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PREDICTING RESPONSES OF GEO-ECOLOGICAL CARBONATE REEF SYSTEMS TO CLIMATE CHANGE: A CONCEPTUAL MODEL AND REVIEW

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Abstract Coral reefs provide critical ecological and geomorphic (e.g. sediment production for reef-fronted shoreline maintenance) services, which interact in complex and dynamic ways. These services are under threat from climate change, requiring dynamic modelling approaches that predict how reef systems will respond to different future climate scenarios. Carbonate budgets, which estimate net reef calcium carbonate production, provide a comprehensive 'snap-shot' assessment of reef accretionary potential and reef stability. These budgets, however, were not intended to account for the full suite of processes that maintain coral reef services or to provide predictive capacity on longer timescales (decadal to centennial). To respond to the dual challenges of enhancing carbonate budget assessments and advancing their predictive capacity, we applied a novel model elicitation and review method to create a qualitative geo-ecological carbonate reef system model that links geomorphic, ecological and physical processes. Our approach conceptualizes relationships between net carbonate production, sediment transport and landform stability, and rates knowledge confidence to reveal major knowledge gaps and critical future research pathways. The model provides a blueprint for future coral reef research that aims to quantify net carbonate production and sediment dynamics, improving our capacity to predict responses of reefs and reef-fronted shorelines to future climate change.

Keywords: Carbonate Budgets; Ecological Modelling; Mental Model Elicitation; Coral Reefs; Reef Islands; Climate Change

Introduction

Coral reefs provide a number of critical ecosystem services. They offer complex habitats for a multitude of marine organisms (Darling et al. 2017) and are critical for maintaining biodiversity that supports economically valuable tourism and fisheries (Spalding et al. 2017). These systems also provide an essential supply of sediment to reef-fronted shorelines and islands (Ogden 1977, Harney & Fletcher 2003, Dawson & Smithers 2014, Cuttler et al. 2019) and act as physical structures that buffer wave energy to protect coastlines (Ferrario et al. 2014, van Zanten et al. 2014). Reef systems rely on the net accumulation of biologically produced calcium carbonate ($CaCO_3$) by reef communities (e.g. corals, crustose coralline algae or CCA), to maintain these ecosystem services. The three-dimensional structure of the reef framework is the result of organisms that produce carbonate (and construct reefs) and the biological, physical and chemical processes that remove carbonate (and deconstruct reefs). Calcifying organisms on reefs include corals, which contribute to the development of the reef structure (Stearn et al. 1977, Hubbard et al. 1990, Perry & Larcombe 2003); CCA, which cement and stabilize the reef framework (Martindale 1992, Rasser & Riegl 2002, Tierney & Johnson 2012); and foraminifera (Hallock 1981), molluscs (Kay & Kawamoto 1983) and algae such as *Halimeda* spp., (Perry et al. 2016; termed direct sediment producers), which contribute to reef sediment sinks upon death (Hallock 2001, Hart & Kench 2007, Browne et al. 2013). Erosion of the reef framework can occur through biological removal by grazing and boring organisms (e.g. parrotfish and molluscs; Frydl & Stearn 1978, Bellwood & Choat 1990, Glynn & Manzello 2015), physical removal by strong wave action and current velocities (e.g. during cyclones; Harmelin-Vivien 1994, Perry et al. 2014) and chemical dissolution (Cyronak & Eyre 2016).

Over time, the balance between reef framework construction and removal (i.e. net carbonate accumulation) results in negative (eroding), limited (static) or positive reef growth (accretionary) potential, also termed the budgetary state of the reef (Chave et al. 1972, Stearn et al. 1977, Scoffin et al. 1980, Hubbard et al. 1990, Perry et al. 2008, Perry et al. 2013b). Both biological and physical processes that erode the reef framework, together with direct sediment producers, generate sediments that are either lost from the reef system (e.g. dissolved or transported off-reef), or incorporated into the reef framework and/or depositional sinks (Kennedy & Woodroffe 2002, Mallela & Perry 2007, Morgan & Kench 2014). Knowledge of these processes can be actualized through the use of a reef carbonate budget, which provides a conceptual approach to capture the geological and ecological processes that drive reef accretion and erosion (Chave et al. 1972, Stearn et al. 1977, Perry et al. 2012, Lange et al. 2020).

A carbonate budget is typically estimated using either (1) the biological census-budget technique (e.g. Browne et al. 2013), (2) the hydro-chemical estimate (e.g. Muehllehner et al. 2016) or (3) from reef cores that are used to determine geological estimates of net carbonate accumulation rates (e.g. Ryan et al. 2001). The census-based approach calculates net carbonate production directly by (1) quantifying biologically produced calcium carbonate based on organism relative abundance and calcification rate (e.g. corals, CCA), and (2) subtracting rates of carbonate removal based on the biomass and/or feeding rates of grazing organisms (e.g. parrotfish and urchins), and abundance and boring rates of internal bioeroding organisms (e.g. bioeroding sponges; Table 1; Stearn et al. 1977, Eakin 2001, Perry et al. 2008). In contrast, the hydro-chemical approach provides an indirect estimate by assessing changes in seawater carbonate chemistry over the reef as a proxy for net calcification, and reef cores estimate historical net carbonate accumulation based upon reef accretion rates (see Lange et al. 2020 for detailed review of carbonate budget methods). Census-based approaches provide a detailed estimate of the net carbonate production over ecological scales (days to years), whereas hydro-chemical estimates provide indirect estimates of net calcification flux over short timeframes (hours to days). Although reef cores provide long-term insight into past reef accretion on geological timescales (centuries to millennia), these *in situ* records of net accretion only provide the cumulative result of constructive and destructive processes rather than a delineation between these processes. Of the >300 reefs globally that have been studied using carbonate budgets, the census-based approach has been applied in 64% of Indo-Pacific and 87% of Atlantic carbonate budget studies (Lange et al. 2020).

Census-based carbonate budgets were primarily designed to provide ‘snap-shot’ estimates of ecological processes, but interest is growing in the potential application of carbonate budgets as a predictive tool for both long-term reef accretion and associated shoreline responses (i.e. accretion/erosion), particularly in relation to climate change (e.g. Morgan & Kench 2016b, Perry et al. 2018b). Understanding how environmental processes interact to enhance or limit carbonate budgets is critical to developing predictive dynamic models of reef accretion, sediment production and landform stability under future climate change. By coupling ecological models and carbonate budgets with future climate scenarios, Kennedy et al. (2013) identified impacts of climate change on the carbonate balance on Caribbean reefs and demonstrated the importance of managing water quality and herbivore fisheries in maintaining carbonate production and reef growth under future climate change. Quantitative dynamic models of carbonate budgets have also been used to assess reef budgetary state at global scales by coupling calcification and bioerosion rates with predicted changes in coral cover under future climate change scenarios (Cornwall et al. 2021). These models quantitatively link ecological processes to environmental drivers to predict responses of constructive and destructive processes on a reef, but how these predicted changes in net carbonate accumulation (based on ecological data from limited temporal and spatial scales) translate to longer-term changes in reef accretion and associated landform stability has yet to be resolved.

The capacity to predict the future trajectory of reefs and associated landforms in the Anthropocene will be of considerable value for future ecosystem conservation and coastal management. To illustrate, thermal coral bleaching events associated with climate change have reduced the abundance and function of carbonate producing organisms globally, resulting in reef degradation, declines in structural complexity and biodiversity, and reduced reef growth (Hoegh-Guldberg et al. 2007, Graham & Nash 2013, Hoegh-Guldberg et al. 2017, Perry & Morgan 2017). These ecological

Table 1 All published (field) census-based carbonate budget studies to date. Studies that utilized indirect measures of net carbonate production (e.g. hydro-chemical or reef cores) have been excluded from this list. For each study, we provide details on the overall approach used, the variables measured (total number of variables in brackets) and related assumptions. Note that only those carbonate budget studies that incorporate gross carbonate production (including corals) are included

Year	Location/s	Approach used and key processes	Key variables and total number used	Assumptions and exclusions	References
1977 and 1980	Bellairs Reef, Barbados	A detailed survey of carbonate production and loss within ecological zones together with a comprehensive assessment of habitat complexity	Living and dead coral cover, CCA cover, sand and rubble cover, rugosity, coral growth rates and skeletal density, coral composition and community size distributions, CCA growth rates (Stearn et al. 1977), fish species, size and abundance, parrotfish gut content analysis and feeding activity, urchin abundance, test size and gut content analysis, macroboring rates, sediment particle size and composition, sediment accumulation rates, dead reef erosion/lowering rate, diagenetic constituents and reef cementation rates (Scoffin et al. 1980; 26 variables across two papers)	• No assessment of carbonate sediment production as it assumes that the contribution of direct sediment producers was so low to have no effect on gross carbonate production rates • Focuses on five coral species for coral gross carbonate productivity rates and ignores other coral species contributions to the budget • Suggests that mechanical erosion is not important based on *in situ* observations	Stearn et al. (1977) and Scoffin et al. (1980)
1979	Discovery Bay, Jamaica	This study provides an assessment of coral carbonate production with detailed sediment accumulation profiles from seismic scanners and sediment cores	Living coral cover and composition, coral growth rates, sand cover, sediment carbonate content, sediment loss and accumulation rates, sediment size fraction, sediment depth layer, mass of reef-derived sediment (ten variables)	• Limited benthic cover data and no site-specific coral growth data • No data on other carbonate producers, e.g. encrusters or direct sediment producers • No data on biological, physical or chemical erosional rates • Several assumptions made regarding sediment compositional links to gross reef carbonate productivity and coral carbonate productivity rates • No assessment of how carbonate production varies among reef zones	Land (1979)

(*Continued*)

Table 1 (*Continued*) All published (field) census-based carbonate budget studies to date. Studies that utilized indirect measures of net carbonate production (e.g. hydro-chemical or reef cores) have been excluded from this list. For each study, we provide details on the overall approach used, the variables measured (total number of variables in brackets) and related assumptions. Note that only those carbonate budget studies that incorporate gross carbonate production (including corals) are included

Year	Location/s	Approach used and key processes	Key variables and total number used	Assumptions and exclusions	References
1979	Onslow Island, Galapagos	This study provides an assessment of coral cover and urchin activity to estimate a net carbonate budget	Live and dead coral cover, CCA cover, coral composition, urchin species, abundance, size and grazing rates, urchin gut content analysis, sediment composition and particle size (11 variables)	• Coral gross carbonate production is a function of live coral cover as opposed to growth rates • Carbonate production from other carbonate producing organisms is not included • No assessment of other bioeroding species (fish, macro- and microborers) • No assessment of physical and chemical erosion	Glynn et al. (1979)
1982	Hawaii to Kure atoll, Hawaiian archipelago	This study uses coral cover data from 14 major islands with detailed coral growth assessments for *Porites lobata*	Live coral cover and composition, coral growth rate and skeletal density (four variables)	• Uses *Porites lobata* to represent all coral species growth rates • Suggests that rates of accretion are equal to maximum rates of gross carbonate production due to site selection characteristics • Assumes that rates of chemical and mechanical erosion are negligible • Assumes that gross production rates are equal to net production rates; hence, there is no assessment of rates of carbonate removal • No assessment of carbonate production from other carbonate producing organisms	Grigg (1982)
1984	Cane Bay, St. Croix	This study uses transects and sediment tagging to assess gross carbonate production and sediment dynamics, respectively	Living and dead coral cover, sand cover, CCA cover, rugosity, coral composition, skeletal growth and density, sediment transport loss and accumulation rates, sediment carbonate content (11 variables)	• Uses previously published skeletal growth and density rates • Uses a depth correction factor to include differences in growth rates with depth • Rare coral growth rates are assumed and grouped as 'other corals' • There is no measure of the calcification rate of other calcifiers even though the coral sediment fraction is only 45%. Instead, this is estimated from reef cores • No data on physiochemical erosional rates due to the assumption that these elements are captured by changes in sediment accumulation and loss	Sadd (1984)

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Table 1 (*Continued*) All published (field) census-based carbonate budget studies to date. Studies that utilized indirect measures of net carbonate production (e.g. hydro-chemical or reef cores) have been excluded from this list. For each study, we provide details on the overall approach used, the variables measured (total number of variables in brackets) and related assumptions. Note that only those carbonate budget studies that incorporate gross carbonate production (including corals) are included

Year	Location/s	Approach used and key processes	Key variables and total number used	Assumptions and exclusions	References
1988	Uva Island and Onslow Reef, Eastern Pacific	A detailed study of urchin bioerosion and sediment production pre and post an El Nino warming event	Living coral cover, coral colony size and shape, rugosity, urchin species, abundance, size and grazing rates, damselfish territories, macroboring rates, bioeroder sediment production, sediment composition (12 variables)	• Net carbonate production values are provided but unclear how they were determined, most likely from percentage of living coral cover • Carbonate production from other carbonate producing organisms likely not included • Data on cumulative bioerosion from non-echinoid organisms (mostly macroborers) are provided, but not details on parrotfish • No assessment of physical and chemical erosion	Glynn (1988)
1990	Tiahura, Moorea	A detailed study on urchin densities and size distributions with changing substrate	Living and dead coral cover, coral composition and condition, rubble and sand cover, urchin species, size and abundance, urchin gut content (ten variables)	• Rates of carbonate consumption were based of published exponential relationships between test size and gut content • Uses published coral growth rates and skeletal density to estimate gross carbonate production • Does not account for other carbonate producing organisms • Does not account for other bioeroding organisms and physiochemical processes that remove carbonates	Bak (1990)
1990	St Croix, US Virgin Islands	This study provides an assessment of carbonate production with an estimation of sediment import, export and accumulation rates	Living coral cover, CCA cover, coral composition, growth rates and bulk density, sediment composition, rugosity, sediment import, export and accumulation rate, reef accretion rates (11 variables)	• Some measured and some published coral growth rates used • No *in situ* measures of coralline algae production rates or other encrusting organisms • Several assumptions made around sediment production from bioerosion (based off the Land 1979 study) • No direct estimates of bioerosion from key bioeroding species	Hubbard (1990)

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Table 1 (*Continued*) All published (field) census-based carbonate budget studies to date. Studies that utilized indirect measures of net carbonate production (e.g. hydro-chemical or reef cores) have been excluded from this list. For each study, we provide details on the overall approach used, the variables measured (total number of variables in brackets) and related assumptions. Note that only those carbonate budget studies that incorporate gross carbonate production (including corals) are included

Year	Location/s	Approach used and key processes	Key variables and total number used	Assumptions and exclusions	References
1996	Uva Island, Eastern Pacific	This study uses *in situ* census-based data together with published carbonate production rates to develop a carbonate budget model	Live and dead coral cover, CCA cover, damselfish lawn cover, coral composition, rugosity, urchin density, sediment size distribution and hydrodynamic properties (nine variables)	• Uses published growth rates for coral and coralline algae as well as erosion rates from urchins, fish and other non-echinoid grazers • Makes assumptions regarding coral skeletal density • Uses published data on net erosion rates of the reef framework • Assumes that direct sediment producers are not important for the budget • Assumes that rates of chemical erosion are comparatively low compared to physical and biological erosion • Estimates rates of sediment retention based on a comparison between size of sediments produced by bioeroders versus those retained on the reef	Eakin (1996)
2000	13 reefs in three regions (Java Sea, Ambon and South Sulawesi) in Indonesia	This study provides an assessment of benthic cover and carbonate production and removal across several reef sites along a water quality gradient	Live and dead coral cover, algal cover, sand and rubble, sponges, coral composition, growth rate and skeletal density, macroboring rates, water clarity, maximum depth of coral growth, temperature, salinity, chlorophyll-a, nitrate and phosphate concentrations, SPM, sediment accumulation and light intensity (20 variables)	• Applies measured growth (and bioerosion rates) from *Porites* spp. for all corals, thereby assuming approximately equal calcification rates • Assumes approximately equal rates of bioerosion for live and dead standing corals • Uses live corals to estimate bioerosion rates • No estimation of direct sediment producers • No estimation of physiochemical rates of erosion	Edinger et al. (2000)
2000	Green Island, Australia	This study focuses on the contribution of foraminifera to the carbonate budget using a census-based approach	Living coral cover, algal and turf cover, *Halimeda* cover, calcareous algal cover, sand cover, coral composition, sediment trap content weight, sediment composition and particle size, foraminifera density and species composition, wind and current data (14 variables)	• Focuses only on gross carbonate production from corals, foraminifera and *Halimeda*, which were used to calculate total carbonate production. Therefore, no assessment of other encrusters or other direct sediment producers • Does not apply a rugosity factor, so coral production estimates likely underestimated • Uses published carbonate production rates for corals, calcareous algae and foraminifera	Yamano et al. (2000)

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Table 1 (*Continued*) All published (field) census-based carbonate budget studies to date. Studies that utilized indirect measures of net carbonate production (e.g. hydro-chemical or reef cores) have been excluded from this list. For each study, we provide details on the overall approach used, the variables measured (total number of variables in brackets) and related assumptions. Note that only those carbonate budget studies that incorporate gross carbonate production (including corals) are included

Year	Location/s	Approach used and key processes	Key variables and total number used	Assumptions and exclusions	References
2001	Uva Island, Eastern Pacific	Study combines *in situ* census-based data with published carbonate production rates to develop a carbonate budget model	Same as Eakin et al. (1996)	• Same as Eakin et al. (1996)	Eakin (2001)
2003	Kailua Bay, Oahu, Hawaii	An assessment of carbonate production and removal that also considers variable production between zones and includes direct sediment production rates	Live and dead coral cover, macro and turf algal cover, CCA cover and growth rates, sand and reef framework cover, rugosity, coral composition, growth rates and skeletal density, urchin abundance and size, macroboring rates, sediment depth layers, sediment carbonate content and composition, mechanical erosion rate (19 variables)	• Coral growth rates sourced from the literature except for three key coral species • Assumes that timeframe of coral rubble availability for macroboring rates related to coral vertical height and growth rates • Estimates of urchin bioerosion rates taken from previous studies • Uses published turnover rates to estimate direct sediment production rates • Physical erosion on *in situ* framework included but based on previously published estimates • No estimates of chemical erosion	Harney & Fletcher (2003)
2007	Rio Bueno, Jamaica	A comprehensive carbonate budget using transects and *in situ* experiments together with environmental data collection	Living and dead coral cover, algal cover, rubble, reef framework and sand cover, rugosity, coral composition, growth and skeletal density, encrusting community composition, cover and growth, fish species, numbers and size, urchin density and size, macroboring and micro-boring rates, sediment accumulation rates, rates of framework infilling, sediment carbonate content and composition, temperature, salinity, DIN, phosphorus, ammonia, light, suspended sediments (31 variables)	• Uses previously published coral growth and density rates • Uses a depth correction factor to include differences in growth rates with depth • Rates of bioerosion from dead coral colonies are based on the assumption that corals were recently dead • Estimates of urchin bioerosion rates taken from previous studies and applies a correction factor to consider reworked sediments • Calculation of fish erosion rates also uses off site data, a correction factor and no assessment of fish behaviour • No assessment of direct sediment production rates • No estimates of physical erosion on both sediments or *in situ* carbonate framework	Mallela & Perry (2007)

(*Continued*)

Table 1 (*Continued*) All published (field) census-based carbonate budget studies to date. Studies that utilized indirect measures of net carbonate production (e.g. hydro-chemical or reef cores) have been excluded from this list. For each study, we provide details on the overall approach used, the variables measured (total number of variables in brackets) and related assumptions. Note that only those carbonate budget studies that incorporate gross carbonate production (including corals) are included

Year	Location/s	Approach used and key processes	Key variables and total number used	Assumptions and exclusions	References
2007	Warraber Island, Torres Strait, Australia	This study assesses gross carbonate production using quadrates and transects within ecological zones	Living coral cover and composition, CCA cover, *Halimeda* cover, sponge and brown algal cover, seagrass cover, sand and reef framework cover, rugosity, sediment depth and type, foraminifera and mollusc abundance (14 variables)	• Uses previously published rates for all calcifying organisms and applies an adjustment factor based on organism abundance • Focuses on gross carbonate production so not a full budget	Hart & Kench (2007)
2012	Bonaire	This study provides the method of a rapid census-based approach termed 'ReefBudget', which focuses on quantifying the relative contributions of key calcifying organisms	Living coral cover, CCA cover, turf and macroalgal cover, *Halimeda* cover, sand, rubble and reef framework cover, rugosity, coral composition, growth rates and skeletal density, encrusting cover and growth rates, parrotfish species, size and abundance, parrotfish bite rates, scars and mass eroded, urchin abundance, size and species, clionid sponge cover, microbioerosion rates (25 variables)	• Uses previously published coral growth and skeletal rates • Uses the average calcification rate for the encrusting carbonate producers • Fish, urchin, sponge and microbioerosion rates based on previously published (off site) data that takes limited account of differences in depth, reef habitat and other environmental drivers of these processes • No assessment of direct sediment production rates • No assessment of physical or chemical erosion rates	Perry et al. (2012)
2013	19 reefs in the Caribbean	This study uses the ReefBudget method to assess carbonate production on several reefs	Same as Perry et al. (2012)	• Same as Perry et al. (2012)	Perry et al. (2013b)

(*Continued*)

Table 1 (*Continued*) All published (field) census-based carbonate budget studies to date. Studies that utilized indirect measures of net carbonate production (e.g. hydro-chemical or reef cores) have been excluded from this list. For each study, we provide details on the overall approach used, the variables measured (total number of variables in brackets) and related assumptions. Note that only those carbonate budget studies that incorporate gross carbonate production (including corals) are included

Year	Location/s	Approach used and key processes	Key variables and total number used	Assumptions and exclusions	References
2013	Middle Reef and Paluma Shoals, Great Barrier Reef, Australia	A comprehensive study of carbonate production and removal in ecological zones with a detailed assessment of sediment dynamics and direct sediment production	Live and dead coral cover, macro- and turf algal cover, CCA cover, encrusting community cover, composition and growth rates, sand, rubble and reef framework cover, rugosity, coral composition, growth rates and skeletal density, fish species, abundance and size, urchin abundance and size, macroboring rates, light, suspended sediments, direct sediment producers, net sediment accumulation rates, sediment export rates, sediment depth layers, sediment particle size, carbonate content and composition (30 variables)	• Coral growth rates of the three most abundant corals measured on site, but the remaining coral growth rates sourced from the literature • Assumes coral rubble samples for macroboring rates have been available for <1 year on the reef • Estimates of urchin bioerosion rates from previous studies • Uses published turnover rates to estimate direct sediment production • No estimates of physical erosion on *in situ* carbonate framework • No estimates of chemical erosion/dissolution	Browne et al. (2013)
2013	Warrabar Reef and Bet Reef, Torres strait	Study combines published census-based data with remote sensing data to provide an estimate of carbonate production for a number of reef habitats	Living coral cover and composition, CCA and *Halimeda* cover, seagrass, sand and reef framework cover, rugosity, sediment depth and type, foraminifera and mollusc abundance, wave exposure (13 variables)	• For Warraber reef, uses site-specific carbonate production rates from Hart & Kench (2007) • For Bet reef, uses published substrate data together with non-site-specific data on carbonate production • Includes additional limitations as outlined for Hart & Kench (2007)	Leon & Woodroffe (2013)

(*Continued*)

Table 1 (*Continued*) All published (field) census-based carbonate budget studies to date. Studies that utilized indirect measures of net carbonate production (e.g. hydro-chemical or reef cores) have been excluded from this list. For each study, we provide details on the overall approach used, the variables measured (total number of variables in brackets) and related assumptions. Note that only those carbonate budget studies that incorporate gross carbonate production (including corals) are included

Year	Location/s	Approach used and key processes	Key variables and total number used	Assumptions and exclusions	References
2013	One Tree Island, Australia	Study compares rates of gross carbonate production from a census-based approach with hydro-chemically derived estimates, and uses remote sensing to classify reef habitat types over broad areas	Live and dead coral cover, macroalgal cover and algal mat, sand, rubble and consolidated rubble cover, reef platform (eight variables)	• Study focuses on gross carbonate production so does not include estimates of carbonate removal • Uses off-site published carbonate production rates for corals, coralline algae and direct sediment producers	Hamylton et al. (2013b)
2014	Vabbinfaru Reef, North Malé Atoll, Maldives	This study provides a detailed census-based carbonate budget of different reef eco-geomorphic zones, which also includes an assessment of sediment flux and a sediment budget	Live and dead coral cover, CCA and Halimeda cover, sand, rubble and reef framework cover, rugosity, coral composition, growth rates and skeletal density, encruster community composition and calcification rate, CCA carbonate production, fish species, abundance and size, urchin abundance and size, macroboring rates, light, suspended sediments, net sediment accumulation rates, sediment export rates, sediment depth layers, sediment particle size, carbonate content and composition, reef island planform morphology, wave energy (30 variables)	• Coral growth and calcification rates calculated for a selection of dominant hard corals • Does not account for chemical dissolution of reef framework • Internal bioerosion rates of lagoon rubble assumed available for 10 years (since 1998 bleaching event) • Uses published rates of urchin bioerosion • Calculates parrotfish erosion rates for dominant initial and terminal phase excavating species (not scrapers) • Microbioerosion rates from published literature and applied uniformly to reef substrates	Morgan (2014)

(*Continued*)

Table 1 (*Continued*) All published (field) census-based carbonate budget studies to date. Studies that utilized indirect measures of net carbonate production (e.g. hydro-chemical or reef cores) have been excluded from this list. For each study, we provide details on the overall approach used, the variables measured (total number of variables in brackets) and related assumptions. Note that only those carbonate budget studies that incorporate gross carbonate production (including corals) are included

Year	Location/s	Approach used and key processes	Key variables and total number used	Assumptions and exclusions	References
2015	75 sites across the Caribbean	This study uses the ReefBudget method (with some additional transect and rugosity data measurements)	Same as Perry et al. (2012)	• Same as Perry et al. (2012)	Perry et al. (2015c)
2015	Great Chagos Bank, Peros Banhos, Salomon	This study presents a modified version of the ReefBudget method for the Indo-Pacific region. Sites were also classified based on wave exposure for modelling purposes	Living coral cover, CCA and non-encrusting coralline algal cover, turf and fleshy macroalgal cover, *Halimeda* cover, sand, rubble and reef framework cover, rugosity, coral composition, shape and size, growth rates and skeletal density, parrotfish species, size and abundance, parrotfish bite rates, scars and mass eroded, urchin abundance, size and species, micro and macrobioerosion rates, sediment production rates by macroborers (27 variables)	Key differences with the previously published ReefBudget method include • The use of published rates of clinoid sponge bioerosion rather than in-water surveys • Inclusion of sediment production rates from macroborers • Coral colony size, growth, density and geometric shape are used to calculate coral carbonate production. In addition, • There is also no assessment of encrusting carbonate production rates (excluding CCA) • Areas where published data are used include coral growth rates and skeletal densities, macro- and microbioerosion rates and some data related to parrotfish erosion activity • No assessment of physical or chemical erosion rates	Perry et al. (2015b)
2016	Curacao and Bonaire, Caribbean	Study focusing on the coral community and applies growth rates from the ReefBudget method	Live coral cover, coral composition and size distributions, dead coral cover (four variables)	• Focuses on coral carbonate production only • Does not apply a rugosity factor so coral production estimates are likely underestimated • Uses previously published coral skeletal growth and density rates • Uses a depth correction factor to include differences in growth rates with depth	De Bakker et al. (2016)

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Table 1 (*Continued*) All published (field) census-based carbonate budget studies to date. Studies that utilized indirect measures of net carbonate production (e.g. hydro-chemical or reef cores) have been excluded from this list. For each study, we provide details on the overall approach used, the variables measured (total number of variables in brackets) and related assumptions. Note that only those carbonate budget studies that incorporate gross carbonate production (including corals) are included

Year	Location/s	Approach used and key processes	Key variables and total number used	Assumptions and exclusions	References
2017	Seychelles Islands	This study was carried out using 5 years of data (1994–2014) along the reef front to track changes in net carbonate production over time	Same a Perry et al. (2015b)	• Same a Perry et al. (2015b)	Januchowski-Hartley et al. (2017)
2017	Zanzibar Island chain, close to Stone Town, Zanzibar	This study uses the original ReefBudget approach to assess net carbonate production with biodiversity indices and coral structural complexity along an offshore gradient	Same as Perry et al. (2012)	• Same as Perry et al. (2012)	Herrán et al. (2017)
2017	Gaafu Dhaalu Atoll, Southern Maldives	This study uses the modified ReefBudget approach for the Indo-Pacific to assess changes in carbonate budgets due to a coral bleaching event	Same a Perry et al. (2015b)	• Same a Perry et al. (2015b)	Perry & Morgan (2017)

(*Continued*)

Table 1 (*Continued*) All published (field) census-based carbonate budget studies to date. Studies that utilized indirect measures of net carbonate production (e.g. hydro-chemical or reef cores) have been excluded from this list. For each study, we provide details on the overall approach used, the variables measured (total number of variables in brackets) and related assumptions. Note that only those carbonate budget studies that incorporate gross carbonate production (including corals) are included

Year	Location/s	Approach used and key processes	Key variables and total number used	Assumptions and exclusions	References
2017	Lhaviyani Atoll, Central Maldives	This study uses a census-based approach to demonstrate spatial differences in carbonate production at the inter-reef habitat scale	Same as Perry et al. (2015b), study, with the addition of *Halimeda* plant volume, number of non-*Halimeda* calcifying green algae, number of articulated red coralline algae, number of epifaunal gastropods, sediment compositional analysis (33 variables)	• Same a Perry et al. (2015b)	Perry et al. (2017)
2018	Cheeca Rocks, Florida Keys	This study uses the original ReefBudget approach conducted annually on the reef from 2012 to 2016	Same as Perry et al. (2012)	• Same as 2012 Perry et al. study • However, site-specific coral growth rates and skeletal density for *Orbicella faveolata* were determined using X-radiographs and CT scanning, respectively • It was then assumed that all other coral species at the site had the same growth dynamics as the measured *Orbicella faveolata* relative to the default ReefBudget values	Manzello et al. (2018)
2018	86 sites across the Caribbean and 68 sites in the Indo-Pacific region	A meta-analysis of carbonate budgets studies, most using the census-based ReefBudget method or adaptations of this method	Same as Perry et al. (2012)	• Same as Perry et al. (2012)	Perry et al. (2018)

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Table 1 (*Continued*) All published (field) census-based carbonate budget studies to date. Studies that utilized indirect measures of net carbonate production (e.g. hydro-chemical or reef cores) have been excluded from this list. For each study, we provide details on the overall approach used, the variables measured (total number of variables in brackets) and related assumptions. Note that only those carbonate budget studies that incorporate gross carbonate production (including corals) are included

Year	Location/s	Approach used and key processes	Key variables and total number used	Assumptions and exclusions	References
2018	Red Sea, Saudi Arabia	This study adapted the original ReefBudget approach and also deployed carbonate blocks to better estimate rates of net reef accretion and erosion	Living and dead coral cover, CCA cover, turf and macroalgal cover, reef framework cover, rugosity, coral composition and growth rates, CCA growth rates, parrotfish species, size and abundance, urchin abundance, size and species, net accretion/erosion rates (blocks), temperature, salinity, pH, nitrite/ate, ammonia, phosphate, TA (24 variables)	• No assessment of direct carbonate sediment production (or chemical dissolution) • Uses literature-based values to calculate grazing fish and urchin bioerosion rates • No estimates of physical erosion on *in situ* carbonate framework	Roik et al. (2018)
2018	Palau & Yap, Western Pacific Ocean	This study combines *in situ* cover of carbonate producing organisms with published production/ removal rates to produce a spatial visualisation of net carbonate production over the reef	Living and dead coral cover, CCA cover, macroalgal and sponge cover, coral composition, growth rates and skeletal density, rugosity, fish species, abundance and size, urchin species, abundance and size (15 variables)	• Uses published coral linear growth rates • Uses published data on CCA carbonate production rates • Estimates on parrotfish and urchin erosion rates based on published data • Macroboring is not measured but related to the surface area available • Uses published bioerosion rate for sponges • No assessment of direct sediment producers • No assessment of physical or chemical erosion	van Woesik & Cacciapaglia (2018)

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Table 1 (*Continued*) All published (field) census-based carbonate budget studies to date. Studies that utilized indirect measures of net carbonate production (e.g. hydro-chemical or reef cores) have been excluded from this list. For each study, we provide details on the overall approach used, the variables measured (total number of variables in brackets) and related assumptions. Note that only those carbonate budget studies that incorporate gross carbonate production (including corals) are included

Year	Location/s	Approach used and key processes	Key variables and total number used	Assumptions and exclusions	References
2019	Cocos Keeling	A geo-spatial assessment of carbonate budget using *in situ* census-based data together with remote sensing to provide a carbonate budget that covers a considerable spatial area (225 km^2)	Living and dead coral cover, CCA cover, turf cover, encrusters cover, seagrass cover, sand, rubble and reef framework cover, rugosity, coral composition, growth rates and skeletal density, sediment composition, sediment export rates, macroborer erosion rate, parrotfish species, size and abundance, urchin abundance and size (21 variables)	• Used published literature for sediment composition, production and export rates • Uses published data for parrotfish bioerosion rates • Some of the coral growth rates are also calculated using published rates • No assessment of chemical erosion or microbioerosion	Hamylton & Mallela (2019)
2019	Great Chagos Bank, Peros Banhos, Salomon in the Chagos Archipelago	This study used the modified ReefBudget approach for the Indo-Pacific to assess the impacts of a warming event on gross carbonate production rates	Living coral cover, CCA and non-encrusting coralline algal cover, turf and fleshy macroalgal cover, *Halimeda* cover, sand, rubble and reef framework cover, rugosity, coral composition, shape and size, growth rates and skeletal density (15 variables)	This study was based the modified ReefBudget approach (Perry 2015b) with the following differences: • Only included an assessment of carbonate production from corals and key algal species • No assessment of erosion (biological, physical or mechanical) was included • Coral growth rates were assumed to be consistent across biogeographic regions and throughout the bleaching event	Lange & Perry (2019)

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Table 1 (*Continued*) All published (field) census-based carbonate budget studies to date. Studies that utilized indirect measures of net carbonate production (e.g. hydro-chemical or reef cores) have been excluded from this list. For each study, we provide details on the overall approach used, the variables measured (total number of variables in brackets) and related assumptions. Note that only those carbonate budget studies that incorporate gross carbonate production (including corals) are included

Year	Location/s	Approach used and key processes	Key variables and total number used	Assumptions and exclusions	References
2019	Mahutigala reef, Gaafu Dhaalu Atoll, Maldives	This study uses the modified ReefBudget approach for the Indo-Pacific to assess the impact of a warm SST anomaly event on net carbonate production for a reef platform	Live and dead coral cover, CCA and algae cover, rubble and reef framework cover, rugosity, coral composition, shape, growth rates and skeletal density, CCA growth rates, parrotfish bioerosion rates, urchin genera, abundance and erosion rates, micro- and macrobioerosion rates (18 variables)	• Same assumptions as the previously published ReefBudget methods (Perry et al. 2012, 2015b) • Study also assumes that parrotfish bioerosion rates are the same as that recorded for the fore reef (as opposed to the reef flat) in 2016 • Zones of high productivity post-bleaching are now *Heliopora* dominated for which there are no calcification rates available • No correction for inter-blade spaces in benthic cover estimates of *Heliopora*, i.e. likely overestimates carbonate production	Ryan et al. (2019)
2019	Bonaire fringing reef, Caribbean	This study uses the original ReefBudget approach to estimate both net carbonate production and associated reef growth	Same as Perry et al. (2012) study, with the addition of maximum reef height and sponge-specific erosion rates (27 variables)	Same as Perry et al. (2012) with some modifications that include • Takes into account the impact of depth on coral growth rates • The contribution of sponges to gross bioerosion was determined using species-specific erosion rates per unit of infested substrate as defined by De Bakker et al. (2018) • There was some modification to estimates of bioerosion from parrotfish	De Bakker et al. (2019)

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Table 1 (*Continued*) All published (field) census-based carbonate budget studies to date. Studies that utilized indirect measures of net carbonate production (e.g. hydro-chemical or reef cores) have been excluded from this list. For each study, we provide details on the overall approach used, the variables measured (total number of variables in brackets) and related assumptions. Note that only those carbonate budget studies that incorporate gross carbonate production (including corals) are included

Year	Location/s	Approach used and key processes	Key variables and total number used	Assumptions and exclusions	References
2020	Offshore coral reefs, Singapore	This study uses the modified ReefBudget approach for the Indo-Pacific to assess net carbonate production for a highly urbanized reef system	Living coral cover, CCA and non-encrusting coralline algal cover, turf and fleshy macroalgal cover, *Halimeda* cover, sand, rubble and reef framework cover, rugosity, coral composition, shape and size, growth rates and skeletal density, CCA calcification rates, parrotfish species, size and abundance, urchin abundance, size and species, *internal bioerosion rates (macro- and microborers), epilithic algal matrix, microbes and microalgae* (27 variables)	This study was based off of the modified ReefBudget approach (Perry et al. 2015) with some further modifications that include: • Uses published fish and urchin ingestion rates as opposed to measuring activity *in situ* • Uses published ReefBudget coral growth rates for Indo-Pacific corals combined with local growth rates where available • Includes additional methods and variables (in italics) including CCA growth rates and internal bioerosion estimates to provide improved site and time specific data on these variables	Januchowski-Hartley et al. (2020)
2020	Heron Reef, Australia	This study uses the ReefBudget approach to provide a carbonate and sediment budget for five distinct reef zones	Living coral cover, CCA cover, turf and macroalgal cover, *Halimeda* cover and biomass, sand, rubble and reef framework cover, rugosity, coral composition and calcification rates, CCA calcification rates and *Halimeda* sediment production rates, parrotfish species, size and abundance, parrotfish bite rates and mass eroded, external and internal macrobioerosion rates, clinoid sponge cover, microbioerosion rates, carbonate sediment production and dissolution, temperature and light (PAR) (27 variables)	A comprehensive carbonate budget study with the following assumptions/ exclusions: • Uses previously published rates of CCA calcification rates (although from the same study site) • CCA are the only encrusters considered • Only direct sediment producer quantified was *Halimeda* • Parrotfish bioerosion rates based on previous models that estimate carbonate removal based on size and life phase • Rates of carbonate removal by worms and bivalves, and internal bioerosion sourced from the literatures • No estimates of physical erosion • No inclusion of rates of sediment import or export	Brown et al. (2020)

responses will lead to increased wave transmission across reefs and decreased shoreline protection, which will be further exacerbated by sea level rise (Harris et al. 2018). Collapse of reef function can therefore result in increased coastal erosion and inundation (Beetham & Kench 2018). Future landform erosion could lead to loss in terrestrial biodiversity, human displacement and in extreme cases loss of life (Ferrario et al. 2014). Incorporating dynamic modelling approaches with data on reef ecological function and carbonate sediment production, and transport at whole-reef scales would provide key insight into the future maintenance of the entire system under future sea level rise and climate change scenarios.

