geochemical and mineralogical) estimates of Ω_{cf} variability, its controls, and its stability across changing ocean conditions.

High Ω_{cf} may lead to increased crystal disorder (FWHM) and unit cell volumes due to rapid calcification, due to incorporation of trace elemental (TE) impurities, or due to TE/Ca substitutions. Although work-to-date suggests a minimal impact of TE impurities (e.g., Mg/Ca or Sr/Ca) on either FWHM or unit cell volumes (DeCarlo et al., 2017; Farfan, Cordes, et al., 2018), increased Ba^{2+} substitution may lead to increased crystallographic disorder (Farfan, Cordes, et al., 2018; Mavromatis et al., 2018). These results suggest that the ionic radius of TE substitutions may play a role in aragonite crystallography, and/or that Ω_{cf} may control the incorporation of TE/Ca proxies under certain environmental conditions. Therefore, additional interdisciplinary studies combining XRD and Raman spectroscopy with geochemical data have tremendous potential to improve our understanding of the links among seawater conditions, CF chemistry, skeletal geochemistry, and crystallography. Such studies are critical for constraining uncertainties surrounding biomineralization and its impact on geochemical proxies, as well as for constraining estimates for the susceptibility of corals to OA.

Finally, Raman spectroscopy has also provided key insights into the ultimate source of skeletal organic matter (SOM), which is thought to serve as the nucleus for calcification during biomineralization (Mass et al., 2013) and may also play a role in the supersaturation of the CF (as reviewed by Tambutté et al., 2011). The extent to which SOM is sourced from seawater and trapped by the growing crystals (e.g., Benzerara et al., 2011) or derived from the coral polyp (e.g., Von Euw et al., 2017) has been debated, as it has large implications for the extent to which corals can mediate calcification across a range of environmental conditions (as reviewed by Tambutté et al., 2011). Initial crystallographic studies on corals and mollusks hypothesized that the unit cell anisotropy of these bioaragonites was caused by the incorporation of biomolecules (although abiotic factors may also contribute) (Pokroy et al., 2004, 2006). Using Raman spectroscopy, DeCarlo, Ren, and Farfan (2018) demonstrate that there is no significant difference in the C—H bond signal of biogenic and abiogenic aragonite minerals, suggesting that the SOM is not unique to biogenic aragonite and may be trapped during calcification (rather than produced by the coral polyp itself). Similarly, Holcomb et al. (2009) note that the morphology of synthetic aragonite precipitated from seawater without a SOM matrix is remarkably similar to that of aragonite acicular needles in coral dissepiments. These results suggest that although SOM may play a critical role in crystal nucleation, seawater temperature and aragonite saturation likely dictate calcification of the bulk of the skeletal material (DeCarlo, Ren, & Farfan, 2018). Such detailed crystallographic studies may therefore reconcile evidence for biological mediation of calcifying surfaces (e.g., via SOM nucleation, increased porosity, and/or surface area: volume ratios in the complex 3D structure; Barnes, 1970; Cohen et al., 2009; Foster & Clode, 2016; Tambutté et al., 2015), with observations of reduced net calcification rates with OA (e.g., Chan & Connolly, 2013). Nevertheless, future work expanding these approaches to suboptimal environments (e.g., upwelling zones, and CO_2 seeps) and to extreme events may help elucidate the limits and costs of biologically mediated calcification processes across a range of environmental conditions.

4.3 | Coral stable nitrogen isotopes

The past decade has brought major advances in our understanding of and ability to measure the nitrogen isotopic composition of the scleractinian coral skeletal organic matrix (hereafter "CS-δ^{15}N," Figure 2e). Since the initial development and early applications of CS-δ^{15}N (e.g., Hoegh-Guldberg et al., 2004; Marion et al., 2005; Muscatine et al., 2005; Ward-Paige et al., 2005), records collected from both scleractinian and gorgonian corals have provided critical insights into the role of anthropogenic nitrogen sources on coral reef ecosystems (Baker et al., 2010, 2013; Erler et al., 2020; Ren et al., 2017; Sherwood et al., 2010; Yamazaki et al., 2011) and their impact on eutrophication (Duprey et al., 2020), disease prevalence and severity (Redding et al., 2013), and coral trophic status (i.e., degree of autotrophy vs. heterotrophic vs. mixotrophy; Erler et al., 2015; Wang et al., 2015). In contrast to most other marine carbonate proxies, which measure the inorganic components of the aragonite (or calcite) mineral skeleton, CS-δ^{15}N is measured on the organic matrix that is thought to serve as the nucleus for calcification during biomineralization (Mass et al., 2013). However, because this organic matrix comprises a small fraction of the skeletal material, early applications of this novel proxy required large samples (Marion et al., 2005; Muscatine et al., 2005), limiting the temporal resolution of the resulting reconstructions. Improvements to the method permit analysis of smaller samples, but many approaches suffer from limited analytical precision (Uchida et al., 2008; Yamazaki et al., 2011, 2013). Building off of a protocol developed for δ^{15}N of organic matter trapped within foraminifera tests (Ren et al., 2012), Wang et al. (2015) developed a new method that has greatly improved both the precision and sample size requirements. These methodological improvements permit CS-δ^{15}N analysis on 5–10 mg of the coral skeleton with a reproducibility of 0.2‰ (1σ, Wang et al., 2015), thereby greatly expanding the utility of this proxy for assessing nitrogen dynamics on coral reefs.