To respond to the dual challenges of enhancing carbonate budget assessments and advancing them to create predictive capacity in the face of global environmental change, our goal was to create a qualitative geo-ecological carbonate reef system model that links geomorphic, ecological and physical processes. First, we reviewed the history and present applications of **census-based** carbonate budgets and highlight their strengths and weaknesses. Second, we employed a novel model elicitation method that aggregated expert knowledge from key disciplines (ecology, sedimentology, biogeochemistry, coastal geomorphology) to develop a new geo-ecological reef system model. This new model was comprised of six sub-system modules (*in situ* carbonate production, acute disturbance events on coral reef communities, coral reef response to sea level rise impacts, bioerosion, net carbonate sediment production and carbonate sediment transport and depositional sinks) that build on existing carbonate budgets and capture connections to sediment dynamics. For each module, we evaluated all known variables through an extensive literature review and selected dominant variables for inclusion in future carbonate budgets and models. In addition, we provided a semi-quantitative assessment of our collective confidence in the model, which highlights knowledge gaps for future research. We anticipate that our qualitative model will provide a blueprint for future reef system studies that aim to quantify net carbonate production and the sediment production processes that influence landform stability, improving the current capacity to predict responses of reefs and reef-fronted shorelines to future climate change.

Census-based carbonate budgets

The first census-based carbonate budget method was published in 1972 and aimed to understand the theoretical relationships between potential carbonate production, gross production and net production (Chave et al. 1972). Following this landmark study, Stearn et al. (1977) were the first to apply this budget method, which they did on Bellairs Reef, Barbados. This work was shortly followed by Land (1979), who conducted a comprehensive study of reef sediment profiles in Jamaica using seismic scanners and sediment cores to assess reef-wide changes in carbonate production and reef framework development. Over the next 20 years, only seven carbonate budget studies of varying focus (e.g. coral carbonate production, bioerosion, sediment dynamics) and complexity (4–11 variables; Table 1) were published. Since 2000, application of the technique has increased, with 29 published census-based studies (Table 1). These studies have focused on community carbonate production rates, with some studies also incorporating site-specific components of benthic cover (e.g. algal, rubble, sediment cover), bioerosion (e.g. fish and sea urchin grazing; Morgan 2014), environmental variables (e.g. light, suspended sediments, nutrients; Mallela 2007) and mechanical erosion (Harney & Fletcher 2003; Table 1). These later, and largely ecological-focused, studies included a greater number of variables than early geological studies (average 20 variables; maximum 33; Table 1) and, as such, provide a more detailed overview of reef ecological state and accretionary potential.

Since the initial publication of the carbonate budget method, however, a number of challenges have arisen. These challenges relate to three main areas: inclusion of ecological complexity; data collection and application; and inclusion of environmental drivers. In addition to these existing challenges, a number of future challenges for census-based carbonate budget studies also exist. These challenges are critical to consider if predictive tools for reef budgetary state and landform stability are to be realized. Future challenges include the integration of carbonate sediment production, loss and transport, and a comprehensive assessment of landform change (Table 2). Furthermore, carbonate budget studies may benefit from improved integration of the three main data collection approaches (census-based, hydro-chemical, coring) to identify mechanisms responsible for changes in budgets that operate over different timescales as well as enabling direct comparisons between methods. Here, we discuss each of these challenges in turn.

Current challenges for census-based carbonate budget studies

Inclusion of ecological complexity

Ecological assessments in census-based carbonate budgets can be biased towards data that is easier to collect, reducing accurate representations of ecological complexity. In other words, the more accessible the data, the more likely it is to be included in an assessment. For example, the most commonly reported variables in carbonate budgets relate to benthic cover (living coral cover – 100%, dead coral cover – 68%, sand/sediment cover – 73% of studies; Table 1). Methods used to estimate benthic cover are relatively easy to carry out (e.g. line intercept transect) because they do not require expensive equipment and can be conducted in a relatively short timeframe (days; English et al. 1997). As such, a large amount of data on benthic cover can be collected quickly.

In contrast, those variables less commonly reported are ones for which the data take longer to collect, such as erosion from borers (39% of studies). Boring organisms are typically small to microscopic, often patchily distributed (e.g. bivalves) and are cryptic in nature (e.g. sponges, polychaetes; Diaz & Rützler 2001, Pari et al. 2002, Hutchings 2011, Schönberg et al. 2017). As a result, their abundance and erosion rates cannot necessarily be determined visually along a transect but instead require, for example, high levels of expertize and expensive analytical equipment (e.g. scanning electron microscopy) to both locate and identify organisms and assess rates of carbonate removal (Enochs et al. 2016, Färber et al. 2016). Other problems arise because internal rates of bioerosion are likely to be non-linear (e.g. Roff et al. 2020), requiring the deployment of experimental substrates over long-time periods (years), onto which these organisms recruit (Pari et al. 1998, Pari et al 2002, Tribollet 2008a,b, Enochs et al 2016, Silbiger et al. 2017). Additionally, their interactions with each other and the environment can be complex (e.g. featuring successional and disruptional feedbacks, Schönberg et al. 2017, Roff et al. 2015b), yet census-based carbonate budget calculations often rely on an 'average' value of bioerosion from snap-shot *in situ* experiments. Long-term studies, expensive equipment and high level of expertize require additional investment of resources, which are limited for many research projects. The consequences of generating assessments that are biased towards easily accessible data (e.g. data from rapid visual assessments) is that key components of the carbonate budget are likely to be under or mis-represented and the estimated net carbonate production may be incomplete or inaccurate.

Data collection and application

Existing studies have typically used different methods to generate data. For instance, estimates of *in situ* calcification rates commonly require the use of two or more different methods to estimate skeletal density and linear growth (review by Fitzer et al. 2019; also see Table 3) due to variable coral morphology (e.g. branching, plating and massive). For example, corals with massive morphologies, and some branching morphologies (e.g. *Isopora* spp.), are long-lived and produce regular annual density bands that enable growth rate measurements along a relatively well-defined growth axis v(Lough & Barnes 1992, Cantin & Lough 2014, Razak et al, 2020). Massive corals, however, grow slowly (~1 $cm{\cdot}yr^{-1}$), and calcification rate measurements require the use of x-radiography to identify

Table 2 Summary of current (1–3) and future challenges (4–5) of census-based carbonate budget studies. For each challenge, we summarize why it exists, potential associated impacts and how it can be addressed

Current challenge	Why it exits	Impact/s	Addressing the limitation
1. Inclusion of ecological complexity	• Logistical difficulties associated with certain variables or processes that results in a bias towards data that are easier to collect • Lack of resources to support those more expensive or time-consuming methodologies • A diversity of organisms to include • Perception that some variables are not important due to a lack of knowledge and/or understanding	• Key variables (or processes) of the carbonate budget are under-represented and the estimated net carbonate production may, therefore, be inaccurate	• *Improve current understanding on which variables are key for carbonate budgets and should be included*
2. Data collection (methods and variables) and application	• Lack of resources (e.g. time and money) • Diversity of methods available • Differences in reef types and settings leading to different variables and related methodologies	• Inability to compare data across sites accurately	• *Improve current understanding on which variables are key for carbonate budgets and should be included* • Develop standardized methods that better quantify key variables, e.g. physical erosion • Conduct studies that quantitatively compare different methods to assess inter-useability
3. Inclusion of environmental drivers	• Carbonate budgets are skewed towards biological carbonate production and loss • Logistical difficulties related to methodological requirements (e.g. sediment transport) • Lack of knowledge and understanding of non-biological processes that influence carbonate budgets (e.g. dissolution)	• Incomplete assessment of net carbonate production on a reef. • Furthermore, the lack of environmental data with carbonate budget data reduces ability to predict future changes in net carbonate production	• *Improve current understanding on which variables are key for carbonate budgets and should be included* • Highlight the value of environmental (cause) data with biological data (effect) for future carbonate models

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Table 2 (*Continued*) Summary of current (1–3) and future challenges (4–5) of census-based carbonate budget studies. For each challenge, we summarize why it exists, potential associated impacts and how it can be addressed

Current challenge	Why it exits	Impact/s	Addressing the limitation
4. Integration of carbonate sediment production, loss and transport	• Methodological difficulties associated with quantifying sediment production • The assumption that the dissolution of existing carbonate sediments is not important (lack knowledge and understanding) • The assumption that carbonate sediments do not contribute to the development of the reef structure	• Rates of carbonate sediment production on coral reefs are poorly quantified, plus a common assumption is that sediments are lost from the carbonate system • Poor understanding of how disturbance-related shifts in reef communities alter rates and types of reef sediment production • Difficult to assess the impacts of future climate change (e.g. OA) on existing detrital sediment reservoirs (e.g. islands)	• *Identify which variables are key to quantifying net carbonate sediment production* • More quantitative studies (including carbonate budget studies) on direct sediment production • More studies that aim to provide better methods (using new technologies) to accurately quantify rates of carbonate sediment production for a range of calcifying taxa
5. Assessments of landform stability	• Limited carbonate sediment production studies due to methodological issues/ difficulties • Logistical and methodological difficulties due to our limited understanding of timescales of biological sediment production and physical sediment transport • Carbonate budgets were never designed to explicitly address these connections	• Difficult to predict how changes in sediment production will influence the stability of associated landforms	• *Identify variables (and processes) key to understanding how changes in reef carbonate sediment production influence landform stability* • Multi-disciplinary (and novel) studies that assess biophysical processes and interactions across a range of timescales • More carbonate budget studies that assess the whole-system (reefs to landforms)

Note: Text in italics indicate areas that are addressed within the geo-ecological carbonate reef system model.

annual growth bands together with quantification of skeletal density using methods such as X-ray computed tomography (Table 3). In contrast, corals with a branching morphology grow relatively fast (3–15 $cm{\cdot}yr^{-1}$; Crabbe & Smith 2005, Browne 2012, Morgan & Kench 2012, Pratchett et al. 2015) and are typically the dominant reef building taxa on structurally complex coral reefs (Perry et al. 2018a). Yet, many branching and plating corals lack density banding and are instead characterized by complex growth morphologies, making estimates of calcification more challenging and time-consuming to measure. For branching and plate corals, these methods include visual estimates of changing branch or plate length (e.g. direct linear measurements); buoyant weighing to quantify changes in skeletal mass; skeletal staining to quantify changes in colony growth; and photogrammetry to capture changes in the size of individual colonies in an area of reef (Table 3). To date, few studies normalize growth rates to colony surface area to enable comparisons between the calcification rates of corals that vary in size or morphology, and no study has quantitatively compared these three methods to determine their inter-useability.

One of the main limitations that arises when different methods (and variables) are used is an inability to compare data across sites accurately. Site comparisons are useful for a number of reasons. For example, they provide comparisons between reef types and regions, which is important for assessing broad-scale ecological and reef budgetary states. In addition, site comparisons can be used to identify those reefs that are either more sensitive and/or resilient to future climate changes, which is critical for conservation management actions. Accurate site comparison relies on studies that use the same measured variables and data collection methods, or methods for converting between different collection methods to provide meaningful comparisons.

The ReefBudget census-based approach published in 2012 has made significant steps towards enabling ecological comparisons across a range of spatial scales (Perry et al. 2012). This approach builds on the traditional census-based carbonate budget (e.g. Chave et al. 1972; Table 1, Land 1979, Hubbard et al. 1990) and provides a standardized and rapid method to calculate reef carbonate production and bioerosion via the collection of abundance data on calcifying and eroding organisms. Prior to 2012, carbonate budgets were estimated using a variety of variables (i.e. organisms and their activity, processes; Table 1) and methods (Table 3). In contrast, the ReefBudget approach combines the collection of site-specific data on over 20 selected variables that can be measured within a few days (e.g. coral cover and composition) with previously published data on variables that require longer timeframes to measure (e.g. coral and CCA growth rates and urchin, fish, macroborers and microbioerosion rates). If employed over several years along permanent transects, the ReefBudget approach can be used to track changes in net carbonate production over time, identify changes in reef state (decline, stable, incline) from natural cycles in reef health (e.g. Manzello et al. 2018) and assess impacts of major disturbance events (e.g. Lange & Perry 2019). Furthermore, the approach allows for comparisons among reef habitats (e.g. Perry et al. 2017, Brown et al. 2020) and across biogeographic regions (Perry et al. 2018b), and has since been used in more than 50% of all census-based carbonate budget studies (Table 1). Despite the benefits of this comparison method, a number of challenges remain.

Inclusion of environmental drivers

Census-based assessments capture direct *in situ* metrics of carbonate production and removal, and as such provide limited or no insight into how these processes are influenced by, or respond to, environmental drivers (e.g. light, temperature, water flow). Our comparison of census-based budgets found that, although all reef and benthic cover variables were well described, very few studies (16%) had quantified local environmental variables (e.g. temperature, light, turbidity) when conducting carbonate budgets (Table 1). Thus, because census-based carbonate budgets capture *in situ* metrics of carbonate potential/removal, they typically lack environmental observations, reducing the ability to assess how production/removal processes are influenced by, or respond to,

Table 3 A summary of the variables currently used in census-based carbonate budgets with associated methods and potential limitations

Area	Organism or process	Variable	Explanation	Associated variables	Common methods	Comments	References
Carbonate framework production	Coral	Calcification rate	Corals are typically the main carbonate producer particularly on tropical coral reefs. Due to variable coral morphology both among and within coral species, there are a number of different techniques that address one or more aspects of coral growth. For branching corals, linear extension refers to an increase in length (cm) along the branches growth axis whereas for encrusting, plating or foliose corals an increase in surface area (cm^2) is more common. For those massive corals other techniques that look at changes in total volume (cm^3) are preferred. These variables can then be used to determine the calcification rate (e.g. linear extension * skeletal density). Coral calcification rate can also be measured using the buoyant weight technique and changes in weight can then be normalized to colony surface area (i.e. grams or kg of $CaCO_3$ per unit of surface area per unit in time). The total alkalinity (TA) depletion method is used to measure coral calcification because TA changes in response to the precipitation and dissolution of $CaCO_3$	Linear extension	1. Direct linear measurement *in situ* using callipers along the branch axis. Small cable ties can be put in place on the branch as a point of reference for repeated measurements	Measures the increase in length of the branch over a known time period, but is time intensive and limited to branching corals	Crabbe & Smith (2005), Morgan & Kench (2012)

(*Continued*)

Table 3 (*Continued*) A summary of the variables currently used in census-based carbonate budgets with associated methods and potential limitations

Area	Organism or process	Variable	Explanation	Associated variables	Common methods	Comments	References
Carbonate framework production (cont.)	Coral (cont.)	Calcification rate (cont.)	See previous page	Linear extension (cont.)	2. Alizarin red to stain corals *in situ* to create a 'time stamp' on the coral skeleton for future measurements. Corals are placed in an enclosed volume (e.g. a plastic bag) into which the dye is injected. The bag is left over the coral colony for ~4 hours before it is removed. Samples from the coral colony or the whole colony is later retrieved. In the laboratory, the coral tissue is removed to expose the under lying skeleton. Newly laid skeleton (post-dying) is white and old skeleton is pink	Provides an estimate of the weight of new carbonate produced over a known time but is time intensive and destructive to coral community. It can, however, be used on all coral morphologies that can be enclosed in an isolated environment (e.g. plastic bag) for staining	Crossland (1981), Browne (2012), Morgan & Kench (2012)
					3. X-radiography of corals to assess annual density banding in massive corals	Typically only useful for massive corals with distinctive growth bands; destructive and expensive as corals have to be removed	Lough & Barnes (1992); Cantin & Lough (2014)

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Table 3 (*Continued*) A summary of the variables currently used in census-based carbonate budgets with associated methods and potential limitations

Area	Organism or process	Variable	Explanation	Associated variables	Common methods	Comments	References
Carbonate framework production (cont.),	Coral (cont.)	Calcification rate (cont.)	See previous page	Linear extension (cont.)	4. Photogrammetry *in situ* to track change in linear extension and volume over time	A non-destructive technique that estimates increases in coral volume of the whole coral colony over a known timeframe but requires expertize in post-processing of photos. Further changes in volume can only identified from photos when a threshold of change has been reached (e.g. a few mm)	Ferrari et al. (2017), Lange & Perry (2020)
				Surface area	1. Bird's-eye photographs of corals collected and analysed for surface area using computer software (e.g. CpCE)	Comparatively easy and quick but accuracy of the surface areas is highly dependent on coral morphology with better estimates for 'flat' corals	Courtney et al. (2007), Holmes et al. (2008); Browne et al. (2015)
				Surface area	1. Paraffin wax and foil wrapping to determine surface area. Individual colonies are either foil wrapped or coated in paraffin wax. The foil can then be unwrapped to determine the surface area. The paraffin wax technique relies on changes in weight (associated with surface area) using a calibration curve (created using objects of known surface area)	Destructive and can be labour-intensive, but can be applied to all coral morphologies	Marsh 1970; Stimson & Kinzie (1991)

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Table 3 (*Continued*) A summary of the variables currently used in census-based carbonate budgets with associated methods and potential limitations

Area	Organism or process	Variable	Explanation	Associated variables	Common methods	Comments	References
Carbonate framework production (cont.)	Coral (cont.)	Calcification rate (cont.)	See previous page	Surface area (cont.)	2. X-ray computer tomography (CT) and 3D scans of branching coral colonies collected and analysed for surface area	This destructive technique is considered to be the most accurate for surface area estimates but can be labour-intensive and requires expensive equipment	Laforsh et al. (2008), Naumann et al. (2009), Foster et al. (2014), Ross et al. (2015)
				Skeletal density	1. X-ray computer tomography (CT) scans of massive coral cores have been used to calculate annual growth rates, skeletal density and coral calcification rates	Destructive and expensive but provides data on a number of key coral parameters	Cantin et al (2010), DeCarlo et al. (2017)
					2. Water displacement technique where a known weight of coral (sealed in wax) displaces a measured volume of water	Comparatively easy and cheap, but has potential for errors if not replicated appropriately	Bucher et al. (1998); Morgan & Kench (2012)
					3. Gamma densitometry: The use of gamma rays provides an important non-destructive method for determining the density along predetermined tracks	Destructive as it requires samples to be cut to a consistent thickness. However, provides excellent high-resolution, coral skeleton density data	Chalker & Barnes (1990), Lough & Barnes (1992)

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Table 3 (*Continued*) A summary of the variables currently used in census-based carbonate budgets with associated methods and potential limitations

Area	Organism or process	Variable	Explanation	Associated variables	Common methods	Comments	References
Carbonate framework production (cont.)	Coral (cont.)	Calcification rate (cont.),	See previous page	Volume change	1. Photogrammetry (as above)	As above	Ferrari et al. (2015); Lange & Perry (2020)
				Total alkalinity depletion	1. Coral colonies are maintained in water chambers with water samples taken for Total Alkalinity (TA) analysis to quantify coral calcification rates	Labour-intensive method that requires expensive equipment and laboratory analysis	Smith & Kinsey (1978), Schneider & Erez (2006), Sawall et al. (2015)
				Buoyant weight	1. Coral colonies are weighed while submerged in water to obtain skeletal weight. Repeat measurements of skeletal weight over time is used to quantify calcification rate	Direct, accurate, and non-destructive. Beneficial for whole coral colonies, especially those with complex morphologies. This method overcomes the issues of intra-colony density variation and skeletal infilling over time for common genera (e.g. *Acropora*) and is non-destructive allowing the same colony to be measured repeatedly over time. Inexpensive but can be labour-intensive	Bak (1973), Jokiel et al. (1978), Roik et al. (2015) for literature review table of calcification rates measured using buoyant weight

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Table 3 (*Continued*) A summary of the variables currently used in census-based carbonate budgets with associated methods and potential limitations

Area	Organism or process	Variable	Explanation	Associated variables	Common methods	Comments	References
Carbonate framework production (cont.)	Coral (cont.)	Abundance	The percentage coral cover (per coral species and/or morphology) is used to calculate the weight of carbonate produced (together with the calcification rate) per area per year	Benthic cover	1. Transects conducted using either line intercept transect or photographs or video of the benthos	Transects are cheap and relatively quick to conduct but relie on appropriate experimental design to accurately capture a true representation of benthic cover	English et al. (1997), Jonker et al. (2008)
					2. Photogrammetry can be used to create detailed three-dimensional habitat maps of the reef	Non-destructive technique but requires expertize in post-processing of photos, and may require expensive equipment (e.g. RoV) to provide a whole reef habitat map	Burns et al. (2015), Price et al. (2019)
		Population	The average size of the coral colony (per species and/or morphology) is required to determine the surface area over which new carbonate will be laid (as the coral grows), i.e. calcification rate is a function of the standing coral population size distribution	Coral size distribution	1. Transects conducted to count number of coral colonies in size classes	Transects are cheap and relatively quick to conduct but relie on appropriate experimental design to accurately capture a true representation of population size structure	English et al. (1997), Jonker et al. (2008)
					2. Photogrammetry can be used to create detailed three-dimensional habitat maps from which coral sizes can be estimated for part or the whole reef coral population	As above	Ferrari et al. (2015), Palma et al. (2019)

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Table 3 (*Continued*) A summary of the variables currently used in census-based carbonate budgets with associated methods and potential limitations

Area	Organism or process	Variable	Explanation	Associated variables	Common methods	Comments	References
Carbonate framework production (cont.)	Encrusters	Abundance	Encrusters include organisms such as CCA, serpulid worms, bryozoans etc. They provide additional carbonate to the reef and play important roles in reef cementation and larval recruitment. To determine their contribution to the carbonate budget, percentage cover of encrusters is required	Benthic cover	1. Deployment of tiles or pipes (ceramic, PVC) for a few months to a few years. On removal, the tiles (or pipes) are photographed and analysed using imaging software to determine the percentage cover for the different encrusting taxa over a known area	Tiles are a quick and easy method to assess cover for key encrusters. Key considerations in tile deployment are the length of time (with longer timeframes >1 year considered to be more accurate) and orientation of tiles to assess potential differences between cryptic versus exposed encrusting communities. Different artificial substrates preferentially attract different encrusting organisms (e.g. PVC promotes CCA). Controls with natural substrates should be run to account for these differences	Mallela (2007), Browne et al. (2013); Morgan & Kench (2014); Kennedy et al. (2017); Mallela et al. (2017)
		Calcification rates	Rates of calcification are typically calculated for the total encrusting population due to the difficulties around separating rates per organism	Calcification rates	1. Deployment of tiles or pipes (ceramic, PVC) for a few months to a few years. On removal, the tiles (or pipes) are placed in acid bath (5% HCl) or vinegar (acetic acid) to dissolve the calcium carbonate. Calcification rates are determined using the weight of carbonate normalized to the known area (cm^2) and unit of time (year)	The calculated calcification rate per tile represents the total encrusting community as it is difficult to separate out different rates for different organisms. Some studies have specified a rate per organism (e.g. CCA, serpulids, bryozoans, etc.)	Mallela (2007), Browne et al. (2013), Kuffner et al. (2013), Mallela (2013), Morgan & Kench (2014), Kennedy et al. (2017)

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Table 3 (*Continued*) A summary of the variables currently used in census-based carbonate budgets with associated methods and potential limitations

Area	Organism or process	Variable	Explanation	Associated variables	Common methods	Comments	References
Carbonate framework production (cont.)	Encrusters (cont.)	Calcification rate (cont.)	See previous page	Calcification rates (cont.)	2. The use of *in situ* respirometry chambers or *ex situ* flume chambers to measure calcification rates of CCA. Water samples from the chambers are taken over short periods of time and then regressed against environmental variables (to integrate 24-hour periods) to assess changes in oxygen, pH and total alkalinity (or isotope incorporation), which are then used to track changes in CCA calcification rates	This method provides a detailed assessment of CCA calcification rates over time and with changing environmental conditions, and is one of the few accurate measurements for understanding adult calcification rates *in situ*. It is, however, a labour-intensive method that requires expensive equipment and laboratory analyses. If insufficient time periods are integrated, or too few individuals, it can also yield substantial variation in data	Chisholm et al. (1990), Chisholm & Gattuso (1991), Tambutte et al. (1995), Chisholm (2000), Martin et al. (2013), Comeau et al. (2015), Cohen et al. (2017), Batista et al. (2020)
Carbonate framework removal and sediment production	Parrotfish bioeroders	Abundance	The number of parrotfish is critical in calculating the total weight of carbonate removed from the reef framework	Number of fish	The number of parrotfish are counted along replicate belt transects (30 m by 5 m)	Relatively easy, quick and cheap to conduct, but is reliant on diver experience and expertize	Frydl & Stearn (1978), Scoffin et al. (1980), Perry et al. (2012)

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Table 3 (*Continued*) A summary of the variables currently used in census-based carbonate budgets with associated methods and potential limitations

Area	Organism or process	Variable	Explanation	Associated variables	Common methods	Comments	References
Carbonate framework removal and sediment production (cont.)	Parrotfish bioeroders (cont.)	Population	The size of the fish is directly related to the erosional rate	Size class	During the belt transects, parrotfish length is estimated into different size classes	Relatively easy, quick and cheap to conduct, but is reliant on diver experience and expertize. The use of a calibrated stereo-video system (DOV) could improve data collection and provide a means of data quality check, but has yet to be employed in published carbonate budget studies	
		Activity	The level of parrotfish bioerosion is also dependent on the feeding behaviour of the fish and size of the bite it takes during feeding	Bite rates	Direct observations of parrotfish feeding *in situ*. The observer records the number bites per min and substrate on which the parrotfish was feeding (e.g. live coral, dead coral, rubble)	Relatively easy, quick and cheap to conduct, but is reliant on diver experience and expertize	Bellwood & Choat (1990), Bellwood (1996), Bruggemann et al. (1994, 1996), Morgan & Kench (2016a); Yarlett at al. (2018)
				Bite volume	During direct observations of parrotfish feeding, the size of the scar on the substrate from the parrotfish is measured *in situ* using callipers and photographed	Relatively easy, quick and cheap to conduct, but volumes calculated are typically an overestimation of the actual volume as the maximum width and length are used to calculate it	

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Table 3 (*Continued*) A summary of the variables currently used in census-based carbonate budgets with associated methods and potential limitations

Area	Organism or process	Variable	Explanation	Associated variables	Common methods	Comments	References
Carbonate framework removal and sediment production (cont.)	Urchin bioeroders	Abundance	The number of urchins (*Diadema* and *Echinothrix* spp.) is critical in calculating the total weight of carbonate removed from the reef framework	Number of urchins	The number of urchins is counted along a belt transect (e.g. 2 m by 10 m)	Relatively easy, quick and cheap to conduct, but urchins are cryptic animals so care needs to be taken to search under ledges and in crevices. It would be beneficial to conduct transects at night as urchins are typically more active during this time	Scoffin et al. (1980), Bak (1994), Perry et al. (2012)
		Population	The erosional rate of urchins is largely a function of size and species with larger individuals causing more erosion	Urchin test size	During belt transects, urchins (per species) are tallied into set urchin size categories		
		Activity	The feeding activity of urchins is directly linked to erosional rates	Erosional rate	Estimates of bioerosional rates can be conducted by analysing gut content or faecal pellets	This method will provide a more accurate estimate of urchin erosion rates as opposed to estimating rates from the urchin test size, but requires additional laboratory analysis. Estimates need to account for carbonate clastic ratios in faecal sediment.	Glynn et al. (1979); Conand et al. (1997); Morgan (2014); Mallela & Perry (2007)
	Other macroborers	Sponge	Sponge cover (similar to density and abundance) is necessary to calculate total carbonate removed	Sponge cover	Estimates are typically made from substrate availability estimates (e.g. dead coral) and take into account the reef complexity (see rugosity below) and a visual estimate of sponge cover from benthic transects	It is very difficult to measure sponge cover accurately as sponges will invade coral skeletons internally. Hence, estimates could potentially be vastly underestimating the amount of sponge in the system	Rutzler (1975); Glynn (1997); Lopes-Victoria & Zea (2005), Schonberg (2015)

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Table 3 (*Continued*) A summary of the variables currently used in census-based carbonate budgets with associated methods and potential limitations

Area	Organism or process	Variable	Explanation	Associated variables	Common methods	Comments	References
Carbonate framework removal and sediment production (cont.)	Other macroborers (cont.)	Sponge (cont.)	Sponge erosion rates are known to be influenced by the substrate (e.g. dead versus live coral) and coral density, and will vary with nutrient concentration and aragonite saturation	Sponge erosion rate	Through the collection of rubble samples or the deployment of carbonate blocks, the rate of carbonate loss can be calculated. Rubble samples are typically cut into cross sections and volume of bioeroded material is estimated from the void volumes per bioeroding taxa and calculated to a rate by determining the timeframe of substrate available for bioerosion. The blocks can also be CT scanned before and after deployment to provide the same variables	Unless rubble samples are C_{14} dated, estimates of timeframes of substrate availability could be inaccurate and would have a considerable influence on the final calculated erosion rates. The use of blocks does overcome this limitation, but the length of time blocks needs to be deployed for to allow the establishment of a 'typical' bioerosional community (e.g. >3 years) may far exceed timeframe available for the study	Stearn & Scoffin (1977), Kiene & Hutchings (1994), Risk et al. (1995), Morgan (2014)
		Polychaetes	Bioeroding worms are considered to occur exclusively in dead coral and can be an important bioeroder for reefs exposed to high amounts of nutrients	Polychaete density	Deployment of carbonate blocks (e.g. *Porites*) for a few months to years. On collection and treatment of the blocks, the number of individuals are estimated per block volume	This method likely provides an accurate assessment of polychaete density but will depend on timeframes for deployment with long timeframes more likely to give a better estimation of polychaete densities on the reef	Sammarco & Risk (1990), Hutchings et al. (2008)
				Polychaete erosion rate	As per sponge erosion rate	As per sponge erosion rate	

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Table 3 (*Continued*) A summary of the variables currently used in census-based carbonate budgets with associated methods and potential limitations

Area	Organism or process	Variable	Explanation	Associated variables	Common methods	Comments	References
Carbonate framework removal and sediment production (cont.)	Other macroborers	Bivalves	Bivalves can also be a key boring organism across a range of reef depths although can occur in patchy distributions	Bivalve density	As per polychaete density	As per polychaete density	Sammarco & Risk (1990), Hutchings et al. (2008)
(cont.)				Bivalve erosion rate	As per sponge erosion rate	As per sponge erosion rate	
	Microborers	Microborers	The importance of microborers for carbonate budgets is poorly understood and little data exists on their bioerosion rates	Microborer density and bioerosion rates	Deployment of carbonate blocks (e.g. *Porites*) for a few months to years. Subsamples of the blocks can then be scanned using either a light or scanning electron microscope (SEM)	Estimates of rates of microbioerosion likely to be relatively accurate (if blocks left out for a few years) but requires extensive time and expertize for the data collection	Chazottes et al. (1995), Chazottes et al. (2002), Tribollet et al. (2002)
	Physical erosion (currently poorly captured in census-based carbonate budgets)	Cyclonic events		Coral breakage threshold	Theoretical modelling based on approximating coral shape as standard geometries (e.g. cylinder) combined with hydrodynamic modelling (computational fluid dynamics, phase-averaged wave models); mechanical/structural integrity testing (compressive/tensile strength tests)	Limited to no direct observations of measured hydrodynamic force leading to coral breakage/fracture (e.g. flume/wave tank experiment)	Rodgers et al. (2003), Madin (2005), Storlazzi et al. (2005), Baldock et al. (2014b)

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Table 3 (*Continued*) A summary of the variables currently used in census-based carbonate budgets with associated methods and potential limitations

Area	Organism or process	Variable	Explanation	Associated variables	Common methods	Comments	References
Carbonate framework removal and sediment production (cont.)	Physical erosion (cont.)	Cyclonic events (cont.)		Volume of breakage	Combined analysis of above (breakage threshold) with *in situ* data on coral cover/ morphology; 'trait-based' approaches		Massel & Done (1993), Storlazzi et al. (2005), Madin & Connolly (2006), Baldock et al. (2014a), Madin et al. (2014)
Direct sediment production	Direct sediment producers	Abundance	Direct sediment producers are those organisms that contribute directly to reef sediments upon death (e.g. molluscs, foraminifera, calcareous algae, echinoids, crustaceans, serpulid casings, sponge spicules). Their abundance in reef sediments is critical to determine their relative importance to the carbonate sediment budget		Reef sediment samples are collected and sieved into sieve fractions (commonly 4, 3, 2, 1, 0, –1 phi). For each size fraction 100–300 grains are identified to taxa level under either a compound microscope or a petrographic microscope following the embedding of sediments into epoxy and thin sectioning	The collection of sediments is quick and cheap, and a lot of data can be collected in a short timeframe. The laboratory analysis requires sedimentology expertize and can take several weeks to months to complete the data collection (depending on the number of grains per sieve fraction)	Harney et al. (2000), Browne et al. (2013), Morgan (2014), Morgan & Kench (2016b), Perry et al. (2019)

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Table 3 (*Continued*) A summary of the variables currently used in census-based carbonate budgets with associated methods and potential limitations

Area	Organism or process	Variable	Explanation	Associated variables	Common methods	Comments	References
Direct sediment production (cont.)	Direct sediment producers (cont.)	Sediment volume	Calcification rates from direct sediment producers need to be normalized to a known volume of sediment, which is turn is converted to a weight (kg) per area (m^2) by taking into account the average sediment depth (m)		The collection of sediments (by hand) from the reef benthos using a container of known volume pressed into the reef benthos	This is a very imprecize method that relies on diver sediment collection techniques and experience. As such, there is a large potential for error in sediment volume estimates	Harney et al. (2000), Browne et al. (2013), Perry et al. (2017)
		Turnover rates	Turnover rates provide an estimate of carbonate release rates into the system when the organism dies. For example, a turnover rate of 2 per year implies that within a year there will typically be 2 populations of living assemblages contributing to reef sediments		To estimate turnover rates, data on annual sediment production rates as well as the weight of the standing living assemblage collected over several months (to determine when organisms die) is required. This method is most commonly used for foraminifera and molluscs	This method requires collection of sediments over several months and the subsequent analysis of both the living and dead assemblages. This is extremely labour-intensive and requires a high level of expertize. There has been no advancement in methods since the 1990s and limited data on this variable is available	Hallock (1981), Hallock et al. (1995)

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Table 3 (*Continued*) A summary of the variables currently used in census-based carbonate budgets with associated methods and potential limitations

Area	Organism or process	Variable	Explanation	Associated variables	Common methods	Comments	References
Direct sediment production (cont.)	Direct sediment producers (cont.)	Turnover rates	See previous page		For calcareous algae (e.g. *Halimeda*), turnover rates are from the number of new segments produced over time using the Alizarin staining method (see corals)	The staining period is short (approx two weeks) due to fast growth but should be replicated throughout the year. Field surveys of algal biomass can be very time-consuming if in high abundance. New algal growth segments are often lightly calcified sediments, i.e. may not be representative of heavily calcified basal segments/whole plant. Once growth and calcification rates are known, you must then convert to a rate and must know number of crops per year, for which there are often very little data available. New growth can be grazed by fish, which can lead to an underestimation of calcification/turnover rates	Multer (1988), Freile & Hills (1997), Vroom et al. (2003), Perry et al. (2016, 2019)
Carbonate sediment loss	Chemical erosion	Sediment dissolution	Dissolution is a loss term as the sediments dissolve into the overlying water	Alkalinity fluxes	Benthic chambers are placed *in situ* on the sediment surface and the change in alkalinity concentration over time is measured	Need to make sure alkalinity flux is only derived from dissolution of carbonate sediments, and not anaerobic processes like sulphate reduction	Cyronak et al. (2013), Eyre et al. (2018)

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Table 3 (*Continued*) A summary of the variables currently used in census-based carbonate budgets with associated methods and potential limitations

Area	Organism or process	Variable	Explanation	Associated variables	Common methods	Comments	References
Carbonate sediment loss (cont.)	Chemical erosion (cont.)	Sediment dissolution (cont.)	See previous page	Alkalinity fluxes (cont.)	Sediment is placed in *ex situ* flumes and the change in alkalinity concentration over time is measured	*Ex situ* so need to make sure conditions reflect *in situ* conditions	Lantz et al. (2020)
				Pore water carbonate chemistry	Pore water wells	Sampling distinct depths is difficult in permeable sands	Drupp et al. (2016)
Reef factors	Habitat complexity	Rugosity (or roughness)	Rugosity is a measure of reef habitat complexity. This variable is used to calculate the actual surface area available for carbonate production by multiplying the planar surface area by a measure of rugosity. Rugosity is defined as a measure of deformation or roughness of the reef surface (Dustan et al. 2013; Denis et al. 2017).		The traditional method of measuring rugosity is to lay a fine chain over the reef benthos ensuring that it closely follows the substrate. The length of the chain is divided by the straight line between the same two points. Values of 1 represent a flat surface whereas values >2 indicate a rugose surface	This method is easy, cheap and quick to carry out, and can be used to collect lots of data points. However, it is difficult to replicate over time given the diver bias associated with laying the chain and it only provides a measure of two-dimensional changes in reef complexity	Risk (1972), Dahl (1973), Friedman et al. (2012), Perry (2012), Dee et al. (in review)

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Table 3 (*Continued*) A summary of the variables currently used in census-based carbonate budgets with associated methods and potential limitations

Area	Organism or process	Variable	Explanation	Associated variables	Common methods	Comments	References
Reef factors (cont.)	Habitat complexity (cont.)	Rugosity (cont.)	See previous page		Using photogrammetry *in situ* to capture three-dimensional habitat maps and changes in reef complexity	The collection of photographs by the diver along set transects is relatively straight forward. However, the post-processing of the data requires specific software, computing power and expertize. This is potentially the best method for capturing reef complexity	Leon et al. (2015), Storlazzi et al. (2016), Bryson et al. (2017), Anelli et al. (2019), Bayley (2019)
					Remote sensing (either from satellites or airborne LiDAR) to collect high-resolution digital elevation models	This technique provides the highest spatial resolution over the largest reef areas. It involves dividing the surface area of the reef (incorporating the fine scale complexity of features such as corals) by the planar surface area, accounting for the slope of the reef surface. However, the technique is expensive and its ability to identify small scales changes in rugosity is heavily dependent on the data collection parameters (e.g. pixel size)	Hamylton (2014), Du Preez (2015), Hamylton et al. (2017), Purkis (2018), Hamylton & Mallela (2019), Dee et al. (2020)

environmental change. Future carbonate budget studies should aim to capture physical drivers (e.g. hydrodynamics, nutrients, temperature and seawater carbonate chemistry) and develop empirical relationships for rate of change between two co-dependent variables (e.g. nutrient concentration and macroboring). Doing so could, for example, enable budgets to be applied to reefs where logistical difficulties prevent the collection of (multiple) data on variables that require more resources (e.g. time and money). For example, Langdon et al. (2000) examined empirical relationships by defining linear coral growth curves for several coral genera that related to aragonite saturation state. These types of studies, particularly those that target highly variable aspects of the carbonate budget (e.g. coral growth rates; Anderson et al. 2017, Lewis et al. 2017), would reduce the use of non-site-specific data and, therefore, increase the accuracy of the carbonate budget. A more complete understanding of the physical and chemical drivers that are typically quantified in geomorphological and biogeochemical studies will also enable the expansion of carbonate budgets beyond censuses and towards reef-scale processes, such as reef framework accretion or shoreline dynamics.

An important example of an environmental driver and associated variables rarely reported is flow velocity and rates of physical or mechanical erosion (1 of the 38 published census-based studies; Harney & Fletcher 2003). Physical erosion relates to the loss of carbonate material due to the force of water over the reef surface (Hubbard et al. 1990). This form of erosion is most obvious during storm and cyclonic events when current flow velocities and wave forces increase, resulting in coral breakage and increased coral rubble production (Massel & Done 1993, Storlazzi et al. 2005). Flow velocity and rates of physical erosion can therefore have significant effects on carbonate budgets as well as the transport of rubble (and sand) from reefs to shorelines (Massel & Done 1993, Madin et al. 2014). Yet, the responses to these acute events (e.g. cyclones) and their impact on carbonate budgets are often difficult to capture due to the need to collect pre- and post-event measurements. To date, estimates of reef accretion from census-based carbonate budget have focused on reef accretion ‘potential’ (RAP; Perry et al. 2018b), which assumes that the impacts of physical erosion are consistent between locations and through time due to a lack of existing data. Yet, the relative importance of environmental drivers, such as flow velocity, will vary among reef types and settings, with associated rates of physical erosion being more critical for shallow reefs and those found in cyclone hotspots (Fabricius et al. 2008, Puotinen et al. 2016). Therefore, consideration of environmental drivers and how they influence reef system processes is key for determining how the system (and budget) will respond to acute events (e.g. bleaching, cyclones) and future climate change.

Future challenges for census-based carbonate budget studies

The application of census-based carbonate budgets as a predictive tool for reef budgetary state and landform stability will require integrating data on sediment dynamics (production, loss and transport) and landform stability. These inclusions will require recognising differences in temporal and spatial scales between ecological processes (days to decades, millimetre to metres), sediment transport processes (seconds to decades, millimetre to kilometres) and reef accretionary processes (decades to centuries, metres to kilometres). In terms of temporal scales, census-based carbonate budgets record ecological processes that occur over annual timescales, yet it is not clear how such processes of coral growth and bioerosion scale up to longer-term (decadal and longer) processes of reef construction, sediment infilling and cementation of reef frameworks (Roff 2020). In terms of spatial scales, understanding how carbonate budgets translate from reef habitats (e.g. reef crest) to whole reef-scale processes is also challenging and requires insight into net carbonate production and sediment flux at larger spatial scales than previously considered in carbonate budget approaches (e.g. Morgan & Kench 2016b).

Integration of carbonate sediment production, loss and transport

Traditionally, carbonate budget studies have inadequately quantified critical processes relating to reef sediments (i.e. the carbonate sediment budget). Although carbonate sediments have no influence on a reef's budgetary state, they influence long-term rates of reef accretion through framework infilling ($mm \cdot yr^{-1}$; Ginsburg 1983, Hubbard et al. 1990, Milliman 1993), as well as providing the carbonate material for shoreline maintenance (Morgan & Kench 2014, Perry et al. 2015a, Cuttler et al. 2019). Of the 38 published census-based carbonate budget studies, only eight provide data on carbonate sediment production rates (e.g. Harney & Fletcher 2003, Browne et al. 2013, Morgan & Kench 2014, Brown et al. 2020), only four provide estimates on sediment transport within and off-reef (e.g. Land 1979, Hubbard et al. 1990), and only one includes sediment dissolution rates (Brown et al. 2020; Table 1). Lack of inclusion of data on carbonate sediment production in most carbonate budgets is likely due to at least one of two main reasons. First, these data could be lacking due to the technical and logistical difficulties in accurately quantifying sediment production and subsequent transport and deposition (Sadd 1984, Harney & Fletcher 2003, Morgan & Kench 2014, Cuttler et al. 2019, Castro-Sanguino et al. 2020). Secondly, and potentially more importantly, the amount of carbonate sediment produced relative to *in situ* carbonate production (e.g. corals) is in most (but not all) cases comparatively small (e.g. Browne et al. 2013). In contrast, the lack of data on carbonate sediment dissolution is most likely because it was not considered important in early carbonate budgets (Eyre et al. 2014). If, however, we are to expand the scope of carbonate budgets beyond the reef framework and consider the larger spatial connection between reefs and associated landforms, the inclusion of the carbonate sediment dynamics will be a necessary step. For example, carbonate budgets could be linked to sediment dynamics through the quantification of 'net sediment available', which would be derived from classical census-based budget calculations. This 'net sediment' is then available for transport through the system and/or deposition within various sediment sinks (lagoons, beaches, etc.).

For those studies that have incorporated carbonate sediments into their budgetary calculations (often termed the carbonate sediment budget), a number of sediment-related variables have been measured to assess the abundance of direct sediment producers per volume of sediment (e.g. sediment composition, particle size, sediment depth). These variables are relatively straightforward to measure because they rely on the collection of surface sediment over a known area and sediment depth (Harney & Fletcher 2003, Browne et al. 2013). The practical difficulties here relate to estimating rates of sediment production (activity of the organisms), which requires determining turnover rates in populations of direct sediment producers (e.g. foraminifera, molluscs, bryozoans, *Halimeda*). Turnover rates, defined as 'fraction of the total amount of a substance ($CaCO_3$) in a component (organism) that is released in a given length of time' (Odum 1959), provide an estimate of carbonate release rates into the system when the organism dies. To measure turnover rates effectively, data on annual sediment production, as well as weight of the standing 'living' assemblage collected over several months, are required (Hallock 1981). Such measurements are logistically difficult to collect because they require extensive (and multiple) field sampling, followed by a considerable amount of microscopic laboratory work by an experienced field taxonomist for a large number of species or molecular analysis. Very few carbonate budget studies have the resources required to support the time and expertize required to complete these analyses accurately.

As a result of these challenges associated with estimating carbonate sediment production, many carbonate budget studies have adopted pre-existing sediment production rates. Studies that calculated turnover rates were largely carried out during the 1970s and 1980s (Hallock 1981, Drew 1983, Kay & Kawamoto 1983, Hallock et al. 1995). These original rates have been extensively used in subsequent carbonate budget studies (e.g. Harney & Fletcher 2003, Browne et al. 2013), despite the likelihood of differences in environmental conditions (e.g. light and nutrients) on reefs, which drive turnover rates. As such, most carbonate budget studies either ignore sediment production or have non-site-specific estimations of sediment production rates. It remains, therefore, very difficult to determine the importance of carbonate sediments to reef framework infilling, density and stability, and evaluate how sediment production will be affected by future climate change, specifically increased sediment dissolution from ocean acidification (Cyronak et al. 2013, Eyre et al. 2014, Cyronak & Eyre 2016). To further determine outcomes of shifts in sediment production for the maintenance and stability of associated landforms, census-based carbonate budget studies need to consider reef-scale carbonate sediment production and transport processes (see Morgan & Kench 2016b).

Assessments of landform stability

To date, no census-based carbonate budget has incorporated links between reef carbonate sediment production and associated landform stability. Yet these links are necessary to capture if we are to quantify how changes in reef budgetary state relate to carbonate sediment supply and coastal sediment budgets. Reef-fronted shorelines (e.g. beaches and islands) are some of the most at risk landforms to climate change due to their low-lying nature and reliance on reef-derived sediment (Storlazzi et al. 2018). However, our ability to quantify, and potentially mitigate, the threats to these shorelines is poor. The hazards to these landforms include both changes in physical drivers (e.g. future sea level rise and changing wave climate) and ecological shifts (e.g. loss in coral cover and reduced carbonate production) in response to warming seas and ocean acidification (Reyns et al. 2013).

Although we can assess the response of physical processes to future change (e.g. model wave or water level variability at the shoreline in response to reduced reef rugosity; Grady et al. 2013; Harris et al. 2018), quantifying links between ecological (sediment generation) and geomorphic processes (sediment transport, shoreline erosion/accretion), and therefore predicting future landform stability, remains a challenge. The link between sediment production and reef-fronted shorelines is further confounded by our limited understanding of the timescales of sediment production, dissolution and transport mechanisms. For example, previous studies have shown that the active sediment reservoir (i.e. lagoon and beach) can be comprised of either contemporary (<100 years old; Yamano et al. 2000, Dawson et al. 2012) or ancient/relic (longer-time scales of sediment supply; Harney et al. 2000, Cuttler et al. 2019) reef-derived material. However, few studies quantify transport mechanisms and rates due to methodological difficulties in tracking sediment particles over large spatial scales (Hubbard et al. 1990, Storlazzi et al. 2004, Becker et al. 2007, Morgan & Kench 2014, Pomeroy et al. 2017, Cuttler et al. 2019), and the effect of dissolution on sediment supply for reef-fronted beaches has yet to be considered. Thus, the timescales of sediment delivery to reef-fronted landforms (beaches, islands) are poorly resolved. Given that the sensitivity of these landforms is strongly linked to ecological shifts in reef organisms that produce carbonate, a multi-disciplinary approach (ecologists, sedimentologists, biogeochemists and coastal geomorphologists) is required to assess and resolve differences in timescales over which these processes operate (e.g. seconds to years to decades).

Integrating census-based, hydro-chemical and geological carbonate budgets

Of the three carbonate budget approaches detailed above, we have focused on the census-based approach because it is the only method that attempts to differentiate among key organisms, drivers and processes (variables) on ecologically relevant (weeks to months) and measurable timescales. These considerations are paramount in the development of a quantitative model that can calculate how changes in variables (over different spatial and temporal scales) lead to changes in outputs, such as net carbonate production and reef accretion. Critically, census-based budgets quantify loss from the system, which is becoming increasingly relevant information to capture as widespread reef degradation begins to switch many reefs into net negative budgetary states (Perry et al. 2013b). Future studies may consider combining, comparing and/or reconciling data among methods to provide further insights into future reef trajectories, although they will have to overcome current limitations as described below.

The main advantage of the hydro-chemical approach is that it provides a higher temporal resolution (real-time) assessment of net reef calcification than the census-based approach and can be used to investigate daily and seasonal differences (Lange et al. 2020). But these instantaneous, snap-shot readings do not provide an accurate representation of longer-term rates (years) of net carbonate production and cannot differentiate between co-varying (dominant) environmental variables or other co-varying processes (Lange et al. 2020), which are better captured using the census-based approach. Recently, Cornwall et al. (2021) conducted a meta-analysis of coral reef taxa calcification and bioerosion rates from 142 studies, ranging from *in situ* and laboratory coral and CCA calcification to full census-based carbonate budgets and hydro-chemical studies, to predict the impacts of climate change on net reef carbonate production rates on 183 reefs worldwide. This study highlighted that the largest issue when attempting to integrate and compare data between census-based and hydro-chemical methods related to rates of carbonate loss (e.g. bioerosion by physical and chemical processes). At present, there are insufficient measurements of the contribution of different bioeroding organisms (that use either physical, chemical or both processes) to total bioerosion. This data paucity makes it difficult to determine the contribution of physical and chemical erosion to total bioerosion rates when using either the hydro-chemical or census-based approach. For example, some components of chemical bioerosion are inherently measured in hydro-chemical budgets, but physical erosion is rarely considered. Given that bioerosion by physical eroders has been found (on some reefs) to be greater than the sum of net carbonate production, estimating long-term net carbonate production via the hydro-chemical method could be problematic in locations where physical erosion is not included.

Geological cores provide net estimates of carbonate accumulation and reef accretion over decades to centuries, but are spatially limited and cannot differentiate rates at fine temporal resolutions (<1–2 years). Few studies have attempted to combine core and census-based data, and of those that have, there has been mixed success. Browne et al. (2013) found that the hindcast rates of reef accretion using contemporary rates of net carbonate production from census-based methods and sediment budget data were remarkably similar to core data collected for two inshore turbid reefs on the GBR. However, Roff (2020) found that ecological processes (as measured using the census-based method) were decoupled from the geological processes (as measured using the geological cores) resulting in different rates of reef accretion. The study provided possible hypotheses that may account for this decoupling including (1) the transportation of carbonate material off-reef, (2) higher rates of bioerosion in core data than observed in present-day carbonate budget assessments and (3) the inclusion of non-carbonate material into the reef framework. Therefore, the extent of decoupling between ecological processes, which heavily focus on carbonate production, and long-term reef accretion will depend on the relative importance of processes that are either poorly understood (e.g. sediment inputs/removal) and/or not typically captured in census-based carbonate budgets. It should be noted, however, that both studies were conducted on turbid reefs where sediments promote rapid reef accretion rates, so it is unclear whether a closer coupling between processes would be observed on clear-water reef systems (e.g. atolls) where external sediment inputs are limited. Regardless, studies that attempt to include both approaches yield important insights into site-specific processes and their relative importance to future reef trajectories.

Summary

Coral reefs are complex systems that exhibit significant spatial and temporal variation. They are influenced by, and in turn influence, a number of geomorphological, ecological and physical processes, which are challenging to both understand and integrate. Advancing beyond census-based carbonate budgets and developing a reliable geo-ecological carbonate reef system model, however, is increasingly necessary as ecological and human communities face the exacerbating threats of climate change. Climate change has the capacity to influence all of the processes within the reef system, leading to considerable implications for populations that rely on these systems.

Here, we develop a geo-ecological carbonate reef system model that goes beyond the scope of the traditional census-based carbonate budget by incorporating sediment production (sediment budget) and sediment transport and sinks (e.g. reef-fronted shorelines; Figure 1). The model also

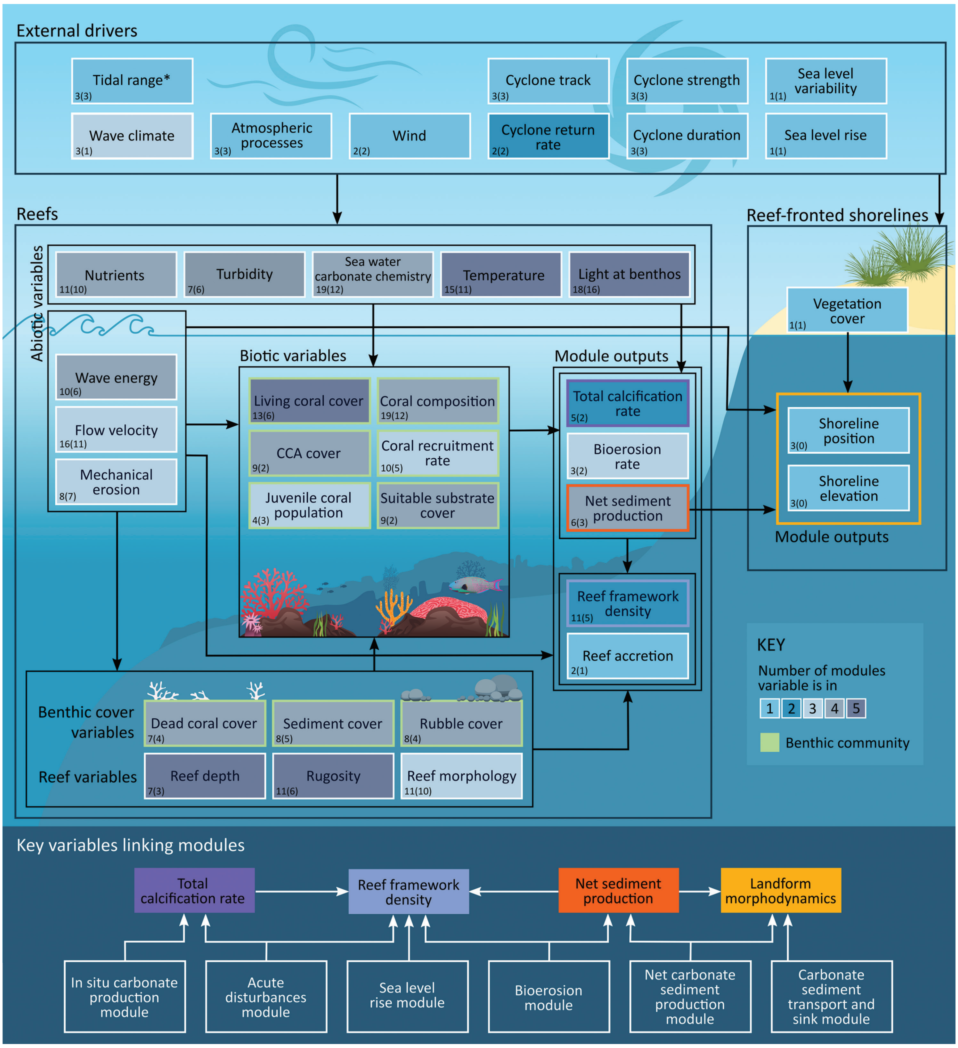

Figure 1 A high-level summary of the geo-ecological carbonate reef system model, which contains 80 variables and 265 relationships. Here, we identify 31 critical variables (with seven output variables) for modelling reef carbonate budgets, sediment transport and landform stability. Variables were considered critical if they were integrated into three or more modules (Reefs box) and/or were root nodes and considered to have a pervasive influence throughout the system (external drivers' box). All external drivers (except 'Tidal range') are influenced by anthropogenic climate change (or are a co-variate), which in turn influence local conditions (e.g. temperature). Additional regional and local anthropogenic impacts (e.g. eutrophication, sediment runoff) are captured in the abiotic variables box (e.g. nutrients and turbidity). Each variable is provided with a number combination in the bottom left-hand corner (measure of centrality). These numbers indicate how connected and influential this variable is among all modules. For example, living coral cover – 13(6) – has a total of 13 arrows connecting it to the system, of which six are influential arrows (leaving the variable). Variables are grouped into categories (e.g. biotic variables), and broad influential relationships between categories are provided by the directional arrows. For specific details, please refer to the module sections. Module outputs are highlighted in the bottom panel (e.g. total calcification rate) together with a 'map' of how the six modules are linked (through their module outputs) within the complete geo-ecological model. Colours used here are also incorporated within module models to illustrate which variables are required within modules to estimate module outputs. For example, all those variables in dark blue (e.g. total calcification rate) in the module models relate to total calcification rates and carbonate production.

responds to the present and future challenges for carbonate budgets (complexity, data collection, environmental drivers, integration of sediments and landform stability) by deconstructing current census-based budgets and examining specifically how the system functions. As such, the first step in producing a geo-ecological carbonate reef system model is to determine (1) which variables are necessary to include; (2) how those variables interact with one another; and (3) what methods or knowledge we have to support the quantification of both variables and the relationships between them. This reconstruction delivers a conceptual, qualitative model that documents the full suite of carbonate reef system variables and their relationships. Below, we outline the method used to develop a conceptual, qualitative geo-ecological carbonate reef system model. This novel framework can provide the context for establishing a new quantitative model that can be used to determine a reliable and comprehensive estimate of net carbonate production for a reef under existing and future conditions.

Our approach – a novel model elicitation method

We developed a novel model elicitation method to develop the first conceptual, qualitative geo-ecological carbonate reef system model. This method was specifically designed for developing a shared, expert-elicited qualitative model (see Table 4 for modelling terminology) of a complex system. Here, we describe the relevant details for this reef model, but for further details, refer to Moon & Browne (2020). The method comprises four phases: (1) module development; (2) elicitation method development; (3) elicitation of individual mental models; and (4) co-creation of the shared qualitative model (Moon & Browne 2020; Figure 2).

Phase 1: Module development

The coral reef and associated landform 'system' was disaggregated into smaller sub-system modules that each represented a functioning unit focused on either a key process or an element (Table 4) of the reef carbonate system (Table 5). For example, the first sub-system module (1) '*in situ* carbonate production', focused on corals and CCA carbonate production where the dominant process is calcification in the form of calcium carbonate ($CaCO_3$). Other modules included acute disturbance events on coral reef communities (2), coral reef response to sea level rise impacts (3), bioerosion (4), net carbonate sediment production (5), and carbonate sediment transport and depositional sinks

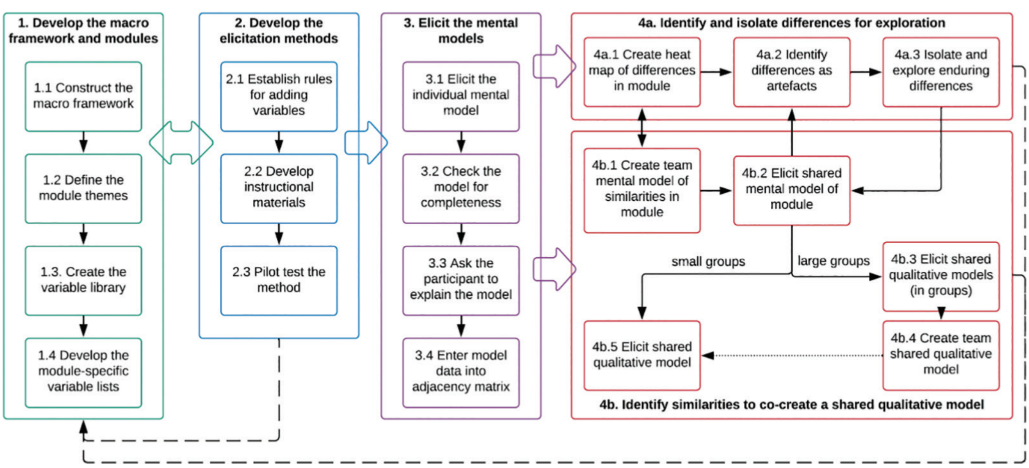

Figure 2 Overview of the mental modelling method for complex systems from Moon & Browne (2020).

Table 4 Definitions for eliciting mental models, and describing variables and relationships within mental models

Term	Definition
Geo-ecological carbonate reef system model	A model that includes all known variables that influence carbonate budgets and tracks reef health with carbonate sediment production and associated landform change. Here, the reef system is broken down into six sub-system modules
Sub-system modules	A sub-system module will focus on a dominant process or element that is integral to the complex system framework. The sub-system module should be a functioning unit of the system framework, i.e. a model in its own right with a defined output
Mental model	A mental model is an individual's internal model of the (sub-) system
Team mental model	A team mental model represents two or more individuals' mental models of a (sub-)system that have been elicited and aggregated
Shared qualitative model	A shared qualitative system model represents two or more individuals' agreed model of a (sub-) system. Development of the shared mental model can be supported by the team mental model
Variable library	The variable library consists of all known variables for all sub-system modules that may be included in the modelling process along with their definitions and associated units
Variable list	Sub-system specific list of variables the modeller uses in the elicitation of their model
Functioning unit	A defined sub-system that can be modelled separately to produce a defined and tangible output
Processes	A series of actions required to achieve an end goal. For example, biological processes include many chemical reactions that result in change and relate to a living organism
System elements	Entities, such as organisms, minerals and chemicals
Rooted nodes	Variables that are the first node in a rooted (directed) graph, which all paths originate from. These variables essentially 'drive' the system as they have a pervasive influence through the whole model
In and out degrees	These refer to the direction of relationships (arrows). In degrees refer to the number of arrows going into the variable in the conceptual model, and out degrees refer to the number of arrows leaving the variable
Variable centrality	The level of variable centrality indicates the number of relationships the variable has. For example, high degree of centrality suggests a number of relationships with other variables

Table 5 A summary of the six sub-system modules outlining the dominant process (P) or element (E.) for modelling together with their dominant driver and module output

Module	Dominant process (P) or system element (E)	Number of variables	Dominant driver	Module output
1. *In situ* carbonate production	Calcification (P)	28	Local environmental drivers (e.g. temperature, light)	Total calcification rate
2. Acute disturbance events on coral reef communities	Coral community (E)	36	Physical erosion (e.g. cyclones) and local environmental drivers (e.g. temperature, DHW)	Total calcification rate
3. Coral reef response to sea level rise	Reef accretion (P)	27	Sea level rise	Reef framework density and reef accretion
4. Bioerosion	Bioerosion (P)	23	Environmental drivers (e.g. nutrients, temperature) and benthic cover	Net sediment production and reef framework density
5. Net carbonate sediment production	Carbonate sediments (E)	28	Environmental drivers (e.g. temperature, nutrients) and physical erosion	Net sediment production
6. Carbonate sediment transport and depositional sinks	Sediment transport (P) and island change (P)	21	Reef hydrodynamics	Shoreline position and elevation

(6; Table 5). These sub-system modules represent targeted knowledge areas for which an individual is more likely to have more comprehensive knowledge and, therefore, a better understanding of how variables are linked within the system.

Phase 2: Elicitation method development

To elicit individual mental models of these six sub-system modules, we developed and tested instructional materials (e.g. instructional video, written instructions, and a variable library with 110 variables) (Phase 2). Model elicitation was conducted remotely and participants self-elicited their mental models, which were digitally recorded in PowerPoint. Models (expressed as digraphs) included three main components: (1) an arrow from one variable to another to indicate the direction of influence, (2) an assessment of participant's perception of the strength of each influence (1= weak to 5 = strong) and (3) an assessment of their level of confidence in their knowledge for each influence (a = low, b= moderate, c = high confidence).

We developed the elicitation method for the qualitative model to serve three main purposes. First, we sought to elicit an individual model from each participant. This output was important in determining both the breadth, but also the diversity and relative confidence of knowledge within a given domain. We elicited the model by asking participants to use the same variables, which enabled quantitative comparison between individual models. Second, we sought to create a team mental model, which involved representing those relationships that were common across sub-system models within modules, but also identifying those relationships that were present in fewer models. Similarities were important to identify because they assisted in determining the overall confidence in underpinning knowledge within the model. Meanwhile, differences were important to identify because they enabled exploration of existing knowledge and associated gaps. Third, we sought to elicit a shared qualitative sub-system model of the module, on the basis of both the individual and team models. The individual and team models supported engagement and discussion on variables and relationships, providing an important 'starting point' for elicitation of the shared model.

Phase 3: Elicitation of individual mental models

For each module, mental models were self-elicited from four to six experts (i.e. a total 28 mental models elicited; Phase 3). We developed the elicitation method to support a modular approach. Modellers were purposely selected according to their area of expertize and assigned a specific module (Table 5). Each modeller was provided with information about the whole geo-ecological carbonate reef system model, including a full list of variables and definitions across all six sub-system modules (Table 6). Modellers were asked, however, to focus on *their* module and its associated output/s.

We developed the elicitation method for the qualitative model with the intention of building towards a quantifiable model. With this goal in mind, we collected data pertaining to each relationship that would provide insight into the likelihood or capacity of quantifying each relationship. We therefore asked each modeller to 'qualify' each of the relationships they recorded. Modellers were asked to classify each relationship on the basis of (1) their perception of the strength of the influence (1 – weak to 5 – strong) and (2) their confidence of the existence of that relationship (a – low to c – high). This step in the elicitation process revealed critical knowledge gaps.