There are several pathways by which CS-δ^{15}N may be altered by natural and anthropogenic processes, leading to significant uncertainties in the interpretation of CS-δ^{15}N variability and trends in systems with complex trade-offs among N sources and/or insufficient baseline measurements before and during anthropogenic alteration of the system. CS-δ^{15}N records are typically interpreted to reflect the δ^{15}N of the inorganic and particulate nitrogen sources in seawater, reflecting more positive δ^{15}N from sewage waste-water effluent (Baker et al., 2013; Duprey et al., 2017, 2020; Redding et al., 2013), or more negative δ^{15}N from agricultural fertilizers (Baker et al., 2010; Marion et al., 2005;

Yamazaki et al., 2011), increased N fixation (Erler et al., 2020; Sherwood et al., 2010), or wet deposition of anthropogenic N from the atmosphere (as a result of fossil fuel burning, Ren et al., 2017; Sherwood et al., 2010). These human activities have led to an estimated 90% increase in bioavailable N globally (Ocean Sciences Board & National Research Council, 2000), a trend that has likely played a role in the degradation of reef ecosystems (Duprey et al., 2020). These impacts are particularly severe near major population centers (Duprey et al., 2020) and tourist destinations (Baker et al., 2013) with poor or unreliable wastewater treatment and wet climates, though anthropogenic N has also been detected on remote oceanic atolls far from N point sources (Ren et al., 2017). However, mixing of isotopically different nitrogen sources may mask anthropogenic impacts on reef systems, leading to erroneous conclusions and delayed management action. Furthermore, CS-δ^{15}N may be altered by changes in upwelling, the trophic food web (Lorrain et al., 2017; Sherwood et al., 2011), N cycling within the coral-zooxanthellae symbiosis (e.g., ammonium "leakage" vs. recycling as a function of feeding rate and availability of DIN sources, Erler et al., 2015; Wang et al., 2015), and/or contamination by non-coral derived organic nitrogen (e.g., if the skeleton is insufficiently cleaned, Erler et al., 2016; however, this is no longer an issue with the latest cleaning methods). These studies emphasize the need for long CS-δ^{15}N records that extend before human impact (e.g., Erler et al., 2016), as well as the need for additional paired δ^{15}N data for coral tissue, zooxanthellae, and source N across species and sites (e.g., Conti-Jerpe et al., 2020; Nahon et al., 2013) to improve mixing models (Baker et al., 2013) and thus the interpretation of CS-δ^{15}N records.

The development of reliable analytical methods for CS-δ^{15}N analyses over the last decades has paved the way for entirely new fields of investigation. For example, if confirmed by other studies, the confounding signal imparted by changes in the coral-zooxanthellae symbiosis may be leveraged as a proxy for bleaching, wherein an increase in heterotrophy (relative to photosynthesis) results in more positive CS-δ^{15}N (as less N is recycled by zooxanthellae and isotopically light ammonium is instead excreted). CS-δ^{15}N records are therefore likely to produce additional insights into the impact of both warming and eutrophication in the coming years.

4.4 | Novel coral proxies of episodic climate events

This section highlights promising new proxies for episodic events in the climate system, whose behavior presents additional challenges for replication and interpretation (Section 3). Nevertheless, significant progress has been made, and these promising proxies should be investigated further at additional sites in the coming years.