The confidence ratings proved useful in two main ways. First, they provided information as to the extent of existing knowledge of the relationships between variables within carbonate reef systems. Of the 265 relationships identified among module models, 74% were rated with high confidence, 17% were rated at moderate confidence, and 9% were rated with low confidence. Second, they provided opportunities to identify knowledge gaps and determine future research needs. Future research needs were revealed by the relationships rated with low confidence and/or where there was

Table 6 List of variables used in model development together with their units and definition

Type	Units	All variables	Definition
Environmental		Atmospheric processes:	Physical processes in the atmosphere (see below for specific variables*)
	ppm	*Greenhouse gases (atmospheric processes)	Atmospheric concentrations of greenhouse gases (i.e. carbon dioxide, methane, nitrous oxide, ozone, water vapour)
	W/m^{-2}	*Solar radiation (atmospheric processes)	Rate of energy received per unit area
	N/A	*Atmospheric convection (atmospheric processes)	Convection currents in the atmosphere (e.g. driver of ENSO)
	$\mu g \cdot L^{-1}$	Chlorophyll-a	Concentration of chlorophyll-a in the surface waters
	hours	Cyclone duration	The duration of the cyclone over a point
	years	Cyclone return rate	Frequency of cyclone occurrences in an area
	scale	Cyclone strength	Cyclone strength measured from 1 to 5 with 5 being the strongest
	km	Cyclone track	The distance in km from the shoreline and the track of the cyclone
	N/A	Degree heating weeks	Degree heating week (DHW) indicates how much heat stress has accumulated in an area over 12 weeks by adding up any temperature that exceeds the bleaching threshold during that time period
	$m \cdot s^{-1}$	Flow velocity	General term for the speed of water motions throughout the reef system including mean currents, tidal currents and wave orbital velocities
	PAR	Light at benthos	Photosynthetic active radiation (PAR) available at the benthos from 400 to 700 nm
	kg or kg yr^{-1}	Mechanical erosion	Amount of reef material broken down by physical processes (waves, grain–grain interaction during transport)
	$\mu mol \cdot L^{-1}$	Nutrients	Using nitrate as a proxy for nutrient pollution
	$L \cdot m^{-2} \cdot day^{-1}$	Pore water advection	Physically driven flow of seawater through permeable sediments
	pH	Pore water pH	pH of the sediment pore water
	$cm \cdot yr^{-1}$	Sea level rise	The rate of current sea level rise at a location
	m	Sea level variability	Non-tidal fluctuation of local sea level above still water depth occurring on seasonal to interannual timescales (excluding sea level rise)
	^{o}C	Temperature	Represents *in situ* temperature at the benthos
		Seawater carbonate chemistry:	Seawater carbonate chemistry (see below for specific variables*)
	mmol kg^{-1}	*Seawater dissolved inorganic carbon (DIC)	Sum of inorganic carbon species
	N/A	*Seawater pH	pH of the seawater

(*Continued*)

Table 6 (*Continued*) List of variables used in model development together with their units and definition

Type	Units	All variables	Definition
Environmental (cont.)	$mmol \cdot kg^{-1}$	*Seawater total alkalinity	Total alkalinity of the seawater
	N/A	*Seawater saturation state (W)	Saturation state of the seawater
	$mg \cdot cm^{-2} day^{-1}$	Sedimentation	The daily rate of sediments settling on the benthos per area
	m	Tidal range	The difference between the average lowest and average highest tidal cycle
	$mg \cdot L^{-1}$	Turbidity	Concentration of suspended sediments in the water column above the reef benthos
	m, s, deg	Wave climate	Regional-scale (order 10s–100s of kms) average wave characteristics (wave height, wave period and direction)
	$kW \cdot m^{-1}$	Wave energy	Local-scale (order kms) wave characteristics that result from the interaction of the regional wave climate with local bathymetry and reef morphology. Wave energy is proportional to the product of wave height squared and wave period
	m	Wave setup	Increase in mean sea level ('still water') due to wave breaking
	$m\ s^{-1}$	Wind	Magnitude and direction of wind
Reef factors	%	CCA cover	The percentage of the reef area covered in CCA
	%	Living coral cover	The percentage of the reef area covered in living coral cover
	%	Dead coral cover	The percentage of the reef area covered in dead coral cover
	%	Macroalgal cover	The percentage of the reef area covered in macroalgae
	%	Rubble cover	The percentage of the reef area covered in rubble
	%	Suitable substrate cover	Indurated limestone (including dead coral, cemented rubble, bioeroded limestone) suitable for coral and algal settlement
	%	Colonisable substrate	Hard surfaces (generally freshly dead coral surfaces, but in cases also living coral, coralline algae) suitable for settlement of internal reef bioeroders
	%	Grazable substrate	Benthic surfaces (generally turf covered framework, but also coralline algae, and in some cases, live coral) suitable for grazing by external bioeroders (bioeroding urchins, fish and molluscs)
	$mm\ yr^{-1}$	Reef accretion	Rate of vertical reef growth
	m	Reef depth	The difference between the height of the reef flat and the bottom of the reef slope where corals stop growing
	$kg \cdot m^{-3}$	Reef framework density	The mass of the reef carbonate framework per unit of volume. This takes into account the weight of carbonate but also the void volume
	N/A	Reef morphology	Geomorphological structural features of an individual reef, characterized by differences in combinations of depth (light), slope and exposure (water flow), dominated by different substrate types and often hosting different benthic communities. Examples include fore reef slope, reef flat, channel width and lagoon
	$m^2 \cdot m^{-2}$	Rugosity	The measure of deformation or roughness of the reef surface
	$min \cdot m^{-2}$	Herbivory	The rate of fish grazing intensity per area of reef substrate
In situ carbonate production	cm	Coral diametre	The average width of corals on the reef

(*Continued*)

Table 6 (*Continued*) List of variables used in model development together with their units and definition

Type	Units	All variables	Definition
In situ carbonate production (cont.)	cm	Coral height	The average height of corals on the reef
	$cm{\cdot}yr^{-1}$	Coral extension rate	The average rate of linear extension of corals on the reef
	$g{\cdot}cm^{-3}$	Coral skeletal density	The average density of the coral skeleton on the reef
	N/A	Coral composition	Term encompassing the different coral morphologies, genus and species on the reef
	N/A	Coral size distribution	Variable that reflects the population size structure of the living coral community
	no. per m^2	Coral juvenile population	The number of juvenile (<5 cm) corals on the reef
	no. per m^2	Coral recruitment rate	Rate of successful coral recruitment to the reef
	kg $CaCO_3{\cdot}m^{-2}{\cdot}yr^{-1}$	Coral calcification rate	A variable that covers all coral calcification on the reef
	N/A	CCA composition	The species CCA composition on the reef
	kg $CaCO_3{\cdot}m^{-2}{\cdot}yr^{-1}$	CCA calcification rate	The average CCA calcification rate
	N/A	OA sensitivity	The sensitivity of corals to changes in the aragonite saturation
	N/A	Temperature sensitivity	The sensitivity of corals to changes in the temperature
	kg $CaCO_3{\cdot}m^{-2}{\cdot}yr^{-1}$	Total calcification rate	A variable that represents the gross carbonate produced on the reef by all calcifying organisms
Bioerosion	N/A	Biotic controls	Includes factors such as recruitment, disease, predation, competition that influence population densities and size-frequency distributions of reef-associated organisms
	cm	Grazer size	Body size (e.g. fish length, urchin test size) of grazing organisms
	no. ind. per m^2	Grazer density	Abundance per unit area of reef of grazing bioeroders (e.g. bioeroding fish, urchins, molluscs)
	no. ind. per m^2	Macroborer density	Abundance of macroboring bioeroders (e.g. molluscs, sponge, crustaceans, worms) per unit volume of reef framework
	no. ind. per m^2	Microborer density	Infestation per unit volume of reef framework of microboring organisms (all fungi, bacteria, algae) – often measured by % surface area and depth of penetration
	kg $CaCO_3{\cdot}m^{-2}{\cdot}yr^{-1}$	Bioabrasion activity	The rate of physical framework removal from all grazing organisms
	kg $CaCO_3{\cdot}m^{-2}{\cdot}yr^{-1}$	Biocorresion activity	The rate of reef framework removal from macro- and microborers
	kg $CaCO_3{\cdot}m^{-2}{\cdot}yr^{-1}$	Bioerosion rate	The total amount of carbonate removed from the reef framework by both bioabrasion and biocorrosion
Sediments	N/A	Sediment characteristics	This term encompasses all sediment descriptives including size, shape, density and porosity
	%	Sediment cover	The percentage of the reef covered in a sediment layer
	m	Sediment depth	The average depth of the sediment layer at a location
	%	Sediment organic content	The percentage of the sediment layer that contains organic material
	years	Turnover rates	The time it takes for a new population of sediment producers to occur in the sediments

(*Continued*)

Table 6 (*Continued*) List of variables used in model development together with their units and definition

Type	Units	All variables	Definition
Sediments (cont.)	mmol·m^{-2}·day^{-1}	Benthic metabolism	Benthic productivity and respiration
	kg $CaCO_3$·yr^{-2}	Sediment dissolution	The rate of sediment dissolution on the reef
	kg $CaCO_3$·yr^{-2}	Sediment loss	The rate of sediment loss on the reef
	kg $CaCO_3$·m^{-2}·yr^{-1}	Direct sediment production	The rate of carbonate sediment production from direct sediment producers such as *Halimeda*, molluscs, foraminifera and bryozoans
	kg $CaCO_3$·m^{-2}·yr^{-1}	Net sediment production	Amount of carbonate sediment produced from direct and indirect sediment producers minus sediment loss from dissolution
	kg $CaCO_3$·m^{-2}·yr^{-1}	Sediment re-incorporation	The rate of sediment infilling of the reef framework
	kg CaCO3·m^{-1}·yr^{-1}	Aeolian transport	The amount of sediment transported by wind
	kg CaCO3·m^{-1}·yr^{-1}	Bed load transport	The amount of sediment transported as bed load
	kg $CaCO_3$·m^{-2}·yr^{-1}	Lagoon infilling	The rate of sediment supply to lagoon areas
	kg $CaCO_3$·m^{-2}·yr^{-1}	Off-reef sediment export	The rate of sediment loss via the transport of sediments off the reef (into deeper water)
	kg $CaCO_3$·yr^{-2}	Suspended load transport	The amount of carbonate sediment transported in suspension
Landforms	%	Beach rock armouring	Percentage of shoreline made up of bedrock
	m	Shoreline position	Horizontal position of the shoreline
	m	Shoreline elevation	Maximum height of the cross-shore beach profile
	%	Vegetation cover	The percentage of the subaerial landform covered in vegetation

Note: Note that there are two variables (atmospheric processes and seawater carbonate chemistry) that include several important processes that have been further defined (*).

a lack of empirical data to support the relationship, representing significant gaps in our knowledge and understanding.

Given our intention of quantifying the model, we sought an additional data set during the individual and group (see Phase 4) elicitation processes. We asked participants to document any literature that supported the relationships in the model/s. This step has allowed us to identify where relevant peer-reviewed literature that provides empirical data that explains or quantifies relationships exists (Table 7).

Phase 4: Co-creation of shared qualitative system model

After the remote self-elicitation process, we invited modellers to attend a two-day workshop. The first day of the workshop involved organising modellers according to their module group. They were asked to elicit a shared model of their module, on the basis of the team model (i.e. aggregated individual models) provided to them. They were also provided with all of the individual models that comprised the team model for sharing and comparison. Each of the phases of elicitation was accompanied by the creation of a knowledge database to support each of the relationships described. This database was deemed critical in moving towards a quantitative geo-ecological carbonate reef system model.

Table 7 Reference list for Figures 3–8 together with a description of sub-system module relationships

Module	Process	Description	Relationships	References
In situ carbonate production	Drivers of the key *environmental* parameters	Atmospheric processes such as increases in anthropogenic CO_2 reduce seawater pH (seawater carbonate chemistry) through a process known as ocean acidification. Macroalgae influences the seawater carbonate chemistry by drawing down CO_2 through photosynthesis and may mitigate the negative effects of OA. Macroalgae productivity is influenced by nutrient flux, temperature and light. Coral reef primary producers modify their seawater carbon chemistry during calcification whereby there is a release of H+ during the conversion of bicarbonate to carbonate	1–6	Atmospheric processes (greenhouse gases) and seawater carbonate chemistry: Caldeira & Wickett (2003), Feely et al. (2004), Sabine et al. (2004), Raven et al. (2005). Macroalgae and seawater carbonate chemistry: Delille et al. (2009), Cornwall et al. (2013). Macroalgae and OA: Cornwall et al. (2013), Rivest et al. (2017), Wahl et al. (2018). Macroalgae and temperature, nutrients and light: Carpenter et al. (1991), Renken et al. (2010), Smith et al. (2010), Reef et al. (2012), Ji et al. (2016). Calcification and seawater carbonate chemistry: Cohen (2003), Jokiel (2011), Ries (2011), Anthony et al. (2013)
		Atmospheric processes influence temperature and DHW because solar radiation penetrating the surface of the oceans is responsible for warming of the surface layers. Greenhouse gases warm the atmosphere, which reduces the amount of heat lost to the atmosphere from the ocean surface, allowing the oceans to steadily warm over time. Water flow velocities influence water residence time and therefore temperature and DHW. Temperature influences the solubility of CO_2 in the surface oceans and the carbonic acid constants	7–10	Temperature and carbon dioxide solubility: Dickson & Millero (1987)
		Flow velocities influence sediment cover	11	Storlazzi et al. (2011)
		Reef depth influences the light reaching the benthos. Chlorophyll-a increases with light and nutrients and causes increased turbidity. Turbidity (water cloudiness) attenuates light in the water column and can reduce light reaching the benthos	12–16	See review by Gattuso et al. (2006)
	Benthic cover, species composition and coral recruitment (*benthic community*)	Seawater carbonate chemistry influences CCA cover	17	Hall-Spencer et al. (2008), Fabricius et al. (2011, 2015), Cornwall et al. (2017)

(*Continued*)

Table 7 (*Continued*) Reference list for Figures 3–8 together with a description of sub-system module relationships

Module	Process	Description	Relationships	References
In situ carbonate production (cont.)	Benthic cover, species composition and coral recruitment (cont.)	Nutrients influences CCA cover	18	Belliveau & Paul (2002), Smith et al. (2010)
		Temperature influences CCA cover	19	*No references for this*
		Light at benthos influences CCA cover due to the production of photosynthetically fixed carbon by the photosynthetic pigments produced by CCA	20	Steneck (1986)
		Flow velocities influence CCA cover	21	*No explicit test of this exists to our knowledge*, but Steneck (1986) discusses some implications
		Suitable substrate cover for colonisation influences CCA cover. Macroalgae (and turf algae) can influence the amount of suitable substrate. High cover of large macroalgae typically has a negative influence, particularly on degraded reefs. For instance, most but not all studies suggest that elevated nutrients drive shifts from high coral cover (low algal cover) to low living coral cover with an accompanying high cover and biomass of fleshy alga influencing the suitable substrate cover. Sediment, rubble and dead coral cover can also influence the amount of suitable substrate cover available	22–24	Suitable substrate and CCA: Steneck (1986). Macroalgae and suitable substrate: Kuffner et al. (2006), Birrell et al. (2008), Hoey et al. (2011), Jorissen et al. (2016). Sediment/rubble/dead coral: Birrell et al. (2005), Cameron et al. (2016). High coral cover to high macroalgae cover: McCook (1999), Hoey et al. (2011), Szmant (2002), Hughes et al. (2007), Jupiter et al. (2008)
		Suitable substrate cover is required for coral recruitment. CCA cover can create more suitable substrate cover for coral recruitment. Some CCA facilitate coral recruitment. Coral recruitment rates can influence the juvenile coral population and therefore influence coral cover. Living coral cover is the adult stock for reproduction, thereby influencing coral recruitment rate, but also coral recruits can arrive from distant (i.e. non-local) adult populations	25–29	Coral cover and recruitment: Bramanti & Edmunds (2016), Hughes et al. (2019). CCA and coral recruitment: Heyward & Negri (1999); Vermeij (2005), Birrell et al. (2008), Tebben et al. (2015), Fabricius et al. (2017)
		Spatial variation in temperature influences the living coral cover. Thermal stress (DHW) resulting in bleaching and/or mortality can also drive changes in living coral cover	30	Moore et al. (2012), Hughes et al. (2018a), Hughes et al. (2019), Gilmour et al. (2019)
		Light at benthos influences coral cover. Different coral taxa have different light preferences	31	Glynn (1976), Harriott & Banks (2002), Francini-filho et al. (2013)

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Table 7 (*Continued*) Reference list for Figures 3–8 together with a description of sub-system module relationships

Module	Process	Description	Relationships	References
In situ carbonate production (cont.)	Benthic cover, species composition and coral recruitment (cont.)	Flow velocities can influence coral cover	32	Grigg (1995), see review by Lowe & Falter (2015)
		Coral and CCA responses to the seawater carbonate chemistry can vary between species and therefore the overall response may vary depending on coral and CCA composition	33	Comeau et al. (2013, 2017a, 2018, 2019a), Schoepf et al. (2013), Cornwall et al. (2017), Okazaki et al. (2017)
		Temperature influences coral composition of species spatially and geographically (e.g. with latitude), and temporally (e.g. repeated stressors over time)	34	Veron (1995), Kleypas et al. (1999), Harriott & Banks (2002), Hughes et al. (2018a,b), Zinke et al. (2018)
		Temperature influences CCA composition of species spatially and geographically (e.g. with latitude) and temporally (e.g. repeated stressors over time)	35	*No assessment of this*
		Reef depth (and hence light reaching benthos) causes vertical zonation and influences coral composition and CCA composition	36	Coral: Kahng & Kelley (2007), Tamir et al. (2019). CCA: Steneck (1986)
	Carbonate production (includes acclamatory and adaption responses, and calcification)	Flow velocities influence OA sensitivity, but the response is species-specific	37	Comeau et al. (2014c, 2019b), Cornwall et al. (2014)
		Coral and CCA composition influences OA sensitivity (different species show different levels of sensitivity)	38	Comeau et al. (2014d, 2017a, 2018, 2019a), Okazaki et al. (2017), Schoepf et al. (2017), Cornwall et al. (2018), DeCarlo et al. (2018), Kornder et al. (2018)
		Light at benthos influences ocean acidification sensitivity	39	Comeau et al. (2013, 2014b), Dufault et al. (2013), Suggett et al. (2013), Enochs et al. (2014)
		Coral and CCA composition will influence temperature sensitivity because different species have varying sensitivity to temperature	40	Coral: Loya et al. (2001), Grottoli et al. (2014). CCA: see review by Cornwall et al. (2019)

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Table 7 (*Continued*) Reference list for Figures 3–8 together with a description of sub-system module relationships

Module	Process	Description	Relationships	References
In situ carbonate production (cont.)	*Carbonate production* (cont.)	Light and flow velocities influence temperature sensitivity (and coral bleaching)	41,42	Light and temperature sensitivity: see review by Fitt et al. (2001), Smith & Birkeland (2007), Brown & Dunne (2008). Water flow and temperature sensitivity: Nakamura & Van Woesik (2001), Nakamura & Yamasaki (2005)
		Changes in coral skeletal density and extension rate (and thus calcification rate) in response to OA will depend on species-specific OA sensitivity	43	Comeau et al. (2014a, 2019a), Okazaki et al. (2017), Cornwall et al. (2018), DeCarlo et al. (2018), Kornder et al. (2018)
		Temperature influences coral calcification rate (skeletal density and extension rate) due to the rate kinetics of aragonite precipitation and temperature driven increases in metabolism. However, the seasonal response of calcification to temperature varies among species and locations	44	Jokiel & Coles (1977), Lough & Barnes (2000), Marshall & Clode (2004), Kuffner et al. (2013), Roik et al. (2015), Ross et al. (2015), Courtney et al. (2017). Variable response of coral calcification rate to temperature: Ross et al. (2018, 2019)
		Nutrients influences coral calcification rate. Very high concentrations can reduce rates of calcification while modest increases can enhance calcification rates	45	Ferrier-Pagès et al. (2000), Koop et al. (2001), Tanaka et al. (2007)
		Changes in external seawater carbonate chemistry can influence the calcification process, given that the calcifying fluid is generally thought to be sourced from seawater. For this reason, seawater carbonate chemistry influences skeletal density and extension rate and thus coral calcification rate. The influence of seawater chemistry on density and extension differs	46, 47	Cohen & Holcomb (2009), Venn et al. (2013), Comeau et al. (2014c, 2017a,b, 2018, 2019a), Schoepf et al. (2017), Cornwall et al. (2018), Kornder et al. (2018), Mollica et al. (2018)
		Temperature sensitivity influences coral calcification rate. Corals are strongly adapted to their local temperatures and different species/genera also show different thermal sensitivities	48	Coles et al. (1976), Jokiel & Coles (1977), Marshall & Clode (2004), Ross et al. (2015), Samiei et al. (2016)
		Water velocities influence coral calcification rate. Water flow influences the boundary layer thickness, and thus, the diffusion of gases, exchange of ions, uptake of nutrients, and transport of metabolites required for physiological processes	49	Patterson et al. (1991), Atkinson & Bilger (1992), Comeau et al. (2014c, 2019b)
		Higher light levels can increase skeletal growth through the increased production of photosynthetically fixed carbon by the symbiont and the production of lipid biomass from translocated photosynthates. Calcification rates are higher in the light than the dark and the relationship between light and calcification rate typically follows a hyperbolic function	50	Chalker & Taylor (1975), Chalker (1981), Gattuso et al. (1999), Marubini et al. (2001), Allemand et al. (2011)

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Table 7 (*Continued*) Reference list for Figures 3–8 together with a description of sub-system module relationships

Module	Process	Description	Relationships	References
In situ carbonate production (cont.)	*Carbonate* production (cont.)	Reef-scale calcification rates would be expected to be positively correlated with higher coral and CCA cover. However, this is not necessarily always the case	51, 59	Coral: DeCarlo et al. (2017), Page et al. (2017), McMahon et al. (2019). CCA: *No specific studies*
		Coral calcification rate is a product of skeletal density and linear extension rate	52	Carricart-Ganivet et al. (2000), Lough & Barnes (2000)
		CCA calcification rate is influenced by light at benthos due to the production of photosynthetically fixed carbon by the photosynthetic pigments produced by coralline algae	53	Ichiki et al. (2001), Lewis et al. (2017)
		CCA calcification rate is influenced by seawater carbonate chemistry	54	Kuffner et al. (2008), Cornwall et al. (2018), Johnson & Carpenter (2018), Comeau et al. (2019a)
		Temperature sensitivity and temperature influences CCA calcification rates	55, 56	Cornwall et al. (2019) (meta-analysis)
		Nutrients influence CCA calcification rates. Nitrogen enrichment (nitrate+nitrite and ammonium) can increase calcification	57	Ichiki et al. (2000), Johnson & Carpenter (2018), Schubert et al. (2019)
		Changes in CCA calcification rates in response to OA will depend on species-specific OA sensitivity	58	Cornwall et al. (2017, 2018), Comeau et al. (2019a)
		CCA and coral calcification rates combined are the total calcification rate	60, 61	Rasser & Riegl (2002), Perry & Larcombe (2003), Tierney & Johnson (2012)
Event (acute)-driven disturbances	Acute climate-driven disturbances on coral reef ecosystems (*physical erosion*)	Cyclone damage depends on the reef's geomorphology and its position with respect to the cyclone track, the cyclone duration and strength	1, 6	Puotinen (2007), Fabricius et al. (2008), Poutinen et al. (2016)
		Cyclones influence reef wave climate and wave energy, which causes direct physical damage to corals via mechanical erosion and mediates community-level calcium carbonate production	2, 3	Dollar (1982), Done (1993), Dollar & Tribble (1993), Storlazzi et al. (2004), Hamylton et al. (2013)
		On the long term, the magnitude of cyclone reef damage will depend on the return time of severe cyclones, which is predicted to increase with warming oceans	4	Webster et al. (2005), Emmanuel et al. (2008), Keim et al. (2007), Elsner et al. (2008), Mumby et al. (2011), Wolf et al. (2016)

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Table 7 (*Continued*) Reference list for Figures 3–8 together with a description of sub-system module relationships

Module	Process	Description	Relationships	References
Event (acute)-driven disturbances (cont.)	Acute climate-driven disturbances on coral reef ecosystems (*cont.*)	Coral bleaching is strongly correlated to heat stress (DHW) and impacts carbonate budget trajectories. Yet, bleaching events can be mitigated by cyclones that may slow down the build-up of thermal stress associated with temperature. Cyclones events have longer-term effects on temperature via wind-induced upwelling and vertical mixing of cooler subsurface water	5	Eakin (2001), Carrigan & Puotinen (2014), June Chang et al. (2016), Januchowski-Hartley et al. (2017), Perry & Morgan (2017), Courtney et al. (2018), Manzello et al. (2018), Hamylton & Mallela (2019), Lange & Perry (2019), Ryan et al. (2019)
	Changes in the abiotic reef *environment* due to acute disturbances	Indirect impacts of cyclones include changes to water quality (WQ) through reduced light availability, increased turbidity, nutrients and chlorophyll-a concentrations. This occurs when sediment is resuspended due to wave action and heavy rainfall (which further exacerbates river flood impacts). These changes in WQ can in turn cause coral bleaching and/or exacerbate bleaching from heat stress. Changes in WQ and high temperature also affect specific coral-growth parameters	7–13, 30–32	Harmelin-Vivien (1994), Larcombe et al. (1995), Jokiel (2006), Anthony & Connolly (2007), Vaselli et al. (2008), Larsen & Webb (2009), Wooldridge (2009), Carricart-Ganivet et al. (2012), Fabricius et al. (2013) Yang & Goodkin (2014), Roik et al. (2016), Edmunds et al. (2019), Evans et al. (2020)
		Changes in light availability will impact colony growth parameters (size, skeletal density and extension rates), which differ among species. This ultimately alters estimates of coral and reef-level calcification rates	20–23, 59, 60	Huston (1985), Meesters et al. (2001), Enochs et al. (2014), Pratchett et al. (2015), Madin et al. (2016)
		Changes in water quality alter the dynamics between corals and algae including macroalgae and CCA, the latter of which is a key component of total reef calcification	25–29, 33, 34, 38, 58, 61	Leukart (1994), Fabricius & De'ath (2001), Diaz-Pulido & McCook (2003), Littler et al. (2006), Castro-Sanguino et al. (2017), Bessell-Browne et al. (2017), Johns et al. (2018), Ceccarelli et al. (2020)
	Spatial and temporal dynamics of *benthic community* composition and *carbonate production*	At the community level, cyclones and bleaching directly reduce the amount of living coral cover and influence the structuring of coral communities given species-specific susceptibilities to each stressor. Hence, the magnitude of the impact of cyclones and bleaching on reef carbonate production will vary spatially depending on the environmental background (water quality conditions), which influences how coral communities are structured (i.e. relative abundance of coral types)	14, 15, 18, 19	Done (1992), Massel & Done (1993), Cheal et al. (2002), Storlazzi et al. (2004), Madin et al. (2006, 2014a), Osborne et al. (2011), Grottoli et al. (2014), Hughes et al. (2018b)

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Table 7 (*Continued*) Reference list for Figures 3–8 together with a description of sub-system module relationships

Module	Process	Description	Relationships	References
Event (acute) driven disturbances (cont.)	Spatial and temporal dynamics of benthic community composition and carbonate production (cont.)	Indirect impacts to the coral community occur via altering ecological interactions of corals with other benthic components such as macroalgae, which rely on free substrate available for colonisation of space. Free space available for colonisation increases after disturbances following coral mortality	36–39, 40–46	Highsmith et al. (1980), Connell et al. (1997), Lirman & Fong (1997), Mallela & Crabbe (2009), Foster et al. (2013), Doropoulos et al. (2014), Graham et al. (2014), Beeden et al. (2015), Elmer (2016), Yadav et al. (2016), Davidson et al. (2019), Hughes et al. (2000, 2019a)
		Coral community composition will determine reef recovery and coral recruitment patterns (sexually or by fragmentation) after disturbance events with cascading effects on the structuring of coral demographics and overall coral size distribution, which ultimately affect coral calcification rates. The balance between carbonate production and loss via growth and mortality processes of calcifier organisms determines the overall volume of reef framework per unit area (density)	24, 52–54, 57, 62, 63	
		Physical coral breakage will affect quantity (and type) of reef sediments and the amount of rubble on reefs, which may affect coral recruitment success and colonisation of other benthic organisms	17, 35, 38, 39, 40, 46	Perry (2001), Fox et al. (2003), Fox & Caldwell (2006), Cameron et al. (2016)
		Cyclones reduce colony size (i.e. diametre and height) impacting reef-scale rugosity via changes in coral size distribution, coral community composition and eventual degradation of dead colonies	16, 47, 48, 55, 56	Crabbe (2009), Graham & Nash (2013), Bozec et al. (2015), Darling et al. (2017)
		Reef-level rugosity may affect the amount of fish grazing necessary to control macroalgal abundance. Macroalgae is also controlled by environmental drivers (e.g. light, nutrients), which interact with grazing. Therefore, water quality degradation due to cyclones and bleaching can also impair grazing upon algae	49–51	Mantyka & Bellwood (2007), Nemeth & Appeldoom (2009), Bennett et al. (2010), Alvarez-Filip et al. (2011), Bozec et al. (2013), Castro-Sanguino et al. (2016)
Coral reef response to sea level rise	Sea level rise drives changes in *environmental* conditions and coral reef processes	Sea level rise changes the initial depth of the reef. The change in reef depth influences the propagation of wave energy into the reef system (see reef hydrodynamics) and the light at benthos, which in turn impact on living coral cover	1, 2, 4, 8	Hearn et al. (1999), Cooper et al. (2007), Baldock et al. (2014a), Beetham & Kench (2018a), Harris et al. (2018)

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Table 7 (*Continued*) Reference list for Figures 3–8 together with a description of sub-system module relationships

Module	Process	Description	Relationships	References
Coral reef responses to sea level rise (cont.)	Sea level rise drives changes in environmental conditions and coral reef processes (cont.)	A change in wave energy directly impacts the mechanical erosion processes on the reef. A change in mechanical erosion will result in differences in dead coral cover and then rubble cover. Different mechanical erosion processes will result in a change to the composition of corals and the CCA cover	3, 5, 7	Storlazzi et al. (2005), Madin & Connolly (2006), Baldock et al. (2014b), Madin et al. (2014)
	Environmental controls on coral reef carbonate production	Turbidity influences water column light attenuation and light at benthos (as a function of water depth). Light availability is an important control on coral cover and community composition	9, 10	Cooper et al. (2007), Tamir et al. (2019)
		Elevated water temperature can cause coral mortality and lead to a change in coral composition, and living and dead coral cover. Ambient temperate can also influence the coral composition and CCA cover. Seasonal changes in temperature also influence the calcification rates of coral and CCA	6, 11–15	Comeau et al. (2013, 2017a, 2018, 2019a), Schoepf et al. (2013), Cornwall et al. (2017), Okazaki et al. (2017)
		Ocean carbonate chemistry can influence the cover of CCA and the suitable substrate cover for coral recruits and the coral recruitment rate. The ability of corals and CCA to calcify are strongly influenced by the carbonate chemistry, so too is the composition of corals likely to be present	16–22	Fabricius et al. (2011), Doropoulos et al. (2012a), Cornwall et al. (2019), Comeau et al. (2019)
	Benthic community dynamics and controls on coral recruitment and calcification rates.	Sediment cover will be an important factor in determining CCA cover and the suitable substrate cover for coral recruitment	24, 25	Fabricius & De'ath (2001), Babcock & Smith (2002)
		Variability in living coral cover is the driver that determines the response of a coral reef to sea level rise. A change to living coral cover will result in differences in other benthic variables such as dead coral cover, suitable substrate cover for coral recruits and coral recruitment rate, and the benthic rugosity of the reef. The cover of living corals will be a key driver of the coral calcification rate	26–30	Perry et al. (2012), Gouezo et al. (2019), Hughes et al. (2019)
		CCA cover can create more suitable substrate cover for coral recruitment. Some CCA facilitate coral recruitment. CCA cover directly influences CCA calcification rate	24, 31, 32, 41	Bak & Engel (1979), Heyward & Negri (1999), Vermeij (2005), Doropoulos et al. (2012a), Ritson-Williams et al. (2014), Tebben et al. (2015), Elmer (2016), Doropoulos et al. (2020)

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Table 7 (*Continued*) Reference list for Figures 3–8 together with a description of sub-system module relationships

Module	Process	Description	Relationships	References
Coral reef response to sea level rise (cont.)	*Benthic community* dynamics and controls on coral recruitment and calcification rates (cont.)	Coral composition is influenced by a number of oceanographic and environmental variables (see links above) and also the juvenile coral population present on the reef (see coral recruitment links below). Live coral cover and the overall calcification rate of the reef is controlled by the composition of corals on the reef	23, 52	Doropoulos et al. (2012a), Perry et al. (2012)
		Rugosity of the coral reef is governed by the different types of benthic cover, primarily live coral cover, dead coral cover and rubble cover. It is an important variable in the propagation of wave energy through the reef system, coral recruitment rate and total calcification rate	28, 33, 35, 36, 38, 39	Smith (1992), Rogers et al. (2001), Wilson et al. (2007), Alvarez-Filip et al. (2009), Perry et al. (2012), Harris et al. (2018)
		Coral recruitment is an important driver for the juvenile coral population and the eventual composition of corals. Suitable substrate cover, CCA cover (see above) and live coral cover as well as seawater carbonate chemistry directly influence the potential recruitment of corals. There is a feedback loop between suitable substrate cover and living coral cover, where suitable substrate cover influences the juvenile coral population and eventual living coral cover	17, 18, 22, 27, 30, 31, 34, 37, 40–43	Doropoulos et al. (2012a,b, 2015), Bramanti & Edmunds (2016), Gouezo et al. (2019), Hughes et al. (2019)
	Balance of coral calcification, removal and sediment incorporation that leads to accretion (*reef geomorphology*)	The total reef accretion is a balance between carbonate production and removal processes. Accretion is also a function of the reef framework density, which describes the structure of carbonate material produced through CCA and coral calcification. Bioerosion rates influence reef framework density and also drives important processes of carbonate framework removal and production of sediment (see bioerosion module). Sediment is also incorporated back into the coral reef influencing the reef framework density	46–52	Perry et al. (2012, 2013b), Morgan & Kench (2016b)
		The combination of coral and CCA calcification rates are the main contributors to the total calcification rate of the coral reef	44, 45	Perry et al. (2012)
		Coral reef accretion leads to change in coral reef morphology and a shallowing of the reef reducing coral reef depth. This forms a feedback loop between the change reef depth due to rising sea levels and the resultant coral reef accretion at a later time point	53, 54	Davies (1983), Neumann & Macintrye (1985), Woodroffe & Webster (2014), Harris et al. (2015b)

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Table 7 (*Continued*) Reference list for Figures 3–8 together with a description of sub-system module relationships

Module	Process	Description	Relationships	References
Bioerosion	*Benthic community* and reef framework (reef framework properties influence erosion)	Reef morphology influences the diversity and distribution of key bioerosional taxa with presence/absence of major bioeroding groups like grazing urchins and parrotfish (grazers), sponges (macroborers) and even light-limited microborers closely linked to reef zonation. It also influences benthic cover. Framework types are also influenced by sub-environment with different benthic communities found in different zones. Feeding activity of grazers are influenced by zonation (parrotfish move to certain zones to graze), and population density size of individuals (e.g. urchins) can be depth dependent. Activity of light limited microborers is also linked to depth/zonation. Reef morphology here is a proxy for light, depth and flow	1–3	Parrotfish and reef morphology: Bruggeman et al. (1996). Urchins and reef morphology: Ruengsawang & Yeemin (2000), Griffin et al. (2003). Marcoborers and reef morphology: Scott (1985), Perry (1998), Chiappone et al. (2007). Feeding rates and reef morphology: Hoey & Bellwood (2008)
		Availability of suitable substrate for either colonisation by internal bioeroders (colonisable substrate, often dead coral cover, although many internal bioeroders can infest living corals) or grazing by external eroders (grazable substrate, namely turfs and CCA) will influence bioerosion through dictating bioeroder biomass	4, 5	Glynn (1988); Eakin (1996)
		Properties of the reef framework determine bioerosion rates, with surface area (Rugosity), volume and ratio of dead to living coral (living coral cover) and substrate density (reef framework density) all influencing bioeroder infestation and boring rates. A feedback loop here as high density of grazers can influence benthic community composition	6–8	Highsmith (1981), Hutchings (1983), Bellwood & Choat (1990), Roff et al. (2020)
		Physical density of the substrate (reef framework density) both affects infestation by internal borers and can stimulate bioerosion rates (particularly in macroborers), or retards it (parrotfish). Low substrate density may aid quicker and deeper penetration, but there is also evidence that dense reef framework enhances endolithic boring rates. Coral composition influences reef framework density. Redistribution of bioeroded calcium carbonate into reef cavities, and eventual recrystallisation and cementation in the cavity also strengthens the reef framework	8–11	Hutchings (1983); Macroborers: Neumann (1966), Highsmith (1981), Highsmith et al. (1983), Rose & Risk (1985), Schonberg (2002), Tribollet & Golubic (2005); Parrotfish: Neumann (1966), Rutzler (1975), Ward & Risk (1977), Ginsburg (1983), Hallock (1988), Ong & Holland (2010), Tribollet et al. (2002)