First, as reviewed by Saha et al. (2016) there has been rapid expansion and refinement of proxies for upwelling (Grottoli et al., 2013; LaVigne et al., 2010, 2016; Watanabe et al., 2017), runoff/river discharge (Brenner et al., 2017; Chen et al., 2020; Grove et al., 2012; Kaushal et al., 2020, 2021; LaVigne et al., 2016; Maina et al., 2012; Saha et al., 2018), and/or sediment flux on to the reef (Carriquiry & Horta-Puga, 2010; Fleitmann et al., 2007; Ito et al., 2020; Mallela et al., 2013; Prouty et al., 2010; Tanzil et al., 2019) from elements with nutrient-like profiles in the water column (Ba/Ca, P/Ca, Y/Ca, Cd/Ca, δ^{13}C) and from skeletal luminescence. For example, while Ba/Ca proxy has been widely applied for some time, the interpretation of these records has varied greatly among sites. An increased focus on replication (Section 3.2) and seawater sampling (Section 6.1) has permitted the first calibrations and quantitative reconstructions from this proxy, while also emphasizing the critical need for species- and site-specific calibration and replication (LaVigne et al., 2016; Tanzil et al., 2019; Weerabaddana et al., 2021). Disagreements among records within sites suggest that other factors may influence the Ba/Ca proxy, such as the incorporation of the large Ba ion into the aragonite lattice during biomineralization (Farfan, Cordes, et al., 2018; Section 4.2) or the spatio-temporal pattern of discharge, TE geochemistry, and sediment availability (Lewis et al., 2018; Saha et al., 2018). In parallel, P/Ca (first proposed by LaVigne et al., 2008; Montagna, 2006) shows considerable promise as a novel proxy for upwelling (LaVigne et al., 2010) and runoff-related phosphate loading (Mallela et al., 2013) on coral reefs. P/Ca may therefore provide critical insights into upwelling and eutrophication and their impact on coral growth (e.g., Montaggioni et al., 2006). Finally, a robust, reproducible luminescence signal has been identified among cores within a watershed due to the conservative behavior of humic acids in seawater, particularly when separated from the density-related signal (Grove et al., 2010, 2012). Furthermore, the strong link between skeletal luminescence, humic acid abundance, and light-absorbent (chromophoric) dissolved organic matter suggests that luminescence records may provide insights into terrestrial carbon fluxes and their impact on coastal productivity (Kaushal et al., 2020, 2021). Luminescence records are also non-destructive and may be less susceptible to non-climatic, low-frequency (red) noise characteristic of other geochemical proxies (Loope, Thompson, Cole, & Overpeck, 2020). Taken together, these studies demonstrate considerable promise for the reconstruction of biogeochemical cycling and nutrient dynamics on coral reefs and emphasize the utility of a multi-proxy approach, replication, and seawater sampling for constraining uncertainties (Grove et al., 2012; LaVigne et al., 2016; Lewis et al., 2018).

Second, in growing recognition of the importance of the Pacific Walker circulation and trade-wind variations in global climate (England et al., 2014; Kosaka & Xie, 2013; L'Heureux et al., 2013; Peyser et al., 2016), a novel Mn/Ca proxy for trade-wind variability (first developed at Tarawa Atoll by Shen et al., 1992) has been further expanded to study long-term wind variations across the 20th century (Thompson et al., 2015). Recent work has also tested the utility of this proxy at other sites with west-facing lagoons both east and west of the dateline (Sayani et al., 2021). At such sites, manganese from wind-blown dust accumulates under reducing conditions in the lagoonal sediments and pore-waters. During westerly wind events (that initiate and sustain ENSO events, Vecchi & Harrison, 2000) this Mn reservoir is remobilized into seawater, where it may be transported to the reef and incorporated into coral aragonite during biomineralization. Despite the complexities of this proposed mechanism, Sayani et al. (2021) demonstrate that the fidelity of this proxy in capturing westerly wind events at two new sites (Butaritari and Kiritimati Atolls), laying the groundwork and methods for this approach to be extended to additional sites. Thompson et al. (2015) demonstrated that decadal changes in reconstructed wind strength contributed to periods of both accelerated and reduced warming over the last century. Nevertheless, complexities in the timing and magnitude of the Mn/Ca-wind signal among sites (Sayani et al., 2021) emphasize the need for replication, as well as further studies into the processes by which Mn is mixed and transported among its key reservoirs. This proxy holds great potential for improving our understanding of trade-wind variations and their role in global climate change.