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Table 7 (*Continued*) Reference list for Figures 3–8 together with a description of sub-system module relationships

Module	Process	Description	Relationships	References
Bioerosion (cont.)	*Benthic community* and reef framework (cont.)	Coral composition not only influences rugosity and other framework properties, but macroborers show strong preferential tendencies towards certain species, perhaps due to skeletal density or nutrition	10, 12	Stearn & Scoffin (1977), Highsmith et al. (1983), Scoffin & Bradshaw (2000), MacDonald & Perry (2003), Chiappone et al. (2007)
	Abiotic *environmental* drivers (both bioeroder densities and activity rates influenced by environmental factors)	Sedimentation negatively affects available substrate for colonisation and grazing, and inhibits macrobioerosion through smothering, especially for sponges. However, it may boost bivalve and polychaete erosion through heterotrophic nutrition. There is some evidence that microborers can thrive under high sedimentation rates	13, 14	Wilkinson (1983), Perry (1996), Holmes (1997), MacDonald & Perry (2003), López-Victoria & Zea (2005), Mallela & Perry (2007)
		Light at benthos is thought to be the number one determinant of microborer density. There is some limited evidence it may also drive rates, although very high irradiance can inhibit boring. This is because microborers are mainly photoautotrophs. Light may also boost macroborer rates, particularly in zooxanthellate sponges through stimulating growth and faster boring rates, but also in sponges more generally	15–17	Rützler (1975), Wilkinson (1983), Hoskin et al. (1986), Vogel et al. (2000), Fine & Loya (2002), Weisz et al. (2010)
		Temperature effects on bioerosion are variable, with some evidence it influences parrotfish grazing rates and sponge boring, and slows microborer activity. High temperatures can also inhibit and damage bioeroders (e.g. in sponges). The best evidence for temperature increasing bioerosion is indirectly, though, increased substrate availability. Seasonal changes and upwelling can also boost bioerosion	16–18	Glynn (1988), Eakin (1996), Reaka-Kudla et al. (1996) Fonseca et al. (2006), Ong & Holland (2010), Achletis et al. (2017), Alvarado et al. (2017), Wizemann et al. (2018)
		Nutrient availability is the most important abiotic control of macrobioerosion, controlling density and to a lesser extent rate. This is because most endolithic macroborers are heterotrophic suspension or filter feeders. There are some evidence nutrients can positively influence microborer densities, although this is not supported by everyone	16, 17, 19	Hallock (1988); Macroborers: Risk & MacGeachy (1978), Highsmith (1981), Rose & Risk (1985), Meesters et al. (1991), Goreau (1992), Edinger & Risk (1994), Holmes (1997), Holmes et al. (2000), Zubia & Peyrot (2001), Callahan (2005), Ward-Paige et al. (2005), Carreiro-Silva et al. (2009). Microborers: Chazottes et al. (1995), Peyrot-Clausade et al. (1995), Kiene (1997), Vogel et al. (2000), Carreiro-Silva et al. (2009)

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Table 7 (*Continued*) Reference list for Figures 3–8 together with a description of sub-system module relationships

Module	Process	Description	Relationships	References
Bioerosion (cont.)	Abiotic *environmental* drivers (cont.)	Flow velocity boosts macroborer (particularly sponge) erosion, both through higher abundances on more exposed fore reefs but also through rates being boosted under high flow conditions, although this effect is variable. Flow is also important in determining how much sediment is re-incorporated back into the framework and how much is removed	16, 17, 20	Naumann (1966), Rützler (1975), Wilkinson (1983), Lopez-Victoria & Zea (2005), Chiappone et al. (2007); Leys et al. (2011)
		Seawater carbonate chemistry influences bioerosion activity. Microborers and sponges increase their growth and activity under ocean acidification. It is believed low pH conditions might promote bioerosion indirectly by weakening framework, or making the cost of acidic excretions less metabolically costly in chemical borers, and also is thought to directly ease the process of chemical bioerosion via reduced alkalinity and pH. It is also assumed to indirectly accelerate bioerosion by stimulating energy capture in phototrophic bioeroders. However, many eroding organisms (e.g. echinoids, molluscs) have calcium carbonate shells and therefore might be expected to be negatively affected. A feedback loop exists as chemical boring influences aragonite locally. Aragonite may also influence framework density through coral skeletal density, and how much sediment gets incorporated into the framework	16, 17, 21–23	Glynn (1997), Tribollet et al. (2009), Wisshak et al. (2012), Enochs et al. (2016), Schonberg et al. (2017)
	Bioerosion (Bioeroder densities and rates affected by biological factors like population characteristics)	Biotic factors (recruitment, disease, competition, predation) directly affect population densities of bioeroding taxa, particularly mobile grazers like urchins and parrotfish, who may also show seasonal shifts in abundance and activity. For example, recruitment is an important driver of polychaete abundance. Population densities influence mean size, and size can be influenced by biological factors like recruitment. A bioerosion loop also exists between macro and microborers and grazer densities. This loop magnifies and distorts bioeroder roles as bioerosion-mediated local changes in environmental conditions, substrate or predation and recruitment control, which then influence densities and rates	24–26	Hutchings (2001), Schoenberg et al. (2017)

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Table 7 (*Continued*) Reference list for Figures 3–8 together with a description of sub-system module relationships

Module	Process	Description	Relationships	References
Bioerosion (cont.)	Bioerosion (Bioeroder densities and rates affected; cont.)	Bioerosion rates by grazers are heavily size dependent (Grazer size), as larger individuals can have a disproportionate effect, e.g. fish smaller than 25 cm have little effect, while a 7 cm diametre *Diadema savignyi* consumes >500 times more carbonate than their 1.2 cm counterparts. Urchin test size is often used as a proxy for bioeroder pressure, while eroding fish bite volume is linked to fish body length. Feedback loop here as grazer density can influence grazer size (e.g. in urchin outbreaks), which reduces the bioerosive power of grazers	26, 27	Bak (1990), Griffin et al. (2003)
		Grazer density is the primary driver of mechanical bioabraision, the mechanical removal of carbonate substrate most usually as an unintentional consequence of herbivory. External eroders (principally reef fish and echinoids) are often apportioned a substantial budgetary contribution. The presence of particular species – such as the excavating fish Bolbometapon – can also be influential. To characterize the contribution of external eroders, they can be further subdivided into scrapers and excavators, the latter of which take substantially more material. Some urchins also excavate cavities. Macroborers contribute to bioabrasion too – most use combination of mechanical and chemical erosion, e.g. the mollusc Lithophaga uses combination of chemical softening (excreting acid from glands along the edge of the mantle) and a mechanical ‘grinding’ involving mechanical scraping of shell	28	Hein & Risk (1975), Bak et al. (1984), Hutchings (1986), Kiene (1988), Bellwood & Choat (1990), Kiene & Hutchings (1994), Pari et al. (2002), Tribollet et al. (2002), Bonaldo et al. (2014)
		Macroborer density has a significant influence on bioerosion, with macroborers adopting biocorrosion, abrasion or both. Sponges are often the most important organisms on the reef capable of erosion rates that exceed mean reef carbonate production rates. But macroborers also include bivalves (Pholadidae (angelwings), Gastrochaenidae (clams) and Mylitidae (mussels)), crustaceans (e.g. hermit crabs), barnacles (e.g. Lithotrya), shrimp (excavate large chambers) and worms including – Phoronids, Polychaetes, Sipunculans. Polychaetes are probably the best studied with polychaete families containing boring species: Eunicidae, Lumbrineridae, Dorvilleidae, Spionidae, Cirratulidae and Sabellidae, all of which employ combinations of mechanical and chemical bioerosion to various extents	29	Smith & Kinsey (1976), MacGeachy (1977), Stearn & Scoffin (1977), Wilkinson (1983), Hutchings (1986), Lazar & Loya (1991), Risk et al. (1995), Nava & Carballo (2008)

(*Continued*)

Table 7 (*Continued*) Reference list for Figures 3–8 together with a description of sub-system module relationships

Module	Process	Description	Relationships	References
Bioerosion (cont.)	*Bioerosion* (Bioeroder densities and rates affected; cont.)	Microborer density influences bioerosion through biocorrosion – erosion by chemical dissolution to penetrate while exploiting fissures and colonising cavities in porous substrates. Defined by the creation of borings <100 µm in diametre, they are small, commonly autotrophic euendolithic microorganisms or microendoliths. Microboring communities colonise reef substrate more rapidly than any other bioeroding group (arriving on freshly exposed substrate within four to nine days of exposure), and may weaken substrate to speed up action of larger borers	30	Golubic et al. (1975), Tudhope & Risk (1985), Chazottes et al. (1995), Vogel et al. (2000), Tribollet (2008), Tribollet et al. (2011)
	Bioerosion output (carbonate removal, net sediment production and framework density)	Bioerosion has three main outputs. First, the total bioerosion rate that relates to the total amount of carbonate removed from the reef framework. Some of this framework removal produces sediments from bioabrasion processes, which feeds into the sediment budget production (net sediment production), and where it connects to the sediment production module. Net sediment production is, therefore, the second output of the module. Some of the carbonate removed is through chemical dissolution, so no sediments are produced. The removal of carbonate from the framework reduces reef framework density (third module output). However, some sediments that are produced from bioerosion may get re-incorporated back into the reef filling in the void volumes (reef framework density)	11, 31–34	Hubbard (1990), Perry & Hepburn (2008), Glynn & Manzello (2015)
Net sediment production	*Environmental* controls on reef calcifiers and sediment producers	Seawater turbidity (i.e. cloudiness) directly influences water column light attenuation and light at benthos (as a function of water depth). Light availability is an important control on coral community distribution and composition	1–3	Cooper et al. (2007), Storlazzi et al. (2015), Morgan et al. (2016)
		Elevated sea surface temperature can cause coral mortality and major increases in dead coral cover and rubble on bleaching-impacted reefs. Climate-disturbance (e.g. temperature extremes) events alter sediment production regimes by changing the relative abundance of calcifiers on reefs. Seasonal changes in temperature also influence the growth, calcification and turnover rates of calcifying algal species and foraminifera (i.e. direct sediment producers)	4, 5, 10, 15	Harney et al. (1999), Perry & Morgan (2017), Hughes et al. (2018a), Prathep et al. (2018); Perry et al. (2019, 2020), Castro-Sanguino et al. (2020), Taylor et al. (2020)

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Table 7 (*Continued*) Reference list for Figures 3–8 together with a description of sub-system module relationships

Module	Process	Description	Relationships	References
Net sediment production (cont.)	Environmental controls on reef calcifiers and sediment producers cont.)	Nutrient loading may increase internal bioerosion activity in live coral heads and detrital coral rubble. Sponge intensity exhibits increases in cover and bioerosion rate across gradients of water quality. Excess nutrients can increase productivity in calcifying green algae (e.g. *Halimeda* spp., *Amphiroa* spp.)	9, 11	Acker & Risk (1985), Holmes et al. (2000), Holmes (2000), Rice et al. (2020)
	Benthic community composition	Reef rugosity and benthic composition determine the total amount of available carbonate for internal boring organisms and grazing bioeroders (e.g. parrotfish and urchins). Higher bioeroder activity will produce greater quantities of detrital sediment	6, 7, 8, 13, 27	Alvarez-Filip et al. (2009), Perry & Morgan (2017)
		Sediment cover on reefs determines available habitat for specific direct sediment producers (e.g. calcifying algae, infaunal bivalves/molluscan species, foraminifera)	14	Schlacher et al. (1998), Van Tussenbroek & Van Dijk (2007), Parker & Gischler (2011)
	Physical erosion/ framework breakdown/grain diminution	Wave breaking and surging currents increase frictional drag on coral and promote physical damage, breakage and dislodgement of corals. The amount of physical stress on corals is related to the local wave climate. Physical breakage results in very coarse sediment clasts (i.e. whole and/or partial colonies) and rubble/gravels (i.e. detrital branches)	27–30	Rasser & Riegl (2002), Madin (2005), Madin et al. (2006, 2014), Baldock et al. (2014b)
		Storm activity (e.g. cyclones/hurricanes) can cause major mechanical destruction of coral reefs by storm waves. Wave energy decreases with reef depth and distance from reef edge (i.e. zones of the highest primary productivity). Damage can occur over large spatial scales (100 km) and coral clasts may form extensive boulder ramparts on the reef flat and/or storm ridges at the coast	27–31	Maragos et al. (1973), Baines & McLean (1976), Ogg & Koslow (1978), Highsmith et al. (1980), Edmunds & Witman (1991), Scoffin (1993), Harmelin-Vivien (1994), Richmond and Morton (2007), Álvarez-Filip et al. (2009)
	Bioeroder (*biological) sediment production* (grazing organisms)	Urchins produce sediment as the by-product of grazing algae growing on dead reef substrates. Sand-sized sediment particles are produced as reef carbonate is excavated, ingested and excreted. Higher urchin densities and grazing rates will increase sediment production	12	Hunter (1977), Ogden (1977), Reaka (1985), Ostrander et al. (2000), Peyrot-Clausade et al. (2000), Morgan (2014)

(*Continued*)

Table 7 (*Continued*) Reference list for Figures 3–8 together with a description of sub-system module relationships

Module	Process	Description	Relationships	References
Net sediment production (cont.)	Bioeroder sediment production (cont.)	Parrotfish graze directly on filamentous algae and endolithic microbes in reef substrate and dead corals. Carbonate material is excavated during feeding, ground by the pharyngeal mill into sand-sized particles. Parrotfish are major producers of new sediment. Parrotfish abundance, size, species and functional group (i.e. scrapers versus excavators) influence the rate of sand production	12	Ogden (1977), Bellwood (1995, 1996), Bruggemann et al. (1996), Perry et al. (2015), Morgan & Kench (2016a)
		Bioeroding sponges (e.g. Cliona sp.) use chemical mechanisms to etch silt-to-sand sized carbonate chips (15–80 μm) from reefs. Chips have a characteristic shape and are easily transported by currents	12	Futterer (1974), Rützler & Macintyre (1978), Acker & Risk (1985), Nava & Carballo (2008), Carballo et al. (2017)
		Other boring organisms (e.g. *Lithophaga*, polychaetes, sipunculids) use chemical mechanisms (i.e. acid) to weaken the carbonate before mechanically removing it. This typically produces silt-sized particles that are transported off-reef	12	Scoffin (1992), Chazottes et al. (1995), Rice et al. (2020)
	Direct (biological) sediment production (e.g. foraminifera, *Halimeda*)	Large benthic foraminifera directly add to sediment reservoirs upon death. Foraminifera are often important in beach and island sediments because of the preferential transport capacity by reef currents and relative durability that promotes preservation. Growth and calcification vary between taxa and are influenced by changes in light and nutrient conditions	16–18, 26	Muller (1974), Hallock (1981), Harney et al. (1999), Fujita et al. (2009), Dawson & Smithers (2014)
		Halimeda are direct sediment producers and are often abundant within sediments. *Halimeda* sediments are typically bimodal: (1) whole or broken plates that are shed through growth or upon death and (2) fine sand- and silt-sized aragonite needles following breakdown	16–18, 26	Folk & Robles (1964), Drew (1983), Hoskin et al. (1986), Multer (1988), Perry et al. (2016, 2017, 2019), Castro-Sanguino et al. (2020)
		Halimeda have rapid growth and turnover rates (produce a new segment every two to four days). Turnover rates can vary seasonally on high-latitude reefs. Understanding rates of turnover/crops per year is crucial for estimating rates of direct sediment production	10, 15–18, 26	Freile (2004), Perry et al. (2016, 2019)
	Carbonate sediment dissolution (chemical)	Carbonate dissolution results in a loss of material when sediment pore waters become under-saturated with respect to the dissolving mineral phase. Undersaturation occurs through sediment metabolic processes and/or seawater composition. Organic matter decomposes in sediments releasing dissolved inorganic carbon (DIC) into the pore water. Reef sediments have a strong diel cycle of productivity and respiration (i.e. organic matter decomposition) that controls dissolution and precipitation	20–25	Cyronak et al. (2013), Eyre et al. (2014, 2018), Courtney et al. (2016), Cyronak & Eyre (2016)

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Table 7 (*Continued*) Reference list for Figures 3–8 together with a description of sub-system module relationships

Module	Process	Description	Relationships	References
Carbonate transport and sinks	*Reef hydrodynamics*	Incident wave climate is primarily driven by regional wind patterns. As regional storms generate waves, these waves propagate until they interact with a local reef	1–11	Young (1999), Young et al. (2011), Hemer et al. (2013), Hoeke et al. (2013), Reguero et al. (2015)
		Reef depth is controlled by water level above the underlying reef geomorphology and can vary on daily (e.g. tidal) timescales as well as seasonal to interannual timescales		Lugo-Fernández et al. (1998b), Potemra & Lukas (1999), Monismith (2007), Taebi et al. (2011), Lowe & Falter (2015), Buckley et al. (2018)
		When swell arrives, the local reef depth, reef morphology, and rugosity directly control wave dissipation		Hardy & Young (1996), Lugo-Fernández et al. (1998a), Massel & Gourlay (2000), Lowe et al. (2005), Becker et al. (2014), Buckley et al. (2014), Rogers et al. (2016)
		Wave dissipation at the reef crest drives wave setup, which in turn determines circulation patterns around the reef system (dependent upon reef-lagoon-channel morphology). When no waves are present, circulation is driven by tidal processes		Hearn (1999), Gourlay & Colleter (2005), Monismith (2007), Hench et al. (2008), Lowe et al. (2009b, 2010, 2015), Buckley et al. (2015, 2016), Quataert et al. (2015)
	Sediment supply and transport	Reefal sediment supply is directly linked to the reef ecosystem and abundance of reef-dwelling organisms (net sediment production)	12–14	Chevillon (1996), Harney et al. (2000), Yamano et al. (2000), Perry et al. (2011, 2015), Dawson et al. (2012), Morgan & Kench (2016a,b)
		The sediment composition ultimately determines the size, shape and density of the sediment reservoir and how it interacts with overlying flows		Sorby (1879), Folk & Robles (1964), Smithers (1994), Kench & McLean (1996), Ford & Kench (2012), Cuttler et al. (2017)
		Sub-aqueous sediment is entrained and transported via mean currents and wave orbital motions; subaerial (beach face) sediment is entrained transported by wind		Shields (1936), Soulsby & Whitehouse (1997), van Rijn (2007a,b), Storlazzi et al. (2011), Grady et al. (2013), Pomeroy et al. (2015, 2016, 2018), Cuttler et al. (2018)

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Table 7 (*Continued*) Reference list for Figures 3–8 together with a description of sub-system module relationships

Module	Process	Description	Relationships	References
Carbonate transport and sinks (cont.)	Island geomorphology and other *depositional sinks*	Alongshore gradients in sediment transport determine areas of deposition and erosion, which directly influence island shape and area	15–22	Kench & Brander (2006), Kench et al. (2006), Mandlier & Kench (2012), Grady et al. (2013), Beetham & Kench (2014), Duvat et al. (2017a), Cuttler et al. (2018), Costa et al. (2019), Ortiz & Ashton (2019), Shope et al. (2019)
		Sediment can be transported to inshore environments (dunes) via aeolian transport or storm over-wash		Stoddart (1964), Kench et al. (2008), Jackson & Nordstrom (2011), Ford & Kench (2014), Mann & Westphal (2016)
		Vegetation cover can stabilize backshore deposits to facilitate dune establishment/growth and long-term sediment storage		Short & Hesp (1982), Flood & Heatwole (1986), Wasson & Nanninga (1986), Buckley (1987), Hesp (2002), Bauer et al. (2009), Charbonneau et al. (2017)
		Sediment can also be deposited in off-reef areas (e.g. fore reef talus deposits) or contribute to lagoon infilling		Hubbard et al. (1990), Kench (1998b), Kench & Mclean (2004), Perry et al. (2013a), Harris et al. (2014), Morgan & Kench (2016a)

Note: Italicized variables (process column) relate to groupings in figures.

The development of the shared qualitative system model was conducted on the second day of the workshop, which focused on combining all shared sub-system models into one shared qualitative system model (i.e. the geo-ecological carbonate reef system model). We randomly organized modellers into three multi-disciplinary groups, each containing a representative from each sub-system module group. We began the modelling process by identifying those high-level variables that were common to two or more sub-system models. These variables were typically influencing environmental variables (e.g. atmospheric processes, wave climate) that acted as 'root nodes' (i.e. the first node in a rooted (directed) graph from which all paths originate). Below, we outline the development of each individual sub-system model and how these fit together to form the qualitative geo-ecological system model.

Developing the qualitative sub-system models of the geo-ecological carbonate reef system

The collective knowledge and understanding that support carbonate budgets provides the building blocks from which we developed the geo-ecological carbonate reef system model (Figure 1). We begin by first outlining the opportunities, limitations and challenges associated with transitioning from carbonate budgets to (predictive) models. Opportunities provide the foundations upon which to develop the qualitative model, whereas limitations and challenges reveal both the knowledge gaps that we should seek to fill, and the immense difficulty in collecting and analysing spatially and temporally relevant data from carbonate reef systems. Second, we provide a model summary and a detailed description of how each sub-system model was developed. The summary details the model's main outputs and influences, providing context for how each sub-system model relates to the geo-ecological carbonate reef system model. These summaries discuss how the model was developed in the context of previously identified opportunities, limitations and challenges of census-based carbonate budgets. Numbers in parentheses (#) relate to the numbered relationships in the sub-system model figures (Figures 3–8), which are further explained with additional references in Table 7. We explore our ability to quantify the relationships of the sub-system models in the 'Towards a quantitative geo-ecological carbonate reef system model' section.

In situ *carbonate production sub-system*

Transitioning from budgets to models

Primary carbonate production from coral and CCA calcification is the core component of conventional carbonate budgets. Estimates of *in situ* primary carbonate production can be obtained by coral (primary carbonate source) and CCA cover, multiplied by the calcification rate. Existing census-based carbonate budget studies typically include coral cover with calcification rates of one or a few coral species within or close to the site (Perry et al. 2012) predominantly due to the challenge of quantifying calcification rates for all coral species on a reef. Most studies include CCA cover (32 of 38 census-based studies; Table 1) and sometimes include CCA calcification rates (7 of 38 studies; Table 1). Other variables that are frequently included are coral composition, macroalgae cover, rugosity, reef topography and reef depth (Table 1). Rugosity and reef topography are critical because they are used to account for reef surface complexity and accurately quantify carbonate production over the three-dimensional (not planar) surface area. Most studies record coral composition (36 of 38; Table 1), rugosity (30 of 38 studies; Table 1) or reef topography, and all include reef depth. A total of 19 studies record the presence of macroalgae and a further six record 'algal' cover, although the type of algae (calcareous or fleshy) is not always specified (Table 1).

Measurements of primary carbonate production are generally short term (<1 year), and therefore, the majority of net carbonate production estimates that use census-based carbonate budgets are essentially snap-shots in time, which aim to assess what is present on the reef at one specific time, and usually in one geographic location. For this reason, there is a growing need to incorporate the ecological (e.g. macroalgae cover, recruitment rates of calcifying taxa, species composition) and physical (e.g. temperature, light, nutrients, seawater carbonate chemistry, water depth, water flow) variables that influence calcification rates, and are thus important for quantifying and understanding variation in *in situ* primary carbonate production over spatial and temporal scales.

Model summary

This model summarizes the drivers of coral and CCA calcification rates (Figure 3). Coral and CCA control primary carbonate production in coral reefs (Hubbard et al. 1990) and create the three-dimensional reef framework through the bio-calcification of their $CaCO_3$ skeletons, providing the foundation of the geo-ecological carbonate reef system model (# 60–61, Figure 3). Together,

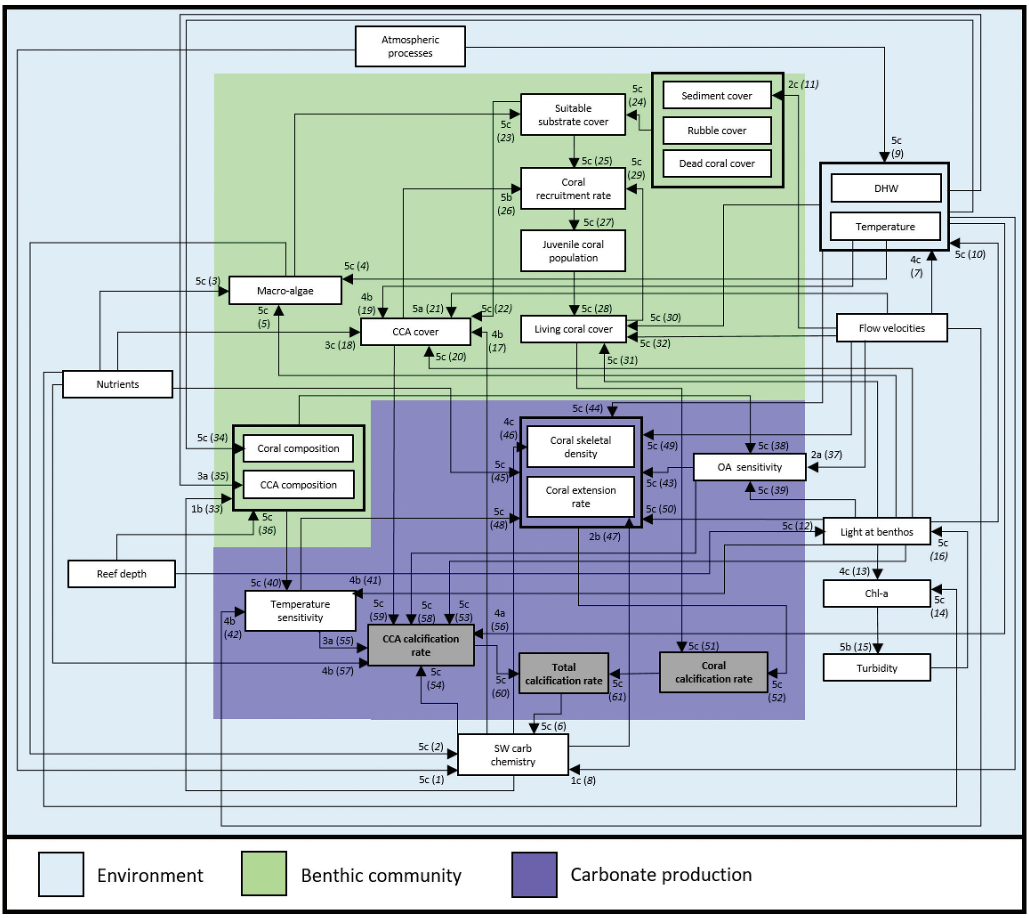

Figure 3 Conceptual model of *in situ* carbonate production. This model contains 28 variables and 61 relationships. Variables are grouped in three broad categories; environment (light blue), benthic community (green) and carbonate production (dark blue). Module output (grey-shaded variables) is from both coral and CCA calcification rate, which together provide total *in situ* carbonate production or total calcification rate. Each relationship is provided with a strength (1 to 5; 5 being the strongest) and confidence score (a–c; c being most confident). Numbers in brackets next to the strength/confidence score relate back to Table 7, which provides details on the relationships with relevant references.

coral and CCA calcification rate dictate the total calcification rate, which is designated as the main output of the model (Figure 3). Corals are the primary framework builders, calcifying rapidly in three dimensions, while CCA bind the reef framework, providing substrate for coral settlement and stabilisation. Thus, the geo-ecological carbonate reef system model requires a module that accounts for the dominant variables responsible for primary carbonate production in coral reef systems (Figure 3; Table 7). Five dominant physical variables explain the overall function of the model, represented by the total number of 'out degrees' (in parentheses; Figure 3): light (9), temperature and degree heating weeks (DHW) (8), water flow velocities (7), seawater carbonate chemistry (5), nutrients (5) and reef depth (2). The dominant ecological variables that are critical for model function include macroalgae cover (2), coral and CCA species composition (2), sensitivity to temperature (2) and ocean acidification (2), and coral recruitment rates (1). The incorporation of these physical variables, in particular flow velocity, directly seeks to resolve a significant limitation of current census-based budgets. These relationships are discussed below.

Photosynthesis and light

Critical to the calcification process is the production of photosynthetically fixed carbon by the microalgal symbionts (*Symbiodiniaceae*) that live within the coral tissue, and the photosynthetic pigments produced by CCA. While not specifically stated or included as a variable in our subsystem module, any variable that affects photosynthetic activity can influence calcification rates (Chalker 1981; Tambutté et al. 2011). This phenomenon, known as 'light-enhanced calcification', is due to the strong influence of light on both rates of photosynthesis and calcification (Chalker 1981) (# 5, 20, 31) with light at the benthos being a function of water depth, turbidity and chlorophyll-a (# 12–16, Figure 3). The influence of light on photosynthesis and calcification rates can be modelled based on the light reaching the benthos (i.e. in the form of photosynthetically active radiation) given that increases in light increase metabolic rates and stimulate calcification until a threshold has been reached, after which photosynthesis and calcification rates 'plateau' (Jokiel & Coles 1977, Chalker 1981, Marshall & Clode 2004, Rodolfo-Metalpa et al. 2008, Ulstrup et al. 2011, Al-Sofyani & Floos 2013, Samiei et al. 2016). Different coral species, however, and even sometimes individuals (e.g. different sized colonies) of the same species, can have different intrinsic rates of calcification that vary between different locations (Pratchett et al. 2015, Ross et al. 2015, Jury et al. 2019). Differences in coral calcification rates ultimately influence community primary carbonate production (# 51, 52). Yet, quantifying this effect is complicated because it requires highly detailed knowledge of the abundance of species within reef communities and the species- and location-specific responses of calcification rates to environmental and ecological parameters (see Kleypas 1997).

Temperature and bleaching

Corals are very sensitive to changes in temperature and are known to be highly adapted to their local seasonal temperature regimes (review by Sweet & Brown 2016). Rising ocean temperatures and the repeated occurrence of abrupt marine heatwaves are driving declines in coral reefs worldwide (Hughes et al. 2018b, Eakin et al. 2019). When sea surface temperatures exceed the local summer maximum monthly mean by just 1°C for three to four weeks, coral bleaching and mortality can occur due to the loss of the Symbiodiniaceae, resulting in declines in calcification and a reduction in live coral cover, respectively (Glynn 1996, Howells et al. 2012, Hughes et al. 2018a). For CCA, the bleaching threshold is based on a few existing studies, yet appears to vary substantially between species, and the negative effects of increasing temperature on calcification rates only seem to appear once temperature exceeds the ambient conditions by 5°C (see meta-analysis by Cornwall et al. 2019). Given that coral and CCA are often already living close to the upper thermal limits in the tropics (Coles & Jokiel 1977, Howells et al. 2012, 2013, Cornwall et al. 2019), further increases to ocean temperatures are expected to cause ongoing losses to coral reef health, species diversity and resilience (Hughes et al. 2017).

Temperature also plays a strong role in *directly* controlling both species distributions worldwide (# 34, 35) and individual rates of coral calcification (# 19, 30, 44, 56; Figure 3). This role is due to the positive effect of temperature on coral metabolism and biomineralisation (Coles & Jokiel 1977, Burton & Walter 1987). Clear trends in coral calcification rates have been observed on seasonal timescales (e.g. Kuffner et al. 2013, Courtney et al. 2017) and along latitudinal gradients in temperature (Grigg 1981, Lough & Barnes 2000). Separating the effects of light and temperature on calcification rates at these spatio-temporal scales can be challenging though, due to the co-variation of temperature and light (Kleypas 1997, Falter et al. 2012, D'Olivo et al. 2019, Ross et al. 2019). With respect to temperature, our model assumes that temperature effects can be modelled based on the local seasonal temperature range, given that increases in temperature drive metabolic rates and stimulate calcification until an 'optimum' has been reached, after which calcification rates decline (Jokiel & Coles 1977, Chalker 1981, Marshall & Clode 2004, Rodolfo-Metalpa et al. 2008, Al-Sofyani & Floos 2013, Samiei et al. 2016). We note, however, that the latitudinal trends and bell curve-shaped responses to temperature are species- and location-specific and not generally applicable to all coral genera, particularly those growing in sub-tropical and temperate environments (Ross et al. 2019). Temperature also plays an important role in controlling rates of CCA calcification (Ichiki et al. 2001, Lewis et al. 2017). Compared to corals, however, the temperature sensitivity of different CCA species is less well understood (# 34, 35, Figure 3; Cornwall et al. 2019).

Nutrients, macroalgae and suitable substrate cover

Nutrients can directly influence coral and CCA calcification rates at the individual level (# 18, 45, 57, Figure 3). Results for corals, however, are highly variable such that very high concentrations can reduce rates of calcification (Ferrier-Pagès et al. 2000) and modest increases in nutrients such as phosphorous can, in some cases, enhance calcification rates (Koop et al. 2001, Tanaka et al. 2007). Similarly, the effects of nutrients on CCA calcification rates are highly variable (# 57). For example, a positive influence of elevated nutrients on CCA calcification rates has been found to offset the negative effects of ocean acidification (Johnson & Carpenter 2018), while others found a negative impact of elevated nutrients on CCA calcification rates (Schubert et al. 2019) and cover (Belliveau & Paul 2002). Thus, although there are established relationships between nutrients and coral and CCA calcification rates, our knowledge of the specific effects of nutrients remains inadequate.

Much work has been done to understand the effects of macroalgae and available suitable substrate on coral recruitment and coral cover, providing a strong framework for modelling these interactions. Several factors, including the flux of nutrients in addition to light and essential elements (e.g. iron), can influence the growth of different algal species (Carpenter et al. 1991, Larned & Atkinson 1997, Renken et al. 2010) (# 3), many of which can compete with CCA and coral for suitable substrate (Szmant 2002, Jupiter et al. 2008, D'Angelo & Wiedenmann 2014). In addition, sediment cover and changes in the physical reef structure (e.g. available suitable substrate) can influence CCA colonisation, coral recruitment rates and coral cover (# 23–26) (Steneck 1986, Birrell et al. 2005, Cameron et al. 2016).

Flow velocities

The influence of water flow velocities is not typically included when modelling carbonate primary production. Water flow velocities, however, have an important influence on suitable substrate cover and calcification rates, because reef-scale hydrodynamics dictate the spatial distribution of algae and suitable substrate for CCA colonisation and thus coral recruitment, including sediment cover, rubble cover and dead coral cover (see net sediment production and sediment transport, # 11). Less is known about the impact of water flow dynamics on the growth of calcified algae, although recent work has investigated the interactive effects of environmental drivers such as temperature, light, nutrients and herbivory on *Halimeda* sp. (e.g. Castro-Sanguino et al. 2017). Higher water flow velocities influence calcification rates by reducing the size of the diffusive boundary layer surrounding coral and CCA, thereby increasing rates of nutrient uptake and exchange of metabolites (Atkinson & Bilger 1992). For this reason, water flow rates have been found to influence ocean acidification sensitivity in certain species of coral and CCA (Comeau et al. 2014c, 2019b); however, these relationships require more research for a range of coral and CCA species encompassing reef-scale diversity (# 37, Figure 3).

Seawater carbonate chemistry

Perhaps, the most complicated variable to relate in the model was the influence of seawater carbonate chemistry on reef-scale calcification rates (# 17, 33, 46, 47, 54, Figure 3). Our current understanding of the effect of ocean acidification on calcification rates is largely based on short-term aquaria experiments that simulate forecasted end-of-century pCO_2. These studies indicate that ocean acidification will result in decreased rates of calcification for many marine calcifiers, including corals and CCA (Kroeker et al. 2013, Comeau et al. 2014d, 2018, 2019a, Kornder et al. 2018). While much work has been done to understand these relationships, the effects of seawater carbonate chemistry are not typically incorporated into census-based carbonate budgets. Characterising these relationships is challenging, in part, due to highly variable species- and location-specific responses to ocean acidification (Gibson et al. 2012). Insights into these responses can be gained from investigating the physiological mechanisms of calcification. For calcification to occur, coral and CCA must take up calcium and dissolved inorganic carbon to precipitate their $CaCO_3$ skeletons internally in a semi-isolated, seawater supplied calcifying fluid located between the living polyp and the skeleton (Cohen & McConnaughey 2003, Gagnon et al. 2012). While coral have some degree of control over their internal carbonate chemistry, the process of calcification is still sensitive to changes in the seawater carbonate chemistry because it alters the internal chemistry of many species (Comeau et al. 2014a, 2017a, 2018, 2019b, Schoepf et al. 2017, Kornder et al. 2018). Thus, there are species-specific responses, with some taxa showing high sensitivity and others showing resistance and resilience to experimentally induced acidification (Schoepf et al. 2013, Comeau et al. 2014d, Cornwall et al. 2018, DeCarlo et al. 2018). The effect of seawater carbonate chemistry on calcification rates can also be buffered or exacerbated by other environmental variables, such as light and nutrients, but these interactive effects are less well documented. Given that the responses to these interactive or additive effects are species-specific, they are challenging to model on the community-wide reef-scale.

Seawater carbonate chemistry is also influenced by the bio-calcification process (Bates & Amat 2010, Anthony et al. 2011). This relationship arises because photosynthesis and respiration results in the metabolic release and/or drawdown of CO_2. In addition, during the calcification process, bicarbonate is converted to carbonate, producing H^+, which are then eliminated from the site of calcification (Allemand et al. 2004). This relationship is included in the model for completeness with the assumption that the relationship operates on short (diurnal) and intermediate (seasonal) timescales more so than interannual or decadal (# 1, 2, 6). Furthermore, we recognize that the diurnal and seasonal variability of seawater pH in coral reefs due to these ecological processes can be highly variable. These fluctuations are generally minor on well-flushed reefs (i.e. 0.1–0.2 pH units), compared to other environments, such as kelp forests and macrotidal pools (Rivest et al. 2017, Cornwall et al. 2018), but can be up to 1.4 pH units on shallower back reefs (e.g. Ohde & van Woesik 1999, Shaw et al. 2012, DeCarlo et al. 2017).

Acute disturbance events sub-system

Transitioning from budgets to models

To understand the processes that drive carbonate production in the face of disturbance events (e.g. bleaching, cyclones), carbonate budgets need to incorporate the effect of changing environmental conditions on ecosystem processes (e.g. growth rates measured during heat stress versus 'normal' conditions) and capture the status of the reef system pre- and post-disturbance events. These conditions are often logistically difficult to measure, resulting in limited evidence on the impact of bleaching events, and even less of cyclone impacts, on reef budgetary state.

To date, only five census-based carbonate budget studies have included carbonate production data pre- and post-bleaching, all of which have been published since 2017 (Januchowski-Hartley et al. 2017, Perry & Morgan 2017, Hamylton & Mallela 2019, Lange & Perry 2019, Ryan et al. 2019). When bleaching has been included, the reliability of the data is related to the time lag between pre- and post-disturbance assessments. Furthermore, these assessments mostly rely on census-based approaches that represent annual production rates for specific reef habitats and, therefore, do not account for event-specific and spatial variability in carbonate production (Perry & Morgan 2017, Lange & Perry 2019, Ryan et al. 2019). Consequently, census-based approaches can result in an overestimation of gross carbonate production compared to approaches that use locally derived calcification rates measured during bleaching years (Manzello et al. 2018).

There is also a distinct lack of pre- and post-cyclone event measurements. These limitations arise from the unpredictable nature of cyclones (Puotinen et al. 2016), making it logistically challenging to mobilize on short notice (e.g. days before a cyclone) to collect pre-cyclone data. Similarly, as cyclones are often destructive, post-cyclone data cannot always be collected immediately post-event (e.g. within a few weeks). Timely pre- and post-cyclone surveys are necessary to understand factors such as initial reef state (e.g. high versus low cover per coral taxa) and local disturbance history, which have the potential to influence the assessment of acute impacts and reef recovery trajectories.

Census-based carbonate budgets are based on the fundamental assumption of spatial additivity (i.e. amount of $CaCO_3$ produced by a single organism per unit area of reef surface covered) and do not consider how interactions between benthic organisms may also modulate carbonate production. This limitation can be exacerbated by acute disturbance events, which differentially influence reef organisms. For example, it has been estimated that the calcifying algae *Halimeda* produces three times as much carbonate when it occupies habitat alongside structurally complex corals such as *Acropora*, which provide refugia from grazing organisms (Castro-Sanguino et al. 2016). Coral bleaching and cyclone events more severely affect branching *Acropora*, which likely has indirect impacts on *Halimeda* carbonate sediment production (Castro-Sanguino et al. 2016, 2020). Consequently, the impacts of acute disturbance events on the reef system are not fully captured using census-based carbonate budgets.

Model summary

This model summarizes the complex interactions between the reef system and acute disturbance events (Figure 4). Alterations in the frequency and timing of acute, climate-driven disturbances, such as tropical cyclones and marine heatwaves, can trigger extensive coral mortality with potentially important impacts on reef carbonate production (Kennedy et al. 2013). We include the effects of wave energy and temperature (as variables for cyclones and heatwaves, respectively) on *in situ* carbonate production in the model in an attempt to encourage future researchers to collect these data, therefore addressing a current limitation of carbonate budgets.

The main outputs of the model are total calcification rate and reef framework density. As a result, the model differentiates the pathways by which disturbance events will influence carbonate production (and reef accretion) via changes in benthic community composition and their ecological

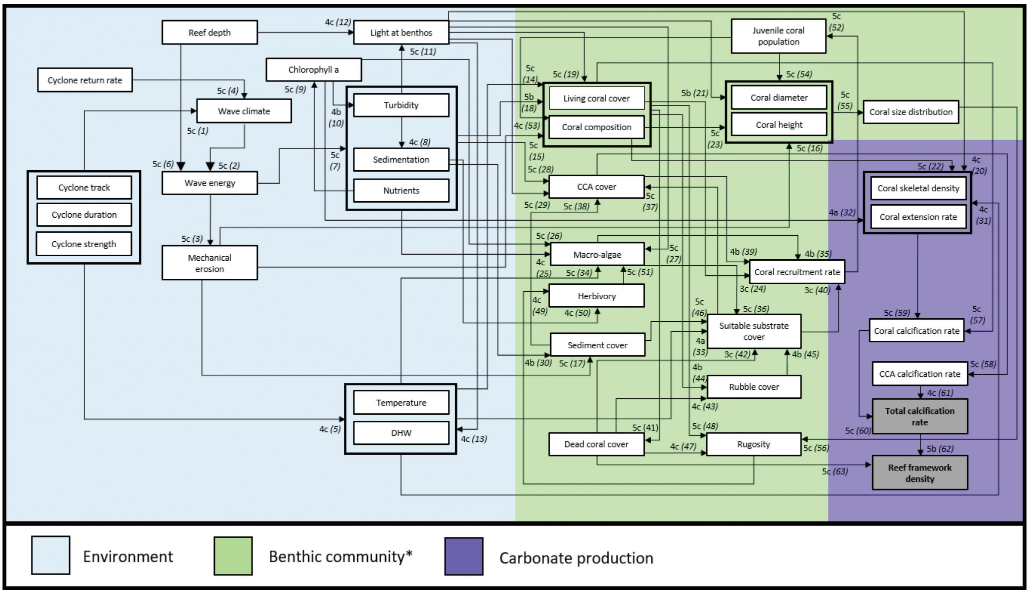

Figure 4 Conceptual model of event-driven (acute) impacts on coral reef communities. This model contains 36 variables and 63 relationships. Variables are grouped into three categories; environment (light blue), benthic community (green) and carbonate production (dark blue). Note that the * next to benthic community is to accommodate the variable herbivory, which is not part of the benthic community. Module outputs (grey shaded variables) include total calcification rate, which feeds into changes in the reef framework density. This module captures the impact of acute events, such as bleaching and cyclones events, and importantly incorporates how changes in benthic community will respond to these large disturbance events. Each relationship is provided with a strength (1–5; 5 being the strongest) and confidence score (a–c; c being most confident). Numbers in brackets next to the strength/confidence score relate back to Table 7, which provides details on the relationships with relevant references.

interactions (Figure 4; Table 7). We note that the variability of the responses from the benthic communities requires generalisations based on one to a few species, potentially limiting the reliability of any subsequent effort at quantification. The model seeks to capture variability of impacts at different spatial and temporal scales by focusing on the influence of wave energy (out degrees = 2; Figure 4) and mechanical erosion (3), temperature (4) and coral composition (6) on total calcification rate and reef framework density.

Wave energy and mechanical erosion

The variation in cyclone damage on a particular reef depends on the reef's position with respect to the cyclone track, the cyclone duration and strength (# 1, Figure 4; Puotinen et al. 2016, 2020). Wave energy variation around a reef provides a direct assessment of exposure to physical stress generated by cyclones (# 2, 3; Massel & Done 1993, Puotinen et al. 2016, Callaghan et al. 2020). The frequency and return period of severe cyclone events (# 4) can also have important implications on long-term ecosystem responses (Mumby et al. 2011, Wolff et al. 2016). Cyclone return rate is particularly important for modelling net carbonate production given the potential effects of global warming on increasing cyclone intensity and frequency (Emanuel 2005, Webster et al. 2005).

The consideration of the direct and indirect mechanisms by which climate-driven disturbances may impact coral communities was critical in building the model. For instance, cyclone waves cause direct physical damage to corals by breaking and dislodging colonies, affecting coral cover and size distribution through colony mortality and reductions in coral diametre and height (# 15–16,

Figure 4). Indirectly, cyclone waves may cause coral mortality via sediment resuspension, leading to coral burial (# 18) and increased turbidity (Edmunds & Witman 1991, Harmelin-Vivien 1994, Larcombe et al. 1995), which can impair coral reproduction and recruitment (Ricardo et al. 2015, Ricardo et al. 2016), and calcification and growth in some species (# 21–24; e.g. Kendall et al. 1985, Freitas et al. 2019). In addition, storm damage generates a considerable amount of loose coral rubble and framework debris that can delay coral recovery by reducing coral recruitment (# 38–40; Fox et al. 2003).

Temperature

For coral bleaching, we considered accumulated heat stress (as degree heating weeks (DHW); Eakin et al. 2010) as a proxy for bleaching severity (e.g. Hughes et al. 2018a). To capture habitat-specific responses to impacts of heat stress (# 12–14, Figure 4; Lenihan et al. 2008, Green et al. 2019) rather than assuming bleaching will occur equally in all habitats from reef crest to deep reef slope, we included variables such as reef depth and rugosity. Bleaching events have increased in severity and frequency due to global warming (Hughes et al. 2017, 2018a). Yet, although thermal stress may be responsible for most large-scale bleaching events, other environmental factors such as high UV radiation (Gleason & Wellington 1993) or reduced salinity associated with cyclones (Goreau 1964, Van Woesik et al. 1995) can also trigger bleaching. These additional processes were captured by incorporating relationships with water quality in the model (e.g. # 7–11).

During warming events, water column mixing induced by cyclones, known as ‘cyclone cooling’ is believed to reduce the heat stress associated with coral bleaching (Carrigan & Puotinen 2014). This process is captured in the model with a relationship between cyclone characteristics and DHW/temperature (# 5). Direct impacts of chronic ocean warming (i.e. increase in seawater temperatures) include effects on species growth and calcification (# 31; Cooper et al. 2008), whereas acute heat stress can trigger coral bleaching and lead to direct coral mortality as well as impaired coral reproduction and growth (Baird & Marshall 2002, Cantin & Lough 2014, Levitan et al. 2014). Indirect impacts include reduced coral larval supply following mass bleaching (Hughes et al. 2019), which has the potential to reduce coral recovery. Furthermore, coral mortality increases substrate availability for macroalgal overgrowth, potentially preventing coral recruitment (Doropoulos et al. 2014, Bozec et al. 2015). The acute disturbance model captures these complex interactions by incorporating feedback loops within components of the benthic community to consider alternative pathways by which coral communities respond to disturbances (# 30–48).

Coral composition

Coral community composition was a central variable in developing the acute disturbances model (Figure 4). Coral species differ in their vulnerability to cyclone-generated waves (Massel & Done 1993, Storlazzi et al. 2005, Madin & Connolly 2006, Madin et al. 2014) and heat stress intensity (Marshall & Baird 2000, Loya et al. 2001, Hughes et al. 2018b). Therefore, shifts in coral community composition due to recurrent disturbance regimes will influence reef-scale carbonate production dynamics (Courtney et al. 2020). Variability in community responses to disturbances is represented in the model with the consideration of species vulnerabilities and life-history traits (Darling et al. 2013, Madin et al. 2016) to inform variations in reef carbonate production (e.g. coral extension rate, coral skeletal density) (e.g. # 59–63).

Coral reef response to sea level rise sub-system

Transitioning from budgets to models

Although sea level dictates a range of environmental conditions that influence reef system development (e.g. accommodation space, light), the effects of sea level rise on carbonate budgets remain inadequately understood. The challenges to our understanding of coral reef response to sea level rise can be considered in the same way as spatio-temporal constraints between 'geological' and 'ecological' perspectives of coral reef change (Woodroffe 2008, Hubbard 2015). Geological approaches benefit from time-averaging processes that operate within a year to provide the average response of a coral reef system to a slow changing boundary condition (such as sea level rise). This approach is robust on temporal scales of millennia but struggles to provide insights into critical ecosystem processes that operate over shorter timescales and influence coral reef accretion (Hubbard 2015). Geological approaches are further limited by the features that can be derived from the stratigraphic record and the sampling regime (which typically consists of a spatially limited distribution of coral reef cores). Conversely, ecological approaches provide data on mechanisms that may drive net carbonate production and are thus more suited to examining the spatial heterogeneity in coral reef response to higher sea levels. Limitations of ecological studies (and carbonate budgets), however, relate to difficulties in translating these short-term ecological processes into long-term geological processes, such as coral reef accretion, that are accurate on scales of decades to centuries (Roff 2020). These limitations are due, in part, to the lack of *in situ* observations of coral reef accretion to recent and/or rapid sea level rise beyond that of the individual response of corals and other calcifiers.

Important recent attempts to cross the temporal gaps in geological and ecological understanding borrow approaches from both perspectives. High-resolution stratigraphic records of coral reef accretion combined with a reconstruction of oceanographic and some ecological processes are now possible (Roff et al. 2015b, Webster et al. 2018). When combined with a transect approach to coring coral reefs, a three-dimensional understanding of coral reef development is also possible (e.g. Cabioch et al. 1999, Dechnik et al. 2016, Webb et al. 2016). Numerical models that incorporate multiple variables from geological and ecological fields are used to hindcast and forecast coral reef accretion under rising sea levels and are starting to provide the links between census-based observations and geological perspectives on reef accretion (Salles et al. 2018, Pall et al. 2020). However, there are a number of interactions on coral reefs that are still poorly understood over the scales relevant to future sea level rise (decades to centuries). Examples include the influence of new substrate (following sea level rise) on coral recruitment and carbonate production (Doropoulos et al. 2012a); the processes that break down coral reefs into rubble and carbonate sediment; and the subsequent re-incorporation of coral reef-derived sediment and rubble into reef framework (Kennedy & Woodroffe 2002).

An ongoing challenge in translating ecological processes to geological timeframes relates to the conversion of *in situ* net carbonate production to reef accretion. To date, most studies that convert carbonate budgets ($kg \cdot m^{-2} \cdot yr^{-1}$) to reef accretion rates ($mm \cdot yr^{-1}$) follow the approach of Smith & Kinsey (1976). While this approach can provide useful insights into the *maximum* potential accretion (e.g. Perry et al 2018a), several assumptions in linking carbonate production to reef accretion remain, including (1) porosity of reef frameworks, which is based upon species-specific estimates from the geological literature (e.g. Davies & Kinsey 1977); (2) accretion derived from annual production estimates, which is assumed to be constant over decadal-centennial timeframes (e.g. De Bakker et al. 2019); (3) sediment incorporation, which is assumed to be constant through time and is uncoupled from framework production (Roff 2020); (4) carbonate production, which is assumed to remain *in situ* with no accounting for off slope transport from periodic storm disturbance (Schlager et al. 1994, Hughes 1999); (5) various conditions and processes, which are assumed constant but will likely change over time (e.g. increased reef flat wave energy under higher sea levels; Hearn 1999, Harris et al. 2018); (6) complex dynamics, such as feedback between reef structure and environmental processes and non-linear system responses, which are ignored (Woodroffe 2008); and (7) increased bioerosion on ecological timeframes, which may weaken reef frameworks resulting in loss of physical structures and reduced reef accretion potential (Glynn & Manzello 2015). These challenges are not easily resolved, but will be critical to understand in more detail if we are to increase our confidence in linking (and modelling) census-based carbonate budget results to the realities of coral reef change.

Model summary

Under rising sea levels, a coral reef system will accrete to mean sea level if the rate of sea level rise does not surpass the maximum rate of coral reef accretion and environmental conditions support carbonate production (Woodroffe & Webster 2014). Therefore, the main goal was to develop pathways that lead to the net vertical accretion of coral reefs in response to higher sea levels. However, the net accretion of a reef is a complex interplay of processes that produce, erode, dissolve, transport and incorporate carbonate material in coral reef systems (Perry et al. 2018b). We attempt to capture this complexity in the model by combining the geological knowledge of coral reef response to climate and sea level change over millennia with the ecological knowledge of coral recruitment, growth, carbonate production and response to environmental conditions over scales of seasons to years (Figure 5; Table 7). Although census-based carbonate budgets have been used to predict how reefs could respond (in terms of reef accretionary potential) to sea level rise, limited attention has been paid to how processes that drive reef ecology and carbonate dynamics might also change. The

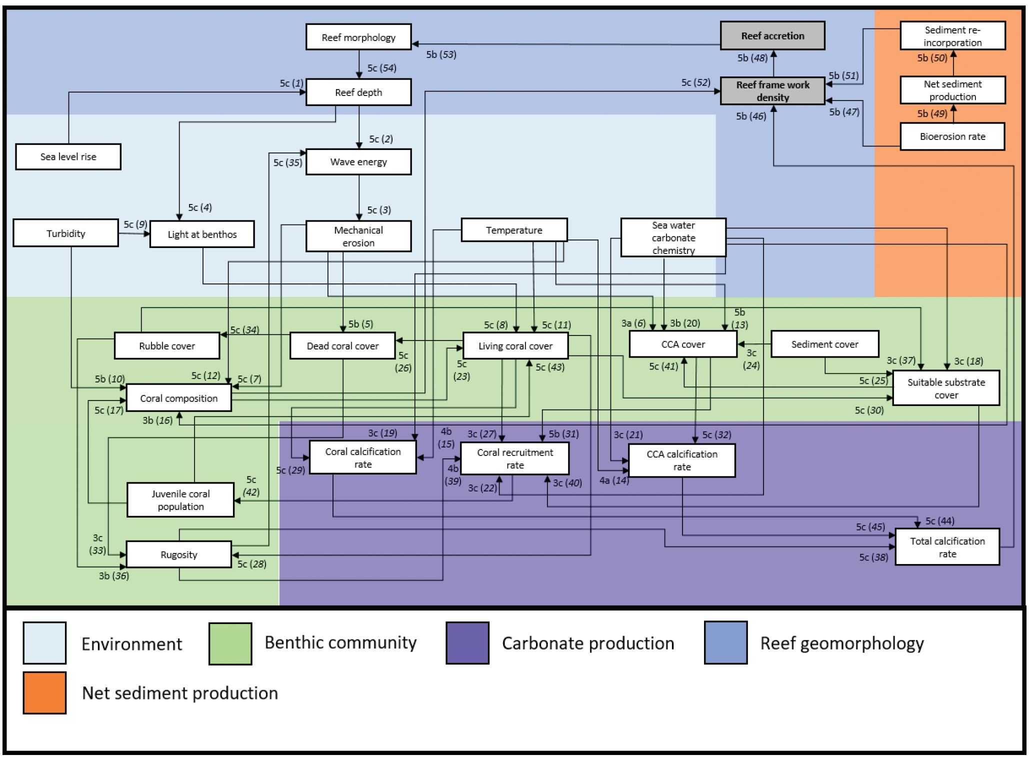

Figure 5 Conceptual model of sea level rise impacts on net reef accretion. This model contains 27 variables and 54 relationships. Variables are grouped in five categories; environment (light blue), benthic community (green), carbonate production (dark blue), net sediment production (dark orange) and reef geomorphology (medium blue). The module combines the geological knowledge of coral reef response to climate and sea level change over millennia with the ecological knowledge of coral recruitment, growth, carbonate production and response to environmental conditions over scales of seasons to years. Module outputs (grey-shaded variables) relate to changes in the reef framework density, which feed into longer-term reef accretion rates together with sediment re-incorporation. The bioerosion rate and net sediment production variables are module outputs from other modules, so includes all variables and relationships captured in these two modules. Each relationship is provided with a strength (1–5; 5 being the strongest) and confidence score (a–c; c being most confident). Numbers in brackets next to the strength/confidence score relate back to Table 7, which provides details on the relationships with relevant references.

coral reef response model seeks to overcome this limitation by articulating the relationships that require future consideration.

The main outputs of the model are reef framework density and reef accretion. As such, the model focuses on how changes in reef ecological process such as coral recruitment (out degrees = 1; Figure 5) and carbonate production (1) and environmental variables such as wave energy (1), light (1) and ocean chemistry (6) could change due rising sea levels and greater accommodation space, and how this could influence reef accretion.

Coral recruitment

A dominant component that differentiates this model to other previous models of reef response to sea level rise is that we specifically include coral recruitment as a central process in a coral reef's response to sea level changes (# 22, 27, 31, 40; Figure 5; e.g. Doropoulos et al. 2015, Bramanti & Edmunds 2016, Gouezo et al. 2019, Hughes et al. 2019). This process is often overlooked due (in part) to the longer temporal scales of most sea level change research when compared to coral recruitment studies. This component, we believe, is essential to consider because it allows an investigation into the processes that lead to rapid or subdued increases of carbonate production rates under rising sea levels.

Intertidal reef flats contain comparatively few, if any, live corals, but under rising sea level, intertidal reef flats will become fully submerged. If the environmental conditions and substrate are favourable, coral reef flats will recruit new corals and allow for the growth of live coral (# 17, 18, 22, 27, 30, 31, 34, 37, 40–43; Figure 5). A key unknown on coral reef response to higher sea levels is the length of time it takes for a reef flat to recruit new corals and begin vertical coral growth (Buddemeier & Hopley 1988, Buddemeier & Smith 1988). This model provides the relationships to investigate these responses by tracking the recruitment of new corals (# 22, 27, 31, 39) on to suitable substrate (# 31, 40, 41). The amount of suitable substrate cover (e.g. m^2) is influenced by rubble (# 37) and sediment cover (# 25) as well as seawater carbonate chemistry (# 18) and living coral cover (# 30). We consider suitable substrate cover to be a key variable that links sea level rise with coral recruitment: as the water depth over the reef increases, it not only increases the accommodation space, but also creates new areas for coral recruitment (i.e. by increase depth over reef flats). Coral recruitment rate is linked to eventual carbonate production because the survival and growth of juvenile corals (# 42) drives the subsequent adult coral composition (# 17), cover (# 43), and rates of coral (# 29) and total (# 44) calcification, together with CCA calcification and rugosity (# 38, 45; Figure 5). The breakdown of corals into rubble and sediment (# 5, 26, 34) via mechanical and bioerosion and subsequent incorporation (# 50, 51; Figure 5) and/or loss of this carbonate material is also an important but poorly understood factor.

Environmental variables

We also include hydrodynamic processes (such as changes in wave energy, # 1–3) and environmental conditions (such as ocean chemistry and turbidity, # 9, 18–22; Figure 5) that could influence carbonate production and the breakdown of live coral. The higher sea levels lead to changes in other environmental conditions that influence coral reef ecosystem functioning, such as light at benthos (Cooper et al. 2007) and wave energy propagating into the reef system (# 1–4; Figure 5; Hearn 1999, Baldock et al. 2014a, Beetham & Kench 2018, Harris et al. 2018). Changes in wave energy and subsequent mechanical erosion will impact the benthic cover (e.g. CCA, coral and carbonate rubble, # 3, 5, 6), and alter coral composition and rugosity (# 7, 23, 28, 33, 36), which are the primary drivers of coral reef carbonate production (# 38, 44,45; Figure 5; Storlazzi et al. 2005, Madin & Connolly 2006, Perry et al. 2012, Perry et al. 2013b, Madin et al. 2014). We also include processes such as net sediment production (# 50) and bioerosion (# 49) that are described fully in the other modules.

Reef framework density and coral reef accretion are the products of processes that produce (coral and CCA calcification) and remove carbonate (mechanical and bioerosion) (# 46–48, 51, 52;

Perry et al. 2013b, Perry et al. 2018b). The rate of reef accretion feeds back into the initial drivers of change in the coral reef system by influencing the difference between mean sea level and depth over the coral reef benthos (# 53, 54). If the rate of coral reef accretion keeps pace with the rate of sea level rise, the change in water depth on the reef flat will be minimal (i.e. similar water depth to present) and therefore conditions on the reef will not change substantially (Beetham et al. 2017, Harris et al. 2018, Perry et al. 2018b). If, however, the rate of sea level rise outstrips coral reef accretion many of the processes will change, leading to different trajectories in coral reef response to rising sea levels (Harris et al. 2018).

Bioerosion sub-system

Transitioning from budgets to models

Bioerosion is a dominant control of net reef accretion, but can be challenging to quantify and is therefore often poorly captured in carbonate budgets (Hutchings 1986, Spencer 1992, Glynn 1997). As widespread loss of corals frees up colonisation space and conditions such as increased nutrient pollution shift the balance in favour of filter feeding organisms, it is predicted that the role of bioeroders on coral reefs will become increasingly important in the future (Perry & Harborne 2016). As such, more reliable measures of bioerosion are paramount to any carbonate budget assessment. The main challenges to modelling bioerosion include (1) the taxonomic diversity and density of bioeroding organisms, which range from microorganisms to large vertebrate grazers (Hutchings 1986), (2) the divergent range of bioeroding mechanisms employed by these organisms, (3) lack of knowledge regarding species-specific responses to external biophysical and water quality variables; and (4) a high amount of variation in bioeroder abundances over time and space. These challenges are discussed below.

Census-based budgets rely on bioeroder density and calcifier abundance data, but rapid field surveys cannot accurately capture density estimates of buried framework eroders (e.g. sponges), motile/transitory grazers (e.g. parrotfish), nocturnal scrapers (e.g. urchins) or microborers invisible to the human eye (e.g. algae). Thus, bioeroders – diverse and largely cryptic – are significantly more difficult to survey than the predominately sessile and conspicuous benthic calcifier community. In the absence of direct measures, proxies are used, which come with underlying assumptions (e.g. that visible infestation of sponges at the surface relates to sub-surface density, or parrotfish numbers on a timed swim relate to activity at that site; Perry et al. 2012, Schönberg 2015). Consequently, many carbonate budgets are published with inadequate knowledge of site-specific bioeroding agents – which agents are present, active and their abundances. These knowledge gaps will have greater consequences in systems where bioeroding organisms are removing a significant portion of carbonate from the system.

Bioeroding mechanisms are as divergent and diverse as the bioeroders themselves – ranging from internal chemical etching by microbes to targeted mechanical excavation by parrotfish. This diversity multiplies the problem of poorly quantified bioeroder abundances when census-based budgets combine existing (i.e. published) activity rates with bioderoder density data to estimate reef-scale bioerosion. Knowledge gaps around activity rates of many species means that estimates are often derived from a few well-cited studies that might not represent the full range of rates across different sites within a species (Ogden 1977, Scoffin et al. 1980, Perry et al. 2012, Lange et al. 2020).

External physical (e.g. temperature, nutrients, sedimentation, wave energy) and biological (e.g. recruitment, competition, predation, disease) variables further propagate complexity by modulating bioeroder diversity, density and activity. For some species, external influences are well parameterized (e.g. multiple lines of evidence for positive association between nutrients and macroborer erosion; Hallock 1988), but for other species, they are not (reviews of knowledge gaps in Hutchings 2011, Perry & Harborne 2016, Schönberg et al. 2017, Lange et al. 2020). Furthermore, because most studies have focused on a single taxon and its relationship to external variable/s, we have insufficient knowledge about the interactive effects of multiple external variables on the bioeroding community's ability to remove carbonate (Hutchings et al. 2005). In addition to external physical and biological variables, bioerosion is also regulated by characteristics of the substrate itself, with factors like framework density, depth and length of exposure (following coral death) affecting bioeroder density and activity (Highsmith 1981, Kiene 1988). To date, substrate characteristics have been insufficiently accounted for in carbonate budgets.

Finally, scaling bioerosion from snap-shot estimates to broader space and time is hugely problematic: bioerosion on a newly exposed reef surface does not occur uniformly either in time (it is strongly successional and also influences itself in feedback loops) or space (bioeroders are often patchily distributed across reefs, so bioerosion pressure is highly variable spatially; Roff et al. 2015b). Bioerosion also fluctuates on orders of magnitude with explosions and crashes in bioeroder population densities (e.g. urchins; Uthicke et al. 2009), which in turn may be influenced by external drivers such as declining water quality, increasing temperatures or removal of predators, as well as showing longer-term trends (e.g. driven by reducing water quality, introduction of diseases).

Model summary

Here, we take an expansive view of bioerosion (due to particularly complex nature) that aimed to capture broad relationships within and between major bioeroding guilds and external (biological, abiotic and habitat) variables. The main model output is gross calcium carbonate removal (termed here total bioerosion rate; # 31, Figure 6), which represents the total material excavated from the framework by bioeroders (# 33; Table 7). How this excavated material is then redistributed (either dissolution, off-reef transport or re-incorporation into the framework) is not something most published budgets attempt to capture. Here, we seek to resolve this limitation by including the relationship between the production of bioeroded sediment and its re-incorporation into the framework (# 11, 20 and 22, 32, 34). Additionally, some sediment will be temporarily stored either on the surface of the reef or inside bioeroder guts ('storage'), and the remainder will be dissolved, ingested or transported to reef depositional sinks or out of the system (see the 'Carbonate Sediment Transport and Depositional Sinks sub-system' section).

Bioerosion is dictated primarily by the *presence* and *activity* of bioeroders; therefore, the model was organized around these two fundamental biological factors: (1) the diversity and density of bioeroding organisms (e.g. Figure 6 Box 1; out degrees = 4) and (2) their activity rate (Figure 6 Box 2; out degrees = 2). Variation in bioeroder density will drive differential bioerosion pressure; thus, the knowledge of the composition and absolute abundance of bioeroders present on reefs is critical to any mechanistic understanding of bioerosion. Likewise, reliable knowledge of activity rates is critical for deriving bioerosion estimates from species abundances (Figure 6 Box 2).

Bioeroder density

To keep the model broad and applicable to different biogeographic regions, bioeroders are classified simply into functional guilds (Figure 6, Box 1). Although several classifications exist (e.g. Golubic et al. 1975, Ginsburg 1983, Hutchings 1986), the most widely applied categorisation groups bioeroders into *grazers* – mainly fish and echinoids that remove surficial material by scraping and excavating often as a consequence of herbivory (# 28, Table 7 for more details); *macroborers* – endolithic sponges, bivalves and worms that either occupy holes or are buried within framework (# 29); and *microborers* – euendolithic microorganisms living in shallow framework creating borings <100 μm in diametre (# 30) (Perry 1999). These groupings allow us to portray different types of bioerosion, such as external versus internal framework removal (Figure 6, Box 1) and mechanical (bioabrasion) versus chemical (biocorrosion) activity (Figure 6, Box 2) and, therefore, group different taxa into trophic groups that are more likely to be influenced by environmental changes in similar ways (Hutchings 1986, Glynn 1997). Microborers, including algae, fungi, cyanobacteria and foraminifera, are both the most ubiquitous and poorest studied of the guilds (Tribollet 2008a). Although the

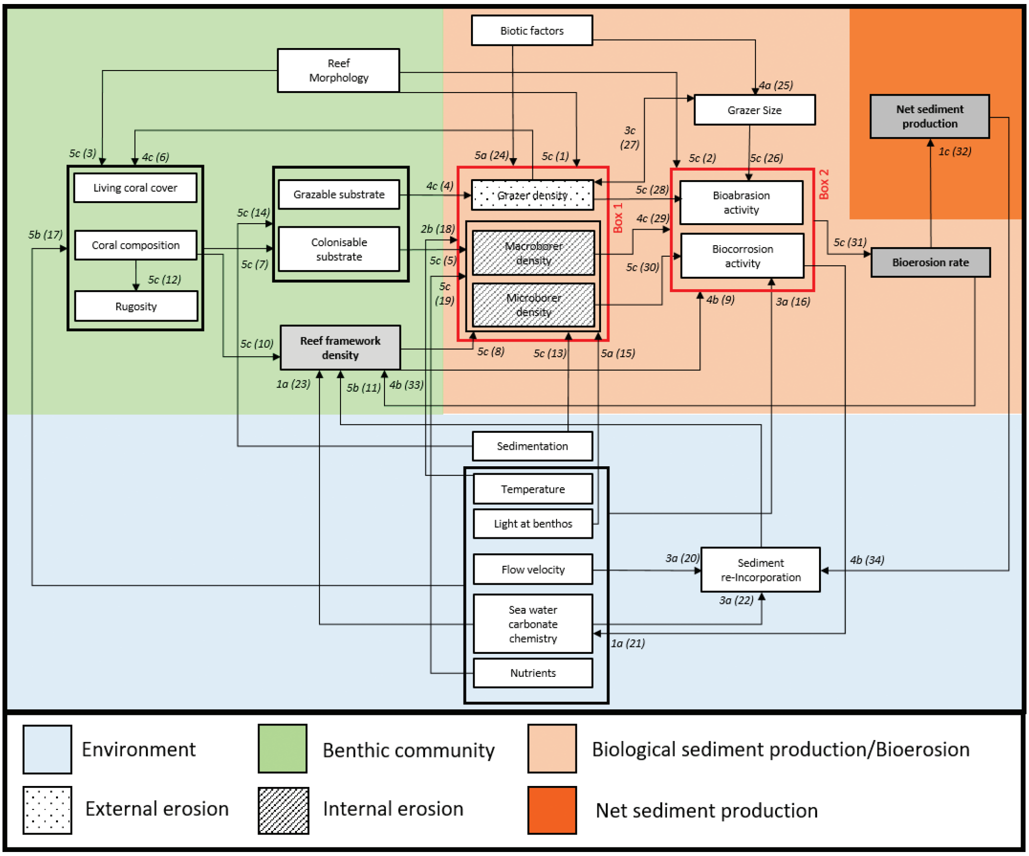

Figure 6 Conceptual model of bioerosion on the reef. This model contains 23 variables and 34 relationships. Variables are grouped into four categories: environment (light blue) and benthic community (and reef properties; green) and bioerosion (light orange). The link to the net sediment production module is also provided (orange box). Module outputs (grey-shaded variables) include the total carbonate removed from the reef (bioerosion rate), some of which (from bioabrasion) feeds into the net sediment production, together with those other biological, physical and chemical processes captured in the net sediment production module. The reef framework density is also a module output as it is influenced by both the removal of carbonate and sediment infilling from bioeroded sediments that are re-incorporated into the reef. The two red boxes relate to bioeroder density (Box 1) and activity (Box 2). In Box 1, we also differentiate between those bioeroders that are external (dotted) and internal (stripped). Each relationship is provided with a strength (1–5; 5 being the strongest) and confidence score (a–c; c being most confident). Numbers in brackets next to the strength/confidence score relate back to Table 7, which provides details on the relationships with relevant references.

roles of grazers and macroborers are better characterized (Bak 1994, Londono-Cruz et al. 2003, Alwany et al. 2009), there is a lack of consensus on their comparative contribution, perhaps due to geographic variation in activity and abundance, and experimental design and focus.