5 | ADVANCES IN PROXY DATA—CLIMATE MODEL SYNTHESIS

5.1 | Proxy system modeling and paleo-data assimilation

Paleoclimate reconstructions are usually developed from paleoclimate archives in the inverse sense: that is the (modern) relationship between the proxy record and climate is inverted to reconstruct past climate from the proxy archive back through time. However, this approach is limited by uncertainties in the paleoclimate data and the proxy-climate calibration, which may be nonlinear, non-stationary, and indeterminate. These problems may be addressed by modeling the proxy record in the forward sense: that is modeling the proxy record from the climate using a PSM (Evans et al., 2013). PSMs represent all the physical, chemical, biological, and/or geological processes by which the climate is translated into a paleoclimate observation (Evans et al., 2013). PSMs are a powerful tool to translate both observed and simulated climate data into proxy language—generating synthetic proxy ("pseudoproxy") records and facilitating the intercomparison of paleoclimate data. Such proxy–pseudoproxy comparisons can be used to assess projections for future climate change (Schmidt et al., 2014; Thompson et al., 2011) and address uncertainties in the observations, climate model simulations, and the PSMs themselves (Comboul et al., 2014; Dee et al., 2016; Loope, Thompson, Cole, & Overpeck, 2020; Stevenson et al., 2013; Thompson et al., 2013). Pseudocorals modeled from long pre-industrial control simulations, initial condition ensembles (see Section 5.2), and/or statistical models (e.g., linear inverse model, Capotondi & Sardeshmukh, 2017; Newman et al., 2009, 2011) can also serve as a benchmark to detect forced changes from internal variability in the climate system (e.g., Abram et al., 2020; Cobb et al., 2013; Grothe et al., 2020).

In recent years, there has been a surge in the development of PSMs and related tools for corals and other archives (Dee, Emile-Geay, et al., 2015; Lawman et al., 2020; Ng et al., 2016; Stevenson et al., 2013; Thompson et al., 2011). PSMs vary widely in terms of the level of complexity (from bivariate linear to multivariate nonlinear) and in the number of processes that are modeled explicitly or parameterized from theoretical or empirical relations. These choices in turn have major ramifications for their modularity across sites and their utility in paleoclimate data assimilation (DA). For example, a simple bivariate PSM has been utilized to model the processes by which temperature and $\delta^{18}O_{sw}$ (precipitation, salinity) is sensed by the coral and subsequently deposited in the coral skeleton, from which we extract oxygen isotope records (Brown et al., 2008; Thompson et al., 2011). Such simplified models can be widely utilized using historical and simulated climate fields, and are typically both modular and scalable across a variety of sites (and even archive types, e.g., Ng et al., 2016). However, simplified models may be missing key processes and/or rely on empirical (and sometimes uncertain) parameterizations (e.g., the $\delta^{18}O_{sw}$—SSS relationship, Conroy et al., 2017; Russon et al., 2013, see Section 6.1), and may therefore underestimate variability under certain conditions (Lawman et al., 2020; Stevenson et al., 2013). For example, to date, coral PSMs have only considered the physical and chemical processes that influence coral proxy records, while the impact of calcification or other "biological" processes (e.g., the physiological constraints on biomineralization) have been folded into a noise term (Thompson et al., 2011) or parameterized statistically (Lawman et al., 2020).

Forward modeling has provided key insights into the data-model mismatch on the spectrum of climate variability, wherein coral paleoclimate proxies are characterized by stronger trends and variability decadal and longer timescales than suggested by earth system models (i.e., reddened spectra, Ault et al., 2009, 2013; Dee et al., 2017; Loope, Thompson, Cole, & Overpeck, 2020; Loope, Thompson, & Overpeck, 2020; Parsons et al., 2017). This is a critical problem to resolve, as the ability of models to capture low-frequency variability in the climate system has major implications for the risk of extreme climate events (e.g., megadroughts, Ault et al., 2014; Cook et al., 2015). Loope, Thompson, Cole, and Overpeck (2020) leverage the PSM framework to demonstrate that the scarcity of coral proxy records contributes to the low-frequency bias in ENSO reconstructions (particularly the scarcity of long records from key ENSO-sensitive regions; see also Comboul et al., 2015), with age-model uncertainties (Comboul et al., 2014) and red noise in individual records both playing a secondary (but important) role. Applications of coral PSMs also demonstrate that SST and SSS both contribute significantly to the magnitude of the 20th-century $\delta^{18}O_{coral}$ trend and that uncertainties or model bias in the magnitude of the hydroclimate change likely contribute to the discrepancy between models and proxies in the magnitude of the forced trend (Thompson et al., 2011, 2013).