Bioeroders demonstrate clear community zonation, directly linked to depth and light (# 1), habitat availability (# 3, e.g. grazable and colonisable substrate: Table 6 for definitions), substrate type and rugosity (# 7), and reef framework density (# 8; Figure 6). Depth ranges (as well as other environmental variables that influence habitat and substrates) are captured in the model under reef morphology, since bioeroders are often related to certain reef zones. Habitat availability for either grazing or colonisation (by endoliths) – which may increase with higher rugosity (# 7 and 12) – is of particular relevance since large shifts in benthic cover in recent decades (# 4, 5) may have caused the escalation in bioeroder abundance (Schönberg et al. 2017). For example, urchin erosion increased 5-fold on Panamanian reefs after bleaching-induced coral losses in 1983 following an El Niño event (Eakin 1996, Glynn 1997). The type of substrate available will also influence the composition and density of bioeroders (# 7). For example, urchins typically graze CCA (Breitburg 1984), most parrotfish selectively graze algal turfs (Bruggemann et al. 1994), and many microborers infest living coral (Zubia & Peyrot-Clausade 2001). Coral community composition becomes important where we see different types of microbioeroding communities inhabit living and dead skeletons, while some macroborers show preference for certain species of coral skeleton (Peyrot-Clausade et al. 1992, Reaka-Kudla et al. 1996). Reef framework density (# 10, 11, 23) can also influence bioeroder density because denser substrates typically attract greater internal infestation, particular for bioeroding sponges (# 8; Schönberg 2002). The fact that bioeroder activity by its very nature influences the habitat locally (e.g. increasing framework porosity, affecting microhabitat complexity, e.g. Roff et al. 2020) further highlights the difficulty in capturing the complex nature of bioerosion in a model.

We include biotic controls on bioeroder population density (e.g. recruitment, disease, competition and predation) that are highly influential but also are too numerous, variable and species-specific to detail (biotic factors; # 24; Figure 6). The 'Bioerosion Loop', for example between grazers, macro- and microborers, represents feedback cycles where bioerosion activity by one guild creates changes in population or substrate that can alter local environmental conditions, further promoting or limiting bioerosion by other guilds (Schönberg et al. 2017).

The influence of abiotic factors, such as light, nutrients, sedimentation and temperature, on the abundance of bioeroding taxa is largely related to mobility, with sessile bioeroders more responsive to variability in environmental conditions. Most endoliths (e.g. macro- and microborers) are either photoautotrophic or heterotrophic filter feeders, and are therefore light or nutrient limited (Hallock 1988, Tribollet et al. 2002). The abundance of microborers is highest where light is abundant, and a reduction in available light will both decrease microborer density and alter the community composition given that certain species are more successful at using the limited light (# 15, Figure 6; Chazottes et al. 1995). Nutrient availability is one of the most influential and well-studied determinants of macroborer abundance, although the influence of nutrients can be both positive and negative (# 19; Chazottes et al. 2002, Wisshak et al. 2012, DeCarlo et al. 2015). The impact of sedimentation on bioerosion is complex, where increased sedimentation can either increase or decrease the abundance of bioeroders (# 13). Ocean warming can also influence the density of microborers (Reyes-Nivia et al. 2013), while temperature-induced bleaching, and subsequent coral mortality, increases the availability of dead coral substrate for subsequent colonisation by bioeroders. (# 18). The species-specific responses to environmental influences challenge any effort to predict how total bioerosion rates will vary with future environmental change.

Bioeroder activity

Bioeroder activity can be classified into either mechanical bioabrasion or chemical biocorrosion (although many macroborers employ a combination of both; Hutchings 1986). Bioabrasion is the mechanical removal of framework and includes both scraping and excavation by grazers, and internal bioerosion from some macroborers. Bioabrasion rates are more strongly influenced by biotic factors, such as the individual size of the eroding species (particularly for external eroders; # 26 and 27; Figure 6), where certain species or larger-sized individuals have a disproportionate impact (e.g. parrotfish < 25 cm have minimal bioerosive effect, while a 7 cm diametre urchin consumes >500 times more carbonate than their 1.2 cm counterparts (Bak 1990)). Biocorrosion is a biologically mediated process involving chemical dissolution of substrate, usually by internal eroders, particularly microborers (Tribollet 2008b). The process affects the local seawater chemistry within the framework and can quickly deplete carbonate content of seawater (# 21). Like any chemical reaction, biocorrosion rates are more likely to be directly influenced by abiotic factors that improve conditions for the reaction (# 16).

Information on how activity rates are influenced by external variables is generally lacking, or context-dependent and specific to individual taxa and locations (Perry & Harborne 2016). In the absence of data on how rates are influenced by external abiotic processes, an understanding of the bioerosion mechanism and organisms can help predict how activity may be modulated by external factors. For example, microborers are largely autotrophic, meaning activity is light-limited, while heterotrophic macroborer activity would be nutrient limited (Zubia & Peyrot-Clausade 2001, Carreiro-Silva et al. 2005). Evidence suggests that ocean acidification has a positive effect on microbioerosion (Reyes-Nivia et al. 2013) with growth and bioerosion increasing (by 48%) under doubled pCO_2 (Tribollet et al. 2009).

As such, our model suggests that temperature, light, flow velocity, seawater carbonate chemistry and nutrients (# 16) influence biocorrosion rates, but at present, more evidence and quantitative data would be required to disentangle these relationships for specific taxa. We also identify reef framework density as having an influence on both bioabrasion and biocorrosion (# 9; Figure 6), the availability of other potential resources within the substrate (e.g. shelter, water and nutrients) that could encourage organisms to bore more rapidly into substrates (# 2), and the influence of substrate properties (e.g. live or dead coral, coral species and morphology) on boring rates (# 7; Goreau & Hartman 1963, Hubbard 1986, Scoffin & Bradshaw 2000).

Net carbonate sediment production sub-system

Transitioning from budgets to models

Sediment production is not considered a central component of a conventional carbonate budget, and therefore, the mechanisms that generate sediments on reefs are rarely included. This omission is made despite their close association with many of the processes that drive reef bioconstruction and erosion. Pioneering studies in the 1970s were principally interested in the geological implications of carbonate budgets for reef development, and therefore often incorporated aspects of sediment dynamics (e.g. off-reef transport, framework infill), but notably excluded sediment dissolution (e.g. Chave et al. 1972, Stearn et al. 1977, Scoffin et al. 1980, Harney & Fletcher 2003). In contrast, more recent carbonate budget studies do not consider sediment produced by living reef communities or have regarded it as a loss to the reef system, particularly as the focus of many carbonate budgets has shifted towards assessing reef biological functioning and health (Januchowski-Hartley et al. 2017, Lange & Perry 2019). Detrital carbonate sediments, however, are widely distributed and have long residence times on reefs (Hubbard et al. 1990, Smithers 1994, Dawson & Smithers 2014, Morgan & Kench 2016b, Cuttler et al. 2019). Moreover, reef-derived sediments also contribute directly to the long-term evolution of the reef structure, as well as to shallow- and deep-water sedimentary reservoirs (e.g. lagoons), and coastal landforms (beaches, islands) (Hubbard 1986, Kench et al. 2005, Gischler 2006, Perry et al. 2013a, Morgan & Kench 2016b). Few studies to date have investigated the sedimentary linkages between living reef communities and carbonate-derived landforms (Hart & Kench 2007, Dawson & Smithers 2014, Morgan 2014), and rarely have measured rates of sediment dissolution been incorporated into budgets (e.g. Courtney et al. 2016).

Model summary

This model summarizes the biological (e.g. coral cover and composition, bioerosion), physical (e.g. wave stress, cyclonic activity) and chemical (e.g. carbonate dissolution) processes that influence the availability of carbonate sources on reefs and their conversion into detrital sediment (Figure 7). Reef-derived sediments are composed of the skeletal remains of reef biota, either as eroded fragments of the primary reef framework (e.g. corals, CCA) or directly as the remains of calcifying reef-dwelling organisms upon death (e.g. foraminifera, molluscs, *Halimeda* spp.). Yet, biological productivity by living reef communities does not directly parallel rates of sediment production, as many carbonate sources require the breakdown by external factors before they can contribute to the

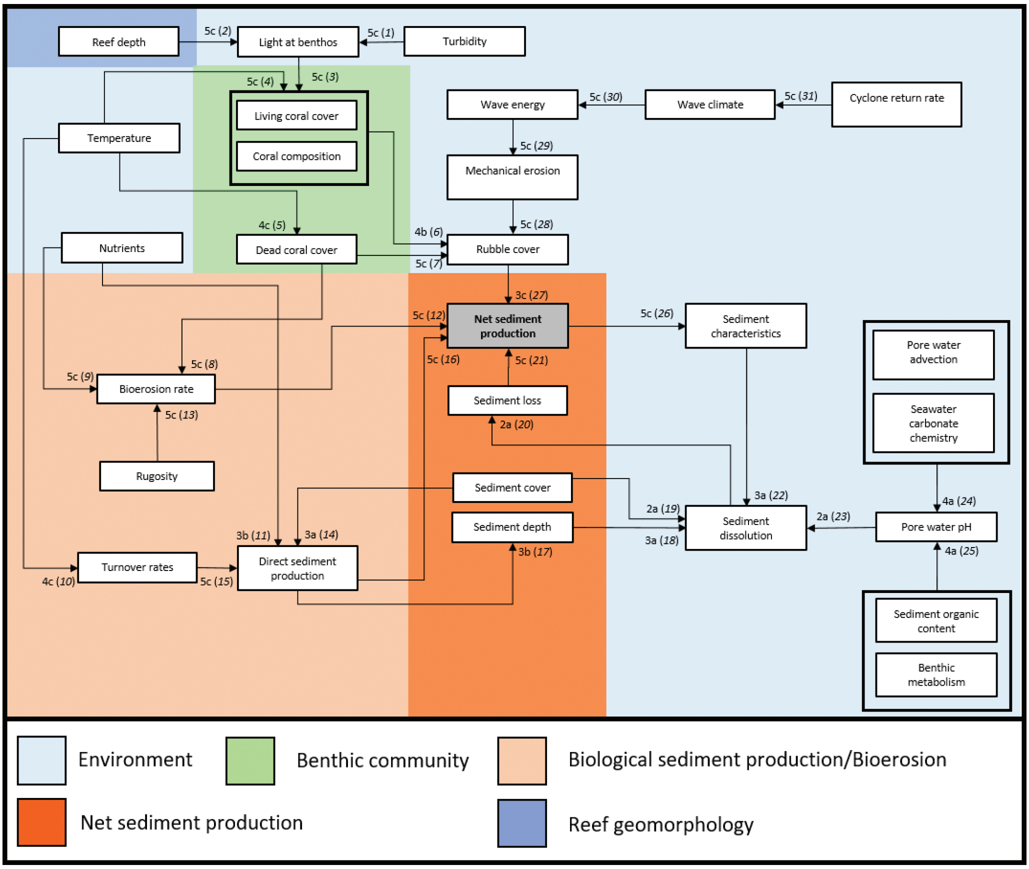

Figure 7 Conceptual model of net carbonate sediment production. This model contains 28 variables and 31 relationships. Variables are grouped into five categories; environment (light blue), benthic community (green), reef geomorphology (medium blue), biological sediment production (light orange) and net sediment production (dark orange). Module output (grey-shaded variable) is net sediment production which represents the gross carbonate sediment production from biological sources (e.g. direct sediment producers, bioerosion) and physical sources (e.g. the breakdown of *in situ* carbonate framework by mechanical erosion) as well as the loss of sediments through dissolution. The bioerosion rate variable is an output from the bioerosion module and represents all variables and relationships in that module. The net sediment produced on the reef then feeds into the carbonate sediment transport and depositional sinks module where sediments are either deposited on the reef system or transported off-reef. Each relationship is provided with a strength (1–5; 5 being the strongest) and confidence score (a–c; c being most confident). Numbers in brackets next to the strength/confidence score relate back to Table 7, which provides details on the relationships with relevant references.

local sediment pool. Here, we identify various biophysical reef processes and describe their influence on net sediment production (Figure 7; Table 7).

The model summarizes both direct and indirect sources of reef-derived sediment production, and loss (e.g. via dissolution), to provide an output of net sediment production. As such, the model focuses on the relationships between key sources of carbonate on reefs (coral cover and composition; out degrees = 1, direct sediment production; out degrees = 3; Figure 7) and the processes that erode (bioerosion; out degrees = 1, physical erosion; out degrees = 1), and remove (sediment dissolution; out degrees = 1) carbonate material. The development of the model highlights the complexities associated with quantifying rates of net sediment production across multiple spatial and temporal scales because of the range of biophysical processes involved. Further, this sub-system model provides a blueprint for including carbonate sediment budgets into census-based carbonate budget studies, which will be critical to improve our understanding on connectivity between reef ecological processes, sediment production and associated landform stability.

Coral cover and composition

Coral cover and composition is the main biological driver of reef-derived sediment because corals are the dominant calcifiers on most reefs, and their structural complexity determines the total source of carbonate framework available for breakdown (Chave et al. 1972, Scoffin 1992, Perry et al. 2012). Moreover, rates and types of sediment supply are derived from the growth traits and skeletal properties of their source organisms (Folk & Robles 1964, Ford & Kench 2012, Perry et al. 2019). Local abiotic conditions (e.g. turbidity, light, temperature, nutrients; # 1–4, 9, Figure 7) can negatively affect coral skeletal properties (e.g. density, micro-hardness), leading to increased rubble generation from hydrodynamic stresses (Risk & Sammarco 1991, Madin 2005, Dunn et al. 2012, Baldock et al. 2014b), or changes in internal bioerosion intensity (Highsmith et al. 1983, Holmes et al. 2000, Hernández-Ballesteros et al. 2013). Mass mortality events (e.g. coral bleaching) create vast amounts of dead coral cover that can be converted into rubble as the framework degrades (Perry & Morgan 2017) or into sand-sized particles following increased herbivory as algal substrates expand (Bellwood 1996, Perry et al. 2020, Taylor et al. 2020). Event-based sediment pulses represent a significant addition of new sediment to reefs (Perry et al. 2020) and have become increasingly more frequent and widespread (Hughes et al. 2018a), but the time lags between coral mortality and sediment generation remain poorly understood.

Bioerosion

Rates of sediment production from bioerosion become significant to local sediment facies when bioeroder activity intensifies (# 12, Figure 7). For example, parrotfish grazing accounted for the production of 85% of island sand (mean grain size of 0.35 mm) in the Maldives because of their high biomass and feeding intensity on reefs (Perry et al. 2015a, Morgan & Kench 2016a). Similar rates and particle sizes are also reported for parrotfish at sites along the Great Barrier Reef (Bellwood 1996). Considerably less is known about sediment production rates by urchin populations, even though individuals also produce sand-sized particles (0.2–0.5 mm) as a by-product of grazing (Hunter 1977, Ogden 1977, Reaka-Kudla 1985, Morgan 2014). Boring organisms (e.g. polychaetes, bivalves, molluscs) typically produce silt-sized particles (<63 µm) that are easily exported off-reef in suspension (Tudhope & Risk 1985). Bioeroding sponges (e.g. *Clinoa* sp.), however, can produce silt-to-sand-sized carbonate chips (15–80 µm) that contribute to local sediment reservoirs where sponge cover is high (Futterer 1974, Rützler & Macintyre 1978, Acker & Risk 1985, Nava & Carballo 2008, Carballo et al. 2017).

Direct sediment production

Direct sediment producers (e.g. *Halimeda* spp., foraminifera) add to detrital sediment pools immediately upon death and are a major source of sediment on some reefs (Kench et al. 2005, Yamano et al. 2005, Hart & Kench 2007, Dawson et al. 2014). In contrast to long-lived corals that are more resistant to breakdown, direct sediment producers have a short lifespan, fast growth and calcification, and high turnover rates (# 15, Figure 7). Although data exist for some key sediment producers (i.e. *Halimeda*) (Freile 2004, Multer & Clavijo 2004, Perry et al. 2016, Castro-Sanguino et al. 2020), limited information on the growth and calcification of benthic foraminifera (Muller 1974, Hallock 1981, Harney et al. 1999, Harris et al. 2015b) and non-articulated calcareous algae is available (Drew 1983, Perry et al. 2016, Perry et al. 2019). More generally, local nutrient conditions and seasonal variability in water temperature and light availability have been shown to influence the growth and calcification of direct sediment producers (# 10, 11; Littler et al. 1988, Teichberg et al. 2013, Castro-Sanguino et al. 2017).

Physical erosion

Physical processes (e.g. wave and currents) drive the production of coarse gravel fragments (>2 mm) and larger dislodged coral clasts on reefs (# 27–31, Figure 7). The greatest physical influence occurs on the reef edge where wave breaking and surging currents increase the physical force on corals and promote damage, breakage and dislodgement (Roberts et al. 1992, Lugo-Fernández et al. 1998a, Brander et al. 2004, Madin et al. 2006). We identify open ocean wave climate as the dominant physical disturbance on reefs (# 29–31). Storm activity (e.g. cyclone/hurricanes) has been documented to cause widespread destruction of coral communities to depths in excess of 20 m (Ogg & Koslow 1978, Highsmith et al. 1980, Edmunds & Witman 1991, Harmelin-Vivien 1994, Alvarez-Filip et al. 2009). These events can produce mass quantities of rubble over large spatial scales (100's km), resulting in the formation of extensive boulder ramparts on reef flats, and storm ridges at the shoreline, which can persist for decades (Maragos et al. 1973, Baines & McLean 1976, Scoffin 1993, Richmond & Morton 2007). The return rate of storms influences the production of rubble as it controls the frequency of destructive events on reefs.

Sediment dissolution

Carbonate sediments can be lost through chemical dissolution (Eyre et al. 2014). Chemical dissolution of carbonate grains is governed by the aragonite saturation state (Ω_{ar}) of the surrounding seawater. Dissolution occurs when $\Omega_{ar} < 1$, which represents the thermodynamic threshold for aragonite precipitation (i.e. $\Omega_{ar} < 1$ and aragonite dissolves; # 23 & 24, Figure 7). Although overlying seawater in most coral reefs is saturated ($\Omega_{ar} > 1$), sediment pore water Ω_{ar} is related to both the metabolic processes and the composition of overlying seawater that is advected into the sediments (Eyre et al. 2014). Organic matter in sediments can decompose, releasing dissolved inorganic carbon (DIC) into the pore water to decrease pore water Ω_{ar} (Figure 7). For example, the starting Ω_{ar} of the pore water is the overlying seawater that is advected into the sediments; in shallow waters where light reaches the benthos, a strong diel cycle of productivity and associated respiration (organic matter decomposition) exist, controlling dissolution and precipitation (Cyronak et al. 2013, Cyronak & Eyre 2016). When Ω_{ar} becomes sufficiently undersaturated ($\Omega_{ar} < 1$), a point called the carbonate critical threshold (Andersson 2015), carbonate material begins to dissolve (# 20). Further carbonate sediment dissolution is driven by additional organic matter decomposition (# 25). The sediments on most coral reefs are currently net precipitating, with some exceptions in organically enriched reefs (Eyre et al. 2018). Carbonate reef sediments, however, may on average transition from net precipitating to net dissolving by 2050 due to ongoing ocean acidification (Eyre et al. 2018).

Carbonate sediment transport and depositional sinks sub-system

Transitioning from budgets to models

The purpose of census-based carbonate budgets is to quantify the balance of carbonate material in the context of net reef accretion, and therefore, no previous study has comprehensively established quantitative links between reef-derived sediment supply and shoreline evolution. Reef system depositional sinks (lagoons, landforms) can act as large reservoirs of carbonate material, but do not necessarily contribute to reef accretion. Yet, quantifying aspects of reef sediment dynamics is critical for predicting the response of landforms (and other depositional sinks) to changes in both contemporary and future process regimes (e.g. sea level rise, wave energy, sediment generation) (Perry et al. 2011).

The balance of sediment supply, transport and deposition dictates the development of reef-associated landforms (e.g. islands, beaches) and other depositional environments on reefs (e.g. lagoons, channels) (Harney et al. 2000, Kench & McLean 2004, Morgan & Kench 2014, Cuttler et al. 2019). In the few cases, when sediment dynamics have been included within carbonate budgets, it has been within a geological context to account for the retention (e.g. sediment re-incorporation, lagoons/channel storage), and/or loss (e.g. off-reef export), of total detrital carbonate from reefs (Land 1979, Sadd 1984, Hubbard et al. 1990, Harney & Fletcher 2003, Browne et al. 2013). Efforts are underway to understand the processes governing the 'carbonate sediment budget', with a focus on the linkages between reef ecology and landform evolution, in other words, the mechanisms of carbonate sediment generation, transport and deposition (Morgan & Kench 2014, Perry et al. 2015a, Morgan & Kench 2016b, Cuttler et al. 2019). These recent studies have highlighted the important role of large bioeroding organisms (parrotfish, urchins) in generating sand-sized sediment suitable for landform construction and maintenance, and have quantified transport rates and mechanisms of sediment delivery (e.g. bedform migration) to nearby depositional sinks (Morgan & Kench 2014,2016a, Cuttler et al. 2019).

Model summary

This model expands the traditional census-based carbonate budget approach, by incorporating sediment dynamics and shoreline morphodynamics, and capturing the full suite of processes driving sediment supply, transport and deposition in reef environments (Figure 8). Reef-fronted beaches and islands are sedimentary deposits formed primarily through the accumulation of biogenic carbonate sediment. These landforms are intimately tied to the rates of local sediment supply derived from the adjacent coral reef communities (see 'Net sediment production sub-system' section). These

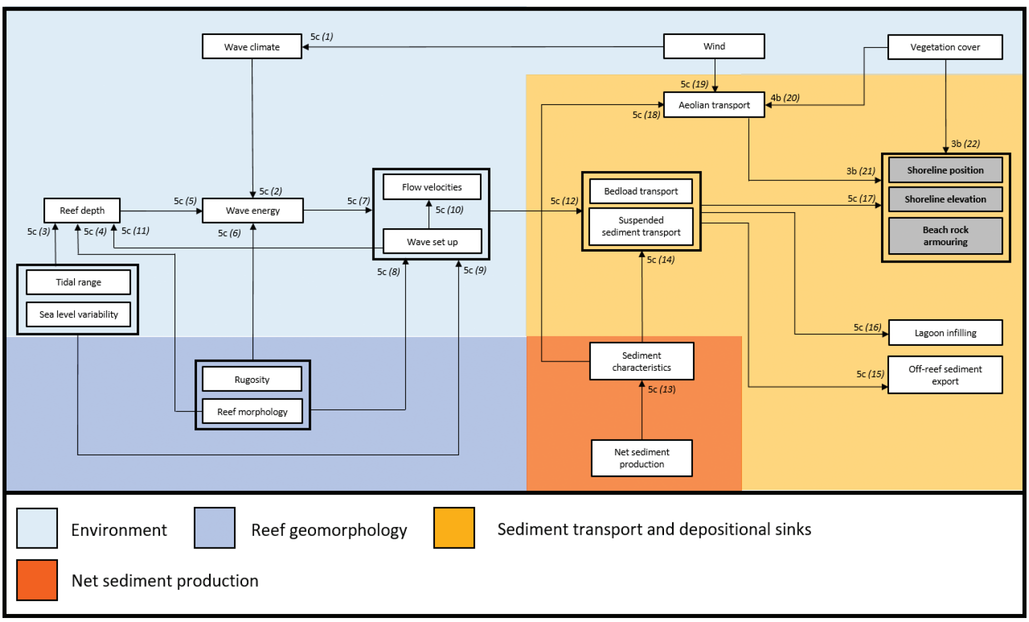

Figure 8 Conceptual model of carbonate sediment transport and depositional sinks. This model contains 21 variables and 22 relationships. Variables are grouped into four categories: environment (light blue), reef geomorphology (medium blue), net sediment production (dark orange), and sediment transport and depositional sinks (yellow). Module outputs (grey-shaded variables) relate to changes in landform morphodynamics. The variable net sediment production is an output from the net sediment production module and represents all variables and relationships in that module. This module captures the processes that mobilize, transport and deposit sediment throughout the reef system, thus representing the links between the ecological processes and landform dynamics. Each relationship is provided with a strength (1–5; 5 being the strongest) and confidence score (a–c; c being most confident). Numbers in brackets next to the strength/confidence score relate back to Table 7, which provides details on the relationships with relevant references.

unconsolidated sedimentary deposits have been shown to be highly dynamic in response to changes in physical forcing (e.g. waves, sea level) and sediment supply, which can cause large-scale modifications to shoreline morphology and elevation. Within many locations throughout the tropics (e.g. atoll reefs), reef-associated landforms provide the only habitable land area for human populations and are of significant ecological value in their support of high levels of terrestrial biodiversity (e.g. seabird populations). Therefore, understanding the processes that deliver reef-derived sediment to the shoreline and govern the formation and morphological stability of these landforms and other depositional sinks across a broad range of timescales (e.g. seasonal to decadal) is of critical importance to the geo-ecological carbonate reef system model.

The model variables are separated into dominant conceptual groups representing: (1) reef hydrodynamics (# 1–11) and sediment supply (# 12–14, 18), and (2) sediment transport and depositional sinks (# 15–17, 19–22; Figure 8; Table 7). Hydrodynamics (wave and sea level variability; out degrees = 6), reef morphology (reef flat width, lagoon and channel geometry, roughness; out degrees = 3) and sediment characteristics (size, shape, density; out degrees = 2; Figure 8) were determined to be the controlling variables of the overall model functionality.

Reef hydrodynamics and sediment supply

Reef hydrodynamics encompasses the wave and water level processes that mobilize and transport reef sediment. Regional wave climate (including extreme events such as cyclone frequency/intensity) determines the incident wave conditions (wave height, period, direction) at a given reef (# 1, 2, Figure 8; Hoeke et al. 2013). Once waves interact with the reef structure, their dissipation and ability to transport sediment is determined by the reef depth (which varies with tidal and non-tidal water levels) and reef morphology (# 3–4, 11). Water depth strongly influences wave breaking (# 5), while reef morphology (i.e. rugosity, fore reef slope, reef flat width) influences wave shoaling, dissipation due to bed friction, and wave setup (the increase in water level that results from wave breaking) (# 6, 8; Gourlay 1996a, Gourlay 1996b, Lowe et al. 2005, Monismith 2007, Lowe et al. 2009a, Buckley et al. 2015, Lowe & Falter 2015, Buckley et al. 2016). Waves generate wave orbital velocities and mean currents (collectively termed 'flow velocities'; # 7, 10, Figure 8) that are responsible for mobilising and transporting sediment (Pomeroy et al. 2015, Cuttler et al. 2019). When no waves are present (i.e. tide-dominated reefs), tidal flows drive the circulation patterns within the reef system (# 9; Lowe et al. 2015, Green et al. 2018).

Sediment produced via the biological and physical erosion of reef communities, or through direct inputs, becomes part of the 'active sediment reservoir' and is available for transport throughout the reef system (see 'Net sediment production' section). Sediment physical characteristics (e.g. shape, size, density) are related to the composition of reef-derived sediments and determine the conditions under which sediment can be mobilized (e.g. fair-weather, storm events) and the mode of transport (bedload, suspended load) (# 12, 14; Sorby 1879, Kench & McLean 1996, Cuttler et al. 2017).

Sediment transport and depositional sinks

Spatio-temporal variability in hydrodynamics drives alterations in sediment transport patterns that lead to the accretion or erosion of depositional sinks (# 15–17, 21, 22, Figure 8). These sinks include (1) off-reef talus deposits, generated by transport down the reef slope or out of channels (# 15; Harney et al. 2000, Morgan & Kench 2016a), (2) lagoon infilling (# 16; Perry et al. 2013a, Harris et al. 2014, Harris et al. 2015a) and (3) shoreline erosion/accretion, which in the context of reef islands is typically observed as changes to island area, height and shape (# 17; Kench & Brander 2006, Beetham & Kench 2014, Mahabot et al. 2016, Cuttler et al. 2019). For landforms, once sediment is deposited on the beach, it can be transported landward via aeolian (wind-driven) transport (# 18–21; Short & Hesp 1982, Sherman & Hotta 1990, Hesp 2002, Aagaard et al. 2004, Bauer et al. 2009) or by storm overwash – an important process for island vertical accretion and sand cay development (# 16; Kench et al. 2008, Woodroffe 2008, Masselink et al. 2020). Furthermore, subaerial sediment can become stabilized through the growth of naturally occurring vegetation (# 22; Hesp 1989, Stephenson & Brander 2003, Jackson & Nordstrom 2011, Charbonneau et al. 2017). Beach sediment can also become cemented *in situ* as ‘beach rock’, through physical and microbial-mediated chemical processes, which causes the precipitation of calcite crystals within the sediment pore spaces that bind individual sand grains (Vousdoukas et al. 2007). This cementation process can result in a natural armouring of the shoreline and potentially protect the landform from erosion by locking in a specific morphology.

Developing the qualitative geo-ecological carbonate reef system model

Above, we detailed the challenges of transitioning from budgets to models and the development of the individual sub-system models for each module. Here, we present a summary of the shared geo-ecological carbonate reef system model. This qualitative model moves beyond carbonate budgets and crosses the geo-ecological divide by providing links between reef ecology, carbonate system dynamics, reef accretion and landform stability.

To assist in understanding the geo-ecological carbonate reef system model, we developed a high-level overview figure that captures the relationships between the sub-system models through their outputs and critical variables (Figure 1). For example, the *in situ* carbonate production and acute disturbance modules produce outputs that feed into the variable ‘total calcification rate’. The bioerosion and carbonate sediment production modules both produce outputs that feed into ‘net sediment production’, which in turn links to the geo-ecological carbonate reef system model outputs, including ‘reef framework density’, ‘reef accretion’ and ‘landform morphodynamics’. We identified ‘critical variables’ according to at least one of three metrics. First, critical variables were those external environmental variables that acted as ‘root nodes’ (Table 4). External environmental variables were typically identified in only one or two modules, but acted as ‘drivers’ of a number of pathways, creating a pervasive influence throughout the system. Second, critical variables had high degree centrality with respect to the number of relationships a variable has with others (Table 8, Figure 1). This measure indicates how influential a variable is within the system. Third, critical variables were those that were common to three or more modules (Table 8; Figure 1). For example, living coral cover was included in five of the six modules (see Table 8) and had a total of 13 relationships (across all modules) with other variables. In addition to identifying relationships among sub-system models and the critical variables, we also grouped variables into broad categories (e.g. abiotic and biotic variables) to assist in providing an overview of relationships within the geo-ecological carbonate reef system model.

The value of the geo-ecological carbonate reef system model lies in its identification of *critical variables* that can be quantified, supporting decision-making for resource-limited research of carbonate system dynamics. The overview model accommodates *system complexity* by combining the current knowledge and understanding of the system; assesses *model confidence* through quantifying knowledge strength and confidence ratings; accounts for *environmental influences and acute disturbances*; and provides *flexibility* in terms of what elements of the system are studied while ensuring they can connect back into the whole system. As a result of these features, which we discuss below, we anticipate that the model will provide a blueprint for future research on reefs and associated landforms, with capacity for quantification of the system’s response to changing environmental conditions.