These findings demonstrate a powerful application of PSMs to address an outstanding uncertainty in $\delta^{18}O_{coral}$ records: quantifying the relative role of temperature and $\delta^{18}O_{sw}$ across timescales (e.g., Hereid et al., 2013; Thompson et al., 2011, 2013). Although Sr/Ca is now routinely measured alongside $\delta^{18}O_{coral}$ to reconstruct the $\delta^{18}O_{sw}$ from the non-temperature related residuals (after removing the Sr/Ca-based temperature signal, Cahyarini, 2016; Ren et al., 2003), such $\delta^{18}O_{sw}$ reconstructions suffer from the propagation of errors or uncertainties in the fidelity of the Sr/Ca-temperature signal, analytical uncertainties, and/or calibration uncertainties (Nurhati, Cobb, Charles, & Dunbar, 2011). Therefore, while this paired approach has been successfully utilized to reconstruct $\delta^{18}O_{sw}$ at numerous sites (e.g., Cahyarini, 2016; Cahyarini et al., 2014; Nurhati, Cobb, & Di Lorenzo, 2011), the noise may obscure the signal, particularly in areas where temperature dominates $\delta^{18}O_{coral}$ variance (and the $\delta^{18}O_{sw}$ signal is thus small relative to the noise). Therefore, the forward approach can be leveraged to assess the relative role of temperature and $\delta^{18}O_{sw}$ in $\delta^{18}O_{coral}$ variability, and assess whether the $\delta^{18}O_{sw}$ confounds or amplifies the temperature signal (e.g., Russon et al., 2013).

Taken together, these studies have therefore not only provided valuable constraints on spatio-temporal patterns of variability but have also improved our understanding of the proxies themselves. In turn, these advancements have led to significant improvements in sensor, archive, and observation models since simple coral PSMs were first developed. Ongoing work by the PAGES Data Assimilation and Proxy System Modeling working group aims to build upon these existing models, expand their application to other marine carbonate archives (spanning animal kingdoms and environments), and compare the utility of PSMs across archives in DA-based reconstructions (i.e., PSM-Model Intercomparison Projects, or "PSM-MIPs"; Evans, 2019).

5.2 | Advances in earth system modeling

Climate models are essential for assessing physically or dynamically plausible mechanisms behind the changes observed in paleoclimate proxy records. The latest generation of models (Earth System Models, ESMs) contributing to the Coupled Model Intercomparison Project Phase 6 (CMIP6) and the Paleoclimate Model Intercomparison Project Phase 4 (PMIP4) have increased in complexity to include coupled biogeochemistry (e.g., Hurrell et al., 2013) and interactive ice sheets (Lofverstrom et al., 2020); significant improvements have also been made to spatial resolution and parameterizations, changes which have improved many structural biases observed in earlier generations of models, including the "double ITCZ" (Eyring et al., 2019). While more comprehensive overviews of CMIP6 and PMIP4 ESMs can be found elsewhere (Eyring et al., 2016; Kageyama et al., 2018, 2020), there are two areas where progress has had a major impact on coral paleoclimate studies.

First, in recognition of their sensitivity to small changes in the global hydrological cycle, stable oxygen and hydrogen isotopes (hereafter water isotopes) are increasingly incorporated as tracers in ESMs to diagnose model representation of key processes (e.g., cloud microphysics, air-sea gas exchange) and to facilitate proxy-model comparisons. The number of such water isotope-enabled simulations has expanded dramatically in recent years—from a handful of simulations (Aleinov & Schmidt, 2006; Jouzel et al., 1987; Mathieu, 2002; Schmidt et al., 2005) to numerous simulations distributed across multiple modeling centers (Brady et al., 2019; Nusbaumer et al., 2017; Risi et al., 2016; Steen-Larsen et al., 2017; Wong et al., 2017; Zhang et al., 2017; Zhu et al., 2017). Isotope-enabled models of intermediate complexity (Dee, Noone, et al., 2015) and regional ocean models (Stevenson et al., 2015) have also been developed. Combined with advances in PSMs and DA tools, these models have facilitated proxy-model comparisons and have improved reconstructions of hydroclimate change (Dee et al., 2016, 2017; Dee, Emile-Geay, et al., 2015; Dee, Noone, et al., 2015; Russon et al., 2013; Stevenson et al., 2015). Expansion of water isotope-enabled simulations across key climate periods should remain a top priority of the modeling community.

The second major modeling effort that has benefited coral paleoclimate studies is the proliferation of large (initial condition) ensembles and long unforced preindustrial control simulations (Hazeleger et al., 2009; Jeffrey et al., 2013; Kay et al., 2015; Kirchmeier-Young et al., 2017; Maher et al., 2019; Menary et al., 2018; Otto-Bliesner et al., 2016; Rodgers et al., 2015; Sun et al., 2018; Wittenberg, 2009). These simulations are critical for estimating internal variability in the climate system (Wittenberg, 2009), assessing the risk of extreme events (e.g., Lehner et al., 2018), and separating structural uncertainties from interannual variability in multi-model mean projections (Deser et al., 2020). These simulations also provide a benchmark against which to detect forced changes that are significant or even unprecedented in the context of natural variability. For example, PSMs run with output from the Last Millennium Ensemble (Otto-Bliesner et al., 2016) have been used to demonstrate that the increase in ENSO and IOD variance in the late 20th century (inferred from $\delta^{18}O_{coral}$) is likely a forced response to anthropogenic climate change, albeit not yet unprecedented (Abram et al., 2020; Cobb et al., 2013; Grothe et al., 2020). Finally, there have also been an increasing number of scientists bridging the divide between paleoclimate proxies and ESMs, as well as large collaborative efforts among modeling and proxy specialists. This acceleration of research and infrastructure at the interface between proxies and models will undoubtedly lead to numerous further innovations.

6 | CHALLENGES AND OPPORTUNITIES

6.1 | Seawater monitoring

Despite considerable advances in the methods for deconvolving the relative role of temperature and $\delta^{18}O_{sw}$ in $\delta^{18}O_{coral}$ reconstructions using both PSMs and paired Sr/Ca-$\delta^{18}O_{sw}$ data, both approaches are severely limited by the dearth of $\delta^{18}O_{sw}$ observations. In the absence of $\delta^{18}O_{sw}$ data with which to calibrate or validate, studies often leverage the strong positive relationship between $\delta^{18}O_{sw}$ and SSS across the tropics (Fairbanks et al., 1997) or (more recently) simulated $\delta^{18}O_{sw}$ from isotope-enabled climate models (Stevenson et al., 2015). However, both techniques are only as reliable as their ability to capture the spatio-temporal variability in $\delta^{18}O_{sw}$. Based on work to date, we know that the $\delta^{18}O_{sw}$-SSS slope varies spatially and through time (e.g. Conroy et al., 2017; Thompson et al., 2013), particularly on millennial and longer timescales, LeGrande & Schmidt, 2011); however, this spatio-temporal variability is still poorly constrained. Spatial relationships from LeGrande and Schmidt (2006) over large geographic regions are typically used but are based on very sparse measurements (Figure 5). This space-for-time approximation may not be appropriate, as the slope of this relationship differs between long-term monitoring and spatial data sets at sites where both are available, particularly across ENSO extremes (Conroy et al., 2017). Furthermore, the slope of the relationship is steeper in the western equatorial Pacific, relative to the central and eastern Pacific (Conroy et al., 2017; Russon et al., 2013) (Figure 5). However, there are still large gaps in the network of available seawater data, and the slope of this relationship remains poorly constrained in many regions. These uncertainties have major ramifications for the interpretation of $\delta^{18}O_{coral}$ records: the contribution of $\delta^{18}O_{sw}$ will be overestimated if the Pacific-wide slope is used at sites with a comparatively weak $\delta^{18}O_{sw}$-SSS relationship and shallow slope (and vice versa, Conroy et al., 2017). A larger network of paired $\delta^{18}O_{sw}$, SSS monitoring sites are required to constrain this relationship and improve the interpretation of coral $\delta^{18}O$ records.

Spatio-temporal measurements of paleo-relevant trace elements in seawater are arguably even more sparse, and largely confined to highly localized studies of runoff and pollution in coastal reef environments. While such variability is presumed to be small (relative to the climate signal) due to the conservative behavior of Sr and other key TE proxies, whether this assumption may break down (de Villiers et al., 1994; Shen et al., 1996) under circumstances is still debated. For example, Sr/Ca departures may occur with riverine and coastal runoff following cyclones and other heavy-rainfall events (e.g., Khare et al., 2021). Other proxy records explicitly leverage spatio-temporal variations in TE concentration (e.g., runoff and upwelling proxies); however, local, long-term monitoring studies are rarely performed to validate these proxies at individual sites. In recognition of this gap and recent advancements in methods for cost-effective, long-term TE monitoring (Khare et al., 2021), there are a growing number of seawater TE monitoring studies to improve the calibration and interpretation of TE proxies (e.g., nutrient availability and upwelling strength from Ba/Ca, LaVigne et al., 2011, 2016; Lewis et al., 2018; Tanzil et al., 2019; P/Ca, LaVigne et al., 2010; Cd/Ca, Grottoli et al., 2013;