Accommodating system complexity

Although data that can be easily collected are more likely to be included in geo-ecological assessments and models, it is nonetheless critical that we seek to represent the complexity of a system. For example, the ReefBudget consists of 33 variables that primarily relate to benthic cover, carbonate

Table 8 Variables listed according to the total level of connectivity (total number of relationships/arrows), number of arrows out (out degrees) and the number of arrows in (in degrees). We also provide a summary of the number of variables included in each module as well as the number of previous census-based carbonate budget assessments that have measured each variable (max 38)

Variables	No. of modules	Total arrows	Arrows out (out degrees)	Arrows in (in degrees)	In situ carbonate production	Acute disturbances	SLR	Bioerosion	Carbonate sediment production	Carbonate sediment transport and sinks	No. of previous carbonate budgets
Seawater carbonate chemistry	4	19	12	7	1		1	1	1		1
Coral composition	5	19	12	7	1	1	1	1	1		36
Light at benthos	5	18	16	2	1	1	1	1	1		5
Flow velocity	3	16	11	5	1			1		1	1
Temperature	5	15	11	4	1	1	1	1	1		4
Degree heating weeks	2	13	9	4	1	1					0
Living coral cover	5	13	6	7	1	1	1	1	1		38
Nutrients	4	11	10	1	1	1		1	1		3
Reef morphology	3	11	10	1			1	1		1	38
Rugosity	5	11	6	5		1	1	1	1	1	30
Reef framework density	3	11	5	6		1	1	1			0
Wave energy	4	10	6	4		1	1		1	1	2
Coral recruitment rate	3	10	5	5	1	1	1				0
CCA cover	3	9	2	7	1	1	1				32
Suitable substrate cover	3	9	2	7	1	1	1				24
Macroborer density	1	9	2	7				1			15
Coral extension rate	2	9	1	8	1	1					27
Coral skeletal density	2	9	1	8	1	1					25
Mechanical erosion	3	8	7	1		1	1		1		1
Sedimentation	2	8	6	2		1		1			9

(*Continued*)

Table 8 (*Continued*) Variables listed according to the total level of connectivity (total number of relationships/arrows), number of arrows out (out degrees) and the number of arrows in (in degrees). We also provide a summary of the number of variables included in each module as well as the number of previous census-based carbonate budget assessments that have measured each variable (max 38)

Variables	No. of modules	Total arrows	Arrows out (out degrees)	Arrows in (in degrees)	In situ carbonate production	Acute disturbances	SLR	Bioerosion	Carbonate sediment production	Carbonate sediment transport and sinks	No. of previous carbonate budgets
Sand/sediment cover	4	8	5	3	1	1	1		1		28
Rubble cover	4	8	4	4	1	1	1		1		23
Macroalgal cover	2	8	3	5	1	1					19
Biocorrosion activity	1	8	3	5				1			16
Microborer density	1	8	1	7				1			16
Turbidity	4	7	6	1	1	1	1		1		4
Dead coral cover	4	7	4	3	1	1	1		1		25
Reef depth	5	7	3	4	1	1	1		1	1	38
OA sensitivity	1	7	3	4	1						0
Temperature sensitivity	1	7	3	4	1						0
Grazer density	1	7	2	5				1			26
Bioabrasion activity	2	7	2	5				1			26
Wave setup	1	7	2	5						1	0
CCA calcification rate	3	7	2	5	1	1	1				7
Chlorophyll-a	2	6	4	2	1	1					1
CCA composition	1	6	3	3	1						0
Net sediment production	4	6	3	3			1	1	1	1	1
Bed load transport	1	6	3	3						1	2
Suspended load transport	1	6	3	3						1	0
Total calcification rate	3	5	2	3	1	1	1				11

(*Continued*)

Table 8 (*Continued*) Variables listed according to the total level of connectivity (total number of relationships/arrows), number of arrows out (out degrees) and the number of arrows in (in degrees). We also provide a summary of the number of variables included in each module as well as the number of previous census-based carbonate budget assessments that have measured each variable (max 38)

Variables	No. of modules	Total arrows	Arrows out (out degrees)	Arrows in (in degrees)	In situ carbonate production	Acute disturbances	SLR	Bioerosion	Carbonate sediment production	Carbonate sediment transport and sinks	No. of previous carbonate budgets
Direct sediment production	1	5	2	3					1		10
Coral calcification rate	3	5	2	3	1	1	1				26
Colonisable substrate	1	5	2	3				1			0
Coral diametre	1	5	1	4		1					10
Coral height	1	5	1	4		1					10
Sediment dissolution	1	5	1	4					1		1
Coral juvenile population	3	4	3	1	1	1	1				0
Sediment characteristics	2	4	3	1					1	1	15
Sediment re-incorporation	2	4	1	3			1	1			1
Pore water pH	1	4	1	3					1		0
Grazable substrate	1	4	1	3				1			0
Aeolian transport	1	4	1	3						1	0
Tidal range	1	3	3	0						1	0
Cyclone duration	1	3	3	0		1					0
Cyclone strength	1	3	3	0		1					0
Wave climate	3	3	1	2		1			1	1	0
Grazer size	1	3	1	2				1			24
Sediment depth	1	3	1	2					1		6
Beach rock armouring	1	3	0	3						1	0
Shoreline position	1	3	0	3						1	0

(*Continued*)

Table 8 (*Continued*) Variables listed according to the total level of connectivity (total number of relationships/arrows), number of arrows out (out degrees) and the number of arrows in (in degrees). We also provide a summary of the number of variables included in each module as well as the number of previous census-based carbonate budget assessments that have measured each variable (max 38)

Variables	No. of modules	Total arrows	Arrows out (out degrees)	Arrows in (in degrees)	In situ carbonate production	Acute disturbances	SLR	Bioerosion	Carbonate sediment production	Carbonate sediment transport and sinks	No. of previous carbonate budgets
Shoreline elevation	1	3	0	3						1	0
Cyclone track	1	3	3	0		1					0
Atmospheric processes	1	3	3	0	1						0
Sea level variability	1	2	2	0						1	0
Wind	1	2	2	0						1	1
Biotic control	1	2	2	0				1			0
Cyclone return rate	2	2	2	0		1			1		0
Reef accretion	1	2	1	1			1				2
Herbivory	1	2	1	1		1					0
Coral size distribution	1	2	1	1		1					10
Turnover rates	1	2	1	1					1		4
Sediment loss	1	2	1	1					1		5
Bioerosion rate	1	3	1	2			1	1	1		22
Pore water advection	1	1	1	0					1		0
Sea level rise	1	1	1	0			1				0
Sediment organic content	1	1	1	0					1		0
Benthic metabolism	1	1	1	0					1		0
Vegetation cover	1	1	1	0						1	0
Lagoon infilling	1	1	0	1						1	0
Off-reef sediment export	1	1	0	1						1	5

Note: Italicized variables are those included in the high-level summary of the geo-ecological carbonate reef system model (Figure 1). These variables are either included in three or more modules, or are key root nodes.

production and bioerosion variables (Perry et al. 2017; Table 1). While this level of complexity is sufficient for estimating rates of *in situ* net carbonate production, it is insufficient for determining how fluctuations in reef health and carbonate production influence reef accretion and/or landform stability over time.

Our geo-ecological carbonate reef system model comprises a total of 80 variables and 265 relationships across six individual but interrelated discipline-specific modules. Of the 80 variables included in the model, 24 are environmental (e.g. light, temperature, seawater carbonate chemistry); 16 relate to sediments (e.g. sediment characteristics and organic content); 14 relate to reef characteristics and benthic cover (e.g. rugosity, living and dead coral cover); 14 to *in situ* carbonate production (e.g. coral and CCA calcification rate); eight to bioerosion (e.g. grazer size and density); and four to landforms (e.g. shoreline position and elevation; Table 6). The diversity of variables provides a more accurate representation of the complexity of these systems.

Of the 80 variables included in our model, only 18 have been reported in the majority (>50%) of census-based carbonate budget studies. These 18 variables represent the bias in existing assessments and models, including benthic cover (e.g. living coral cover, macroalgal cover), grazing rates by urchins and parrotfish, coral growth and reef characteristic variables (e.g. depth, morphology; Table 8). Those variables, such as microborer densities, were less common due to either methodological difficulties or perceptions that it was not as important for carbonate budget estimates.

In addition to accounting for a more comprehensive collection of ecological variables, our model also accounts for the geological environment. These variables represent the 'geo' of the geo-ecological carbonate reef system model, which includes 15 new variables that go beyond the reef and relate it to sediment transport and shoreline dynamics. The inclusion of these variables provides the first model to integrate reef ecological change with landform stability. Representing this complexity is essential for developing quantitative models that will more accurately represent reefs and associated landform systems.

Assessing model confidence

One of the main contributions of the geo-ecological carbonate reef system model is an assessment of the existing knowledge base within each of the modules. Differences in confidence ratings between modules were a reflection of the extent of *existing* knowledge. Such assessments are critical in determining where knowledge gaps exist, particularly in terms of what data are available to enable comparisons between sites.

The sub-system models with the highest confidence ratings related to the *in situ* carbonate production module (77% high, 8% low confidence), acute disturbance model (82% high, 3% low confidence) and the carbonate sediment transport and sinks module (86% high, 0% low confidence), reflecting the vast amount of research and understanding associated with coral calcification processes, and physics-based processes central to carbonate sediment transport. In contrast, modules with the lowest confidence ratings included the bioerosion module (62% high, 23% low confidence) and the sediment production module (64% high, 26% low confidence), reflecting unknowns around environmental variables and rates of cryptic boring organisms, and drivers and rates of sediment production and dissolution, respectively. Areas with the lowest confidence rating were largely associated with four areas: CCA cover and calcification rates, boring organism density and activity, sediment dissolution and reef framework density.

An interesting outcome of the modelling process was a correlation between a person's confidence in their knowledge of a relationship and the perceived strength of that relationship. Modellers rated relationships (influences between variables) in their model based on their perceptions of the strength of those relationships (1 = weak, 5 = strong). Approximately 67% of the total number of relationships were classed as strong relationships and <5% were classed as weak. Weak relationships included the influence of temperature on CCA calcification rates; seawater carbonate chemistry on reef framework density; flow velocity on coral and CCA sensitivity to ocean acidification; environmental drivers of rates of bioerosion; and the influence of sediment dissolution on sediment loss rates. Interesting, of the 25 low confidence relationships, 60% were found to have a low to medium (1–3) strength rating. This correlation points to a bias in what might be considered important within a complex system on the basis of how much data we have on the different variables within that system.

Accounting for environmental influences and acute disturbance events

Environmental influences include both physical (e.g. climate and sea level variables) and abiotic (e.g. seawater carbonate chemistry, light, nutrients) variables. They are necessary to include in any predictive application of the geo-ecological carbonate reef system model because such predictive models ultimately seek to quantify the relationships between environmental variables (cause) and ecological change (effect) (Cacciapaglia & van Woesik 2020, Lange et al. 2020). For example, of the 31 critical variables identified, the majority (19) were environmental variables, 11 of which were (physical) external drivers (Figure 1). The 11 external drivers included atmospheric processes (light, temperature) and wind, wave climate and sea level variables, cyclone-related variables, and landform vegetation cover (Figure 1). These variables were typically only present in one module and acted as 'root nodes'.

One of the most important contributions of the geo-ecological carbonate reef system model is the inclusion of the acute disturbance module. This module contains 63 relationships that connect 36 variables that describe the influence of these events on carbonate production, including variables that specifically relate to disturbance events such as degree heating weeks, cyclone characteristics and mechanical erosion. The acute disturbance module provides a comprehensive blueprint for future carbonate production assessments that seek to assess how these large events influence carbonate production over time (e.g. during the recovery period). The blueprint can be used to support researchers in making decisions around which variables should, and can, be quantified with available resources to estimate current and/or future carbonate production.

The variables and relationships of the acute disturbance module are thus important to capture for modelling changes in carbonate production. Existing census-based carbonate budget assessments typically only provide a 'snap-shot' of present-day carbonate production rates. Few assessments have conducted repeat measurements through time to enable an estimate of change in carbonate production and reef budgetary state in response to changing conditions (Manzello et al. 2018); and pre- and post-disturbance event assessments (Perry & Morgan 2017, Lange & Perry 2019). Yet, it is these events (e.g. bleaching and cyclones), which are predicted to increase in frequency and severity in coming years (Carrigan & Puotinen 2011, Hughes et al. 2017) that are most likely to have large-scale effects on carbonate production. Importantly, we currently lack data on how net carbonate production will change during and following these events. As such, current estimates of the influence of acute events on reef carbonate production and growth are potentially inaccurate, creating the need to develop a predictive quantitative model.

Given that future climate change will likely change ocean conditions (e.g. high temperatures, lower pH, lower light, more frequent and intense cyclones; Hoegh-Guldberg & Bruno 2010, Hughes et al. 2017), it is imperative that physical and abiotic variables are included in geo-ecological carbonate reef system modelling. To provide environmental context, we encourage researchers to include in future carbonate studies site-specific data (in-water) on light, temperature, seawater carbonate chemistry, sediments and nutrients, and wave energy and current velocity. In the absence of direct *in situ* measurements of these variables, there are some readily available data sources (e.g. global wave hindcasts, satellite-derived measures water quality and temperature) that could be (relatively) easily incorporated into future quantitative models that seek to predict ecological change with environmental change. But it should be noted that these data sources operate over larger spatial scales

(>100 m) so likely do not reflect changes in processes at the reef habitat scale. Finally, to quantify cyclone impacts more accurately within geo-ecological carbonate reef system models, we need to also include variables that influence coral breakage thresholds, such as the strength of the substrate upon which colonies are attached (Madin 2005) and intrinsic coral properties (e.g. coral morphology, coral size, coral porosity; Baldock et al. 2014a). These data would allow us to improve modelling of cyclone impacts on coral communities.

Achieving model flexibility

One of the main strengths of our modular approach is that it provides flexibility for future researchers working on part (or all) aspects of the entire geo-ecological reef system. For example, if the focus of the research was on fluctuations in coral and CCA calcification rates with environmental change, researchers could include data on variables and relationships identified in the *in situ* carbonate production module. If researchers were interested in understanding how changes in benthic cover and coral community characteristics (e.g. coral size distributions), following a bleaching event, influenced total calcification rate, they could use the acute disturbance event module. If researchers were aiming to predict reef accretion with future climate change impacts, they could include all models except the carbonate sediment transport and sinks module. The flexibility of the overall geo-ecological qualitative model could also prove critical for future quantitative modelling because a lack of data in one module does not limit the development and application of other modules.

Towards a quantitative geo-ecological carbonate reef system model

Above we detailed how each of the modules of the geo-ecological carbonate reef system model was developed and integrated into the geo-ecological carbonate reef system model. We now turn our attention to current knowledge gaps and related future research directions for each sub-system module. Identifying data needs is critical in quantifying relationships within each module, and thus the overall model, providing the opportunity to develop predictive capacity. In other words, the development of a quantitative model requires both a comprehensive qualitative model and empirical data that describes the relationships of the qualitative model. Below we discuss modelling challenges related to our current knowledge and understanding within each of the sub-system models across changing spatial and temporal scales, and briefly consider the feasibility of developing a quantitative model given current knowledge gaps and computational issues. Lastly, we identify future research directions that would aid the development of a predictive geo-ecological carbonate reef system model.

In situ *carbonate production*

The *in situ* carbonate production model includes 28 variables and 61 relationships (Figure 3). Modellers were highly confident in the majority (77%) of relationships in the model, which reflects the either well-studied or commonly assumed nature of many of the relationships. Well-established relationships were often those between environmental variables. Examples include reef depth affecting light at benthos and the variety of physiochemical controls on seawater carbonate chemistry (e.g. calcification, photosynthesis, atmospheric CO_2 and temperature; Figure 3). Lower confidence ratings were often those relationships *between* environmental and ecological variables, such as the influence of nutrients, temperature and seawater carbonate chemistry on CCA cover (Figure 3).

Relationships with low confidence ratings highlight the need to improve our understanding of the influence of dominant environmental variables on coral and CCA cover, and calcification rates. For example, the influence of wave characteristics on flow on reefs and water velocity has been shown to affect the sensitivity of corals to ocean acidification in some laboratory experiments (Comeau et al. 2014a, 2019b), but we have inadequate knowledge (relationship rated as '2a'; Figure 3) on how strongly this relationship might apply across different coral species or reef environments. We also have inadequate knowledge of the relationships between seawater carbonate chemistry and species composition (relationship rated as '1b'; Figure 3). For instance, ocean acidification has differential effects on calcification among coral species in laboratory studies (Comeau et al. 2017a, 2019a), which theoretically could lead to changes in species composition assuming that the more resilient species flourish while the abundance of more sensitive species declines. Moreover, changes in species composition have been previously reported along pH gradients (Barkley et al. 2015), indicating the role of ocean acidification in structuring coral reef communities. Evidence to date therefore suggests that a relationship should exist, but more studies are required to quantify the relationship.

Understanding (and modelling) the effects of thermal stress and temperature sensitivity (Figure 3) on CCA calcification rates (rated as 'a') and percent cover (rated as 'b') is challenging given that there is inadequate knowledge about the bleaching thresholds of CCA. This lack of knowledge is partly due to the challenges of maintaining CCA in aquaria, in addition to the minimal field-based data available for documenting CCA responses to thermal stress events (Cornwall et al. 2019). Moreover, the identification of CCA species based solely on morphology is challenging (Gabrielson et al. 2018), and many species may have been incorrectly ascribed, resulting in a lower confidence of species-specific responses to different environmental variables.

Quantifying temporal trends in coral and CCA calcification is important for characterising reef maintenance, reef function and the potential for structurally extensive coral reef development. Yet, inadequate knowledge is available relating to long-term (i.e. decadal) changes of coral calcification rates for those taxa that are morphologically complex and/or lack annual density banding (e.g. key reef-building acroporids). With respect to CCA, fewer studies have quantified calcification rates or investigated the response of calcification rates to environmental variables. Furthermore, we have a relatively limited understanding on how short-term acute disturbance events impact the longer-term (>5 years) rates of calcification for both coral (i.e. reef-building taxa) and CCA.

To improve the development of a quantitative carbonate production model, the primary focus area for future research should be the characterisation of long-term (e.g. decadal) changes in coral and CCA calcification rates for multiple taxa across different reef environments (Table 9). An increased understanding of the complex interplay between organism morphology, organism metabolic activity and the degree of mass transfer variability would also provide a clearer framework for modelling these interactive effects. Specifically, future research directions should include

1. The influence of temperature, thermal stress and temperature sensitivity on CCA calcification rates, percent cover and species composition, both geographically and over time, particularly following disturbance events.
2. The individual and combined effects of water flow velocities, nutrients and OA sensitivity on CCA and coral calcification rates and percent cover
3. The different calcification rate responses to temperature of coral taxa from a range of locations
4. The long-term (interannual to decadal) quantifiable changes in coral and CCA calcification rates for key species.

Acute disturbance events

The acute disturbance events model includes 36 variables and 63 relationships, of which 82% were rated with high confidence and 3% with low confidence. Areas of high confidence included the direct and indirect effects of cyclones on the abiotic environment (e.g. waves and water quality);

Table 9 Summary of research questions and knowledge requirements for developing a quantitative model

Module	Research question	Why gap exists	Research needs
In situ carbonate production	1. What is the influence of temperature and thermal stress on coralline algae calcification, % cover and species composition both geographically and over time, particularly following repeated disturbance events?	Logistical difficulties (e.g. challenges in maintaining CCA in aquaria because they often bleach in the control tanks); Lack of knowledge and/or understanding (e.g. generally limited field-based data before/after thermal stress events)	Requires understanding of temporal and geographical changes in CCA growth and % cover across latitudinal gradients, and in response to thermal stress events and for a range of taxa
	2. What are the individual and combined effects of water flow velocities, temperature, light and OA on CCA and coral calcification rates?	Logistical difficulties; lack of knowledge and/or understanding	Requires controlled aquaria studies to better understand both the individual and interactive effects
	3. Why do coral taxa from a range of locations show different calcification rate responses to temperature (i.e. why some corals show a positive or curve-shaped temperature-growth relationship while others do not)?	Lack of knowledge and/or understanding	Further exploration of physiological acclimation/adaptation mechanisms (e.g. photo-physiology and bio-calcification) is required to decipher why some corals show a positive or Gaussian-shaped temperature-growth relationship while others do not, particularly for coral species with distributions that extend to tropical and temperate zones
	4. What are the drivers of long-term (interannual to decadal) changes in coral and CCA calcification rates for key species?	Logistical difficulties; lack of resources (time)	Requires long-term growth rate studies for key taxa, such as the reef-building corals (particularly branching taxa) and CCA that are important for binding the reef substrate
Event (acute)-driven disturbances	1. How does stress (during and following) from acute disturbance events influence rates of carbonate production (and loss)?	Site access	Account for temporal and spatial variability in species sensitivity and recovery to disturbance in stress vs unstressed environments (e.g. revised bleaching thresholds for turbid reefs)
	2. What are the long-term temporal dynamics of benthic components after an acute disturbance event?	Site access	Requires integrating decadal changes in the size structure and species composition of calcifiers after disturbance but also projecting the fate of carbonate material produced by the disturbance, with consideration of possible interactions with calcifier recovery rates in space and time

(*Continued*)

Table 9 (*Continued*) Summary of research questions and knowledge requirements for developing a quantitative model

Module	Research question	Why gap exists	Research needs
Event (acute)-driven disturbances (cont.)	3. How do interactions between various benthos influence response of community carbonate production to acute disturbances?	Lack of knowledge and/or understanding	Requires laboratory experiments on interactions between benthic calcifiers to understand how loss/gain of one calcifier after acute disturbance may have flow on effects for other calcifiers
Coral reef response to sea level rise	1. How do we rectify the varying temporal scales of geological and ecological processes operating on reefs?	Methodology limitations; lack of knowledge and/or understanding	Requires long-term ecological studies (e.g. multi-decadal or longer) to understand how short-term dynamics (seasonal to annual) relate to longer-term processes
	2. Can we increase the spatial coverage and temporal resolution of geological reconstruction of coral reefs?	Methodology limitations	Advances in high precision U-Series dating on multi-reef core transects, in regions with well-constructed sea level curves, can provide high spatial resolution of past reef evolution with the change in benthic composition over time. This can be combined with emerging research on the inclusion of rare earth elements and bioeroders to detail the paleo oceanographic and environmental conditions during coral reef development
	3. What are the key hydrodynamic and oceanographic processes that drive rates of carbonate production, erosion and incorporation into the reef framework over decadal timeframes?	Methodological limitations	Requires a wider spatial (and longer term) deployment of *in situ* data loggers to capture oceanographic and environmental conditions across a number of different reef habitats and types. These data should be combined with data from carbonate budgets and reef geological studies (using high precision dating)
	4. Can we develop probabilistic models that can quantify uncertainty among processes that drive reef change?	Lack of knowledge and/or understanding	Requires the application of statistical and/or machine learning to start applying uncertainties to carbonate budget outputs and reef accretionary models. This will provide an important measure of model confidence
Bioerosion	1. What are the critical environmental controls on biocorroding organisms diversity, density and activity?	Lack of knowledge and/or understanding; organism traits	Requires long-term detailed studies that combine site-specific (habitat) environmental data with differences in micro/macroborer abundance and activity data
	2. How does reef framework factors such as substrate density influence bioerosion rate?	Lack of knowledge and/or understanding; organism traits; methodological difficulties	Requires an assessment of reef framework composition with bioerosion rate, potentially using complementary data from reef cores and ecological surveys

(*Continued*)

Table 9 (*Continued*) Summary of research questions and knowledge requirements for developing a quantitative model

Module	Research question	Why gap exists	Research needs
Bioerosion (cont.)	3. How do variations in bioabrader composition, abundance and activity relate to changes in gross sediment production and reef building processes?	Lack of knowledge and/or understanding; organism traits; methodological difficulties	Requires long-term studies that accurately quantify bioerosion rates with an assessment of where the carbonate removed ends up (e.g. in the reef framework or off-reef)
Net sediment production	1. What are the impacts of climate change (e.g. increasing temperature, OA) on sediment production regimes?	Organism trait; methodological issues	Requires new quantitative methods to measure sediment production by a range of reef calcifiers to determine how large-scale disturbance events will alter the magnitude and rate of sediment supply from reefs. Further information also required on how environmental change will influence organism growth, calcification and turnover rates
	2. Do currently used estimates of direct sediment production accurately represent true sediment production over space and time?	Organism trait; methodological issues	Developing new field survey methods for quantifying the abundance of direct sediment producers. Methods should be established for a wide range of sediment-producing organism and focus of relatively rapid field approaches for documenting reef sediment production, and their growth and calcification rates
	3. Can we better quantify the lag times between sediment production and landform deposition?	Organism trait; methodological issues; lack of understanding and/or knowledge	Establish quantitative methods to track sediment from living reefs to landforms. Requires a detailed reconstruction of sediment transport pathways on reefs, an overview of sediment chronology and the interpretation of mixed old and new sediment assemblages within detrital reservoirs
	4. Can we quantitatively assess the influence of carbonate dissolution on sediment production and existing sediment reservoirs?	Organism trait; methodological issues	Provide assessments on the factors that influence sediment dissolution on reefs, their overall impact to detrital carbonate sinks and how reef conditions will change in the future under varying climate scenarios
Carbonate transport and sinks	1. How do common empirical sediment transport models perform for biogenic sediments?	Lack of knowledge and/or understanding	Establishment of entrainment relationships for biogenic sediment at the individual component scale as well as bulk sediment scale
	2. What are the key mechanisms and rates of sediment transport in reef systems?	Lack of knowledge and/or understanding	Increased observations of sediment transport across various sub-reef environments (fore reef, reef flat, lagoon) to determine transport rates and mechanisms of sediment to depositional sinks

(*Continued*)

Table 9 (*Continued*) Summary of research questions and knowledge requirements for developing a quantitative model

Module	Research question	Why gap exists	Research needs
Carbonate transport and sinks (cont.)	3. What are drivers of reef-fringed shoreline dynamics from seasonal to decadal timescales?	Lack of knowledge and/or understanding	Increased observations of reef-fronted shoreline dynamics at intermediate timescales (seasonal to decadal) to determine the relative roles of physical processes (waves, water levels) and sediment supply in maintaining reef-fronted coasts
	4. What is the role of vegetation in the accretion and erosional stabilisation of coral reef island landforms?	Lack of knowledge and/or understanding	Account for the role of vegetation type in geomorphological development of islands through the use of *in situ* species abundance surveys and remote sensing LiDAR technologies. This should target role of vegetation colonisation in short to long-term accretion, stability and erosional protection. There is a lack of knowledge regarding the interaction of climate processes (wind and metocean) with vegetation and how this affects long-term stabilisation of reef islands
All modules	Can we upscale local processes to more meaningful units (e.g. entire reef complex and sedimentary landforms) without losing accuracy?	Time, money and expertize	Role for earth observation approaches that draw on satellite and UAV imagery to generate spatially continuous estimates of carbonate dynamics across the range of sub-environments around reef platforms

specific interactions between benthic components (e.g. higher sediment cover reduce suitable substrate cover for CCA); and the importance of species-specific coral traits (e.g. skeletal density and extension rates) to assess carbonate production. Low confidence relationships reflect the difficulty in predicting community responses to spatially and temporally variable stress exposure (Figure 4).

The variable, and potentially interactive, nature of disturbance events creates model uncertainty and emphasizes the need for an improved understanding of how inherent environmental conditions interact with disturbance regimes to shape coral community structure at specific locations (e.g. Morgan & Kench 2017, Safaie et al. 2018, Sully & van Woesik 2020). For example, recent studies have reported that turbidity reduces coral bleaching relative to nearby clear-water reefs during thermal anomalies (Sully and van Woesik 2020, Oxenford & Vallès 2016, Morgan & Kench 2017). These studies suggest that reduced exposure to high solar radiation associated with turbidity can decrease bleaching and mortality levels; however, once turbidity reaches a certain threshold, the effect of both stressors can become cumulative (Fisher et al. 2019). When cyclones and bleaching events occur simultaneously, potential exists for interactive effects that can lead to both positive and negative impacts on carbonate production. For example, a moderate cyclone may counteract bleaching events by cooling water temperature through cloud shading, rain, wave action mixing warm surface layers with cool deeper waters and turbid run-off also reducing solar radiation (Carrigan & Puotinen 2014, Oxenford & Vallès 2016). Alternatively, reductions in reef structural complexity caused by severe cyclones (Fabricius et al. 2008, Roff et al. 2015a) are typically larger after bleaching events because dead coral skeletons have a weaker resistance to shear stress (Williams et al. 1999); or the turbidity from wave action and riverine run-off may place even greater stressors on the bleached corals, thus having a negative impact (Wooldridge 2009). These complex interactions among stressors are location and event specific, highlighting the need for site-specific observations pre- and post-disturbance to ensure appropriate modelling of net carbonate production over time.

Understanding cyclones and bleaching impacts on carbonate reef system models demands a thorough understanding of site-specific processes due to their complex (and potentially interactive) interactions with the coral reef ecosystem. Reef vulnerability and recovery from disturbance differ among coral communities, based on their specific physical and ecological environment (Moustaka et al. 2019, Evans et al. 2020) and the patchiness of acute disturbance events (e.g. cyclones and warming; Fabricius et al. 2008). This patchiness leaves some living corals in deeper or sheltered locations that can help recovery on the damaged sections of reef (Halford et al. 2004). Furthermore, extensive coral mortality is not always followed by rapid coral recovery but instead can lead to community shifts (i.e. macroalgal-dominated), which are difficult to anticipate (e.g. Hughes 1994, Diaz-Pulido et al. 2009, Graham et al. 2015, Roff et al. 2015a). Predicting these dynamics is challenging because it requires capturing complex processes (e.g. competition for space, grazing, ecological facilitation) that typically operate at small spatial and temporal scales (e.g. within habitats and at monthly intervals; Bozec et al. 2019). Ultimately carbonate reef system models need to include long-term dynamics of coral cover *under* stress regimes to improve assessment of recovery capacity from future disturbances, particularly given the predicted increase in frequency of cyclones (Elsner et al. 2008) and bleaching events that will likely outpace the rate at which systems can respond to any positive effects of disturbance events.

In summary, to improve the development of a quantitative carbonate model, key areas for further research include (Table 9):

1. The quantification of carbonate production in stressed versus unstressed conditions, accounting for species-specific responses
2. The integration of long-term (multi-annual) dynamics of benthic components after disturbance to project the fate of net carbonate production under different scenarios of stress regimes
3. The assessment of how interactions between various benthos influence responses of community carbonate production to acute disturbance events.

Coral reef response to sea level rise

The coral reef response to sea level rise model includes 27 variables and 54 relationships that detail the complex interactions that drive net carbonate production and coral reef accretion. Of the 54 relationships, 67% had high confidence, 30% had moderate confidence, and 4% had low confidence. Relationships with high confidence included the relationship between sea level rise and reef depth (including the associated change this imparts on reef hydrodynamics), and the processes driving the recruitment of new corals and the pathways that lead to interannual changes in coral composition and cover. Areas of low confidence largely relate to relationships influencing reef accretion such as coral composition, reef framework density and sediment incorporation (Figure 5).

This sub-system model attempts to bridge the gap between ecological and geological processes that operate on different spatial and temporal scales. A challenge here, therefore, was to provide links between these two areas of coral reef research without introducing substantial errors that override any useful result. For example, extrapolation from short- to long-term scales will introduce errors associated with multiple cycles of short-term processes and interpolation from long to short-term scales will overlook important processes that act in the short term. Such errors will influence the values of carbonate production and erosion and the residual accretion rate of the reef. The geologic record can be used to mitigate potential errors associated with interpreting rates of reef accretion (and carbonate accumulation) and changes in benthic assemblages over shorter-time scales (i.e. years). One approach is to apply high precision radiometric dating (i.e. sub-annual to sub-decadal resolution) to coral cores extracted along transects or in high spatial density (e.g. Roff 2020). By taking multiple samples from several reef cores, these data sets are approaching temporal timescales that are captured using the census-based methods, although they only provide an assessment of production and not carbonate loss. Despite recent advances in dating precision, connecting ecological and geological understanding to annual and interannual scales is still a long-standing challenge and crucial knowledge gap in both perspective and knowledge (Woodroffe 2008, Hubbard 2015).

Uncertainty also continues to exist over the hydrodynamic and oceanographic processes that lead to the generation of different benthic cover types, such as rubble, and reef rugosity (Madin et al. 2014). Gross accretion rates of primary reef calcifiers are well known over short-term scales but the role of other processes such as the production, erosion and incorporation of carbonate material into coral reef framework is still poorly understood. While understanding these processes presents substantial challenges, methods are continually advancing that may bridge the gaps in knowledge, with this model providing a guide to the processes that are essential to driving reef response under rising sea levels.

Census-based carbonate budgets and the conversion of net carbonate production to reef accretion rates rely on a number of assumptions (outlined in the 'Developing the qualitative model subsystems' section). At present, the effects of these assumptions on model outputs (e.g. reef accretion rate) are unknown. Understanding these effects, however, is critical for providing confidence in results and quantifying uncertainty. As such, future carbonate budgets should seek to describe the impact of underlying assumptions by providing confidence ranges. Furthermore, the incorporation of a probabilistic approach to census-based carbonate budgets will also help manage the uncertainty introduced by the assumptions of the carbonate budget. Such approaches are commonly used when providing forecasts for complex systems (e.g. Cowell et al. 2006; Vitousek et al. 2017), and we consider a necessary future step to increase the relevance and importance of carbonate budget approaches as tools for coral reef managers and researchers.

In summary, to facilitate improved descriptions of reef change on the scales of decades to centuries and move towards a quantitative geo-ecological carbonate reef model, future research should include (Table 9):

1. Long-term (decadal-scale) studies across different reef environments and habitats that capture both ecological and reef geomorphic changes as a means of linking the varying temporal scales that these processes operate across. This can combine traditional (e.g. diver surveys) and advanced (e.g. drone flights) approaches to mapping ecological communities with advanced approaches to mapping change to the physical structure of coral reefs (e.g. drone, lidar and structure-from-motion surveys).
2. High precision radiometric dating on coral reef core transects to provide higher temporal and spatial resolution on coral reef accretion and reconstruction of benthic community composition.
3. A wider spatial range of *in situ* logging of oceanographic (e.g. waves, tides and currents) and environmental conditions (e.g. temperature and light) in different reef environments and habitats.
4. The application of numerical models that incorporate a wider range of processes (e.g. Salles et al. 2018) and, importantly, uncertainties between the processes that drive reef change via probabilistic approaches and statistical/machine learning (e.g. Pall et al. 2020).

Bioerosion

The bioerosion model includes 23 variables and 34 relationships, of which only 62% were rated with high confidence and 23% with low confidence. Although each relationship is supported by empirical evidence in at least one species or location, 'exceptions to the rule' apply to almost all relationships and many environmental drivers show both positive and negative effects, depending on the species (e.g. sedimentation positively influences some macroboring species but negatively impacts others). Areas of low confidence related to synergistic effects of environmental variables on internal reef bioerosion. More broadly, limitations to modelling bioerosion relate to difficulties in estimating temporal variability in bioerosion due to its non-linearity over time, complex feedbacks and missing or contradictory data. Furthermore, limited data and knowledge exist on rates of bioerosion sediment production and sediment re-incorporation processes (Figure 6).

Bioerosion is highly variable across geographies and among reef zones (across which population densities and environmental influences will naturally vary). This paucity of knowledge not only concerns species biogeography (e.g. greater influence of urchins in the Caribbean), but also in environmental responses – with nutrients found to increase microboring on Caribbean reefs (Carreiro-Silva et al. 2009), but not on Pacific reefs (Vogel et al. 2000). In particular, there has been limited consideration of regional variability of reef framework properties (e.g. density, rugosity) on rates of bioerosion. As such, spatial differences in bioerosion and our understanding of its patterns and processes remain ongoing challenges.

Temporal changes are also a challenge to capture: bioerosion can naturally fluctuate daily (e.g. parrotfish grazing pressure) and seasonally (e.g. Browne et al. 2019), as well as rapidly with large changes in abundance driven by environmental drivers such as pollution events (sponges), diseases (urchins) or habitat changes like coral loss (microborers). Over short timescales (weeks to years), bioerosion shows ecological succession (i.e. is not stable, but also does not necessarily increase proportionally or linearly with time; Kiene 1988, Tribollet 2008a, Schönberg 2015), with freshly exposed substrates showing differential removal rates over weeks to months as microborers and later macroborers colonise, weaken and change the framework (Chazottes et al. 1995). Given these successional changes, long-term studies that track changes in bioerosion rates with environmental and habitat differences (e.g. suitable substrate and reef framework density) are needed to provide a more accurate estimate of 'average' bioerosion required for modelling.

In addition to the short-term challenges of quantifying bioerosion, another major limitation is the calculation of bioerosion itself. 'Net bioerosion' only describes the redistribution of material and not export from the system: removal of material may depend on the grain size produced by the boring organism (could be related to organism size, e.g. urchin test size), habitat factors (e.g. porosity of the substrate) and local conditions (e.g. flow). While bioeroders are important in breaking down reef structure (Hutchings 1986, Eakin 1992, 1996), they also perform numerous other roles critical to the healthy functioning of a reef, such as the recycling and redistribution of reef-produced calcium carbonate. Sediments that are re-incorporated back into the reef framework play a critical role in maintaining reef structure and are therefore an important component of reef building processes (Davies 1983, Perry 1999, Mallela & Perry 2007). Relating carbonate degradation by bioeroder activity to subsequent sediment export or deposition is difficult, but these data are necessary to understand sedimentary processes on coral reefs.

In summary, to improve the development of a quantitative carbonate model, we need more data on bioeroder (across all taxa) responses to interacting (and multiple) environmental variables (e.g. temperature, pH, nutrients, light), from both field and experimental studies. Knowledge gaps that currently limit bioerosion estimates relate primarily to understanding (Table 9):

1. The environmental controls (including interaction of multiple effects) on internal (macro- and microborers) organism diversity, density and activity
2. The influence of reef framework factors such as substrate density and complexity on bioerosion rate
3. The rates