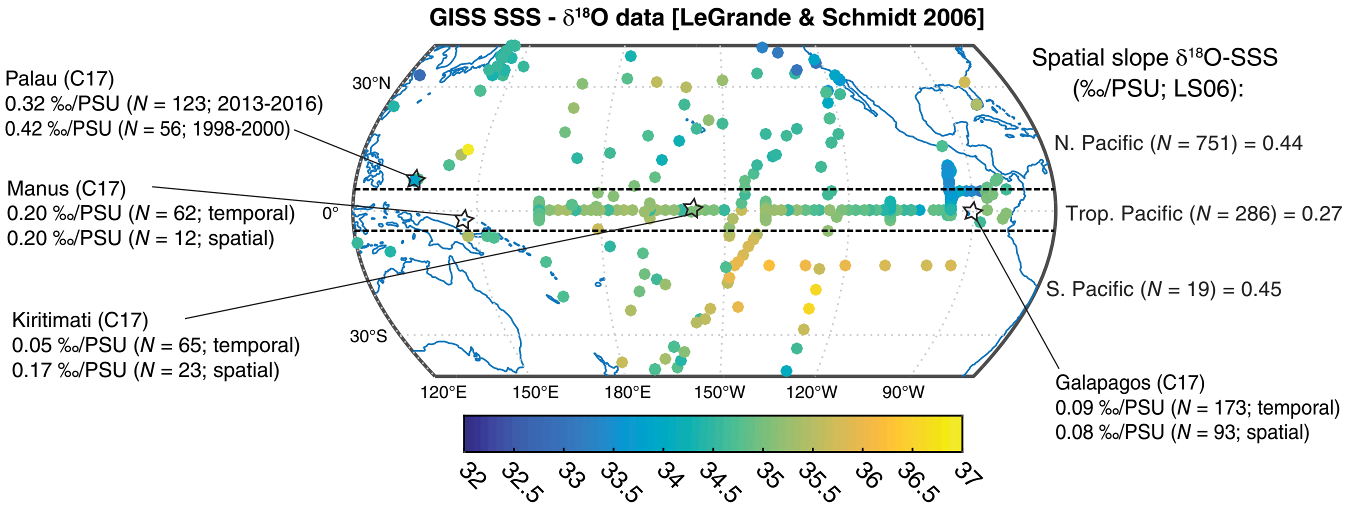

FIGURE 5 Sea-surface salinity (SSS) at sites with existing paired $\delta^{18}O_{sw}$—SSS measurements in the GISS isotope database (LeGrande & Schmidt, 2006; accessed December 3, 2017). The slope of the $\delta^{18}O_{sw}$—SSS relationship across the North Pacific ($N = 751$), Tropical Pacific ($N = 286$) and South Pacific ($N = 19$) from LeGrande and Schmidt (2006) are shown ("LS06"). Stars indicate approximate location of long-term monitoring at Manus, Papua New Guinea (2.06°S, 147.43°E), Koror, Palau (7.32°N, 134.46°E), Kiritimati, Republic of Kiribati (2.00°N, 157.48°W), and Santa Cruz Island, Galápagos, Ecuador (0.74°S 90.30°W) (Conroy et al., 2017). The slope of the $\delta^{18}O_{sw}$—SSS relationship from short-term spatial (spatial) and long-term monitoring (temporal) surveys by Conroy et al. (2017) are shown for comparison ("C17")

and multi-TE/Ca proxies, Lewis et al., 2018). While the relationships among these proxies and climate have been reasonably well replicated among sites (e.g., Grove et al., 2012; LaVigne et al., 2010; Sayani et al., 2021), complex circulation and mixing patterns may complicate the interpretation among sites and cores (Lewis et al., 2018). Community seawater monitoring networks must therefore also prioritize TE sampling, following established clean protocols.

6.2 | Quantitative density paired with geochemical proxies

Despite advances in the methods for quantitative density measurements (Section 2.2), there have been few studies pairing wholistic coral growth measurements (linear extension, density, and calcification) with skeletal geochemistry (as reviewed by Lough & Cooper, 2011; e.g., Kuffner et al., 2017; Reed et al., 2021; Smith et al., 2006). Yet, we know from previous work that coral growth is strongly modulated by climate (e.g., temperature and solar radiation, Lough & Barnes, 2000). Such changes in coral calcification may in turn have an impact on the geochemistry of the skeleton, and thus the climate signal of interest (Section 3). Historically, coral geochemical records have been screened for growth-related artifacts using linear extension rates measured between annual (warm or cold season) tie points in the geochemical record. However, recent studies have demonstrated that skeletal density (and thus net calcification) may be a more sensitive indicator of growth-related artifacts, and often varies independently of (or inconsistently with) extension rate (Mollica et al., 2018; Reed et al., 2018, 2021). As recent advances in quantitative densitometry have dramatically reduced the processing time, wholistic growth measures should be routinely analyzed and reported alongside geochemical proxies. When extended across locations, species, and colonies, this integrative approach has the potential to vastly improve our understanding of the impact of coral physiology on coral climate reconstructions, and assess the response of coral growth to changing environmental conditions.

7 | CONCLUDING REMARKS: CORAL ARCHIVES UNDER CHANGING OCEAN CONDITIONS

Corals remain a critical and reliable high-resolution archive of past climate variability, filling essential gaps in the spatial and temporal coverage of historical and paleoclimate data. Advances in identifying and constraining uncertainties have greatly improved the climate information obtained from these records and have led to the advancement of PSMs.

However, this invaluable archive is an increasingly finite resource. As oceans warm and acidify, corals are becoming more frequently stressed by temperature extremes and reduced aragonite saturation, which is likely to lead to widespread bleaching, mortality, and reduced calcification, unless corals can adapt to the current and projected rates of ocean change (e.g., Cantin et al., 2010; Logan et al., 2014). Repeated global bleaching events have already caused mass mortality on many atolls with invaluable paleo-information (e.g., the Line Islands, Barkley et al., 2018; Donner et al., 2017; Hughes et al., 2017, 2018; Magel et al., 2019; Sully et al., 2019). Thermal stress thresholds may be crossed nearly annually by the mid-21st century if we continue on a high greenhouse gas emission pathway (van Hooidonk et al., 2013, 2014, 2016). Nevertheless, not all reefs will fare the same (e.g., van Hooidonk et al., 2016), as the local response will be ultimately shaped by factors such as the historical frequency of thermal stress (Thompson & van Woesik, 2009), larval source regions (Kleypas et al., 2016; Thompson et al., 2018), temperature extremes (McManus et al., 2020), timeframe for recovery (Hughes et al., 2017), and other compounding natural and human stressors. Fortunately, several "bright spots" have been identified across the tropical-subtropical oceans, where coral reefs may show exceptional resilience to ocean change (Cinner et al., 2016).

As a paleoclimate community, it is imperative that we treat these essential archives as a fragile and dwindling resource, and actively band together (with the support of key funding agencies) to:

1. Develop lasting, two-way partnerships with local communities and stakeholders to draw on local knowledge, identify local research priorities, involve locals in the scientific process, and increase transparency.
2. Leverage and expand tools (e.g., Comboul et al., 2015) for identifying critical gaps in the spatio-temporal coverage of high-resolution coral data.
3. Develop community consensus and leverage international agencies and collaborations to identify reconstruction targets and funding opportunities.
4. Collect modern cores from critical locales, following ecologically and culturally sensitive approaches (e.g., bioerosion protection, avoiding the use of hydraulic fluid, etc.) to expand coverage and replication of high-resolution proxy data over the historical period (since ~1850), thereby improving proxy calibration, constraining proxy uncertainties, and improving model-proxy comparisons.
5. Expand community archival and collaborative exchange of physical samples (Dassié, 2017), particularly those that have been underutilized since their collection. X-ray and/or CT images and age-depth models should be published alongside new geochemical records and made publicly available to ensure their utility in synthesis efforts, particularly as new advancements in the field require archived data to be reprocessed and/or reinterpreted.

These community-driven approaches to harness valuable climate information from coral reefs will benefit local management efforts and facilitate collaborative opportunities and advances. The latter is particularly critical for junior scientists, for whom a career can no longer be built exclusively on new sampling efforts. As with other international paleoclimate synthesis efforts (e.g., PAGES), such an approach will strengthen the community and lead to advances not yet foreseen.

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CONFLICT OF INTEREST

The author has declared no conflicts of interest for this article.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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RELATED WIREs ARTICLE

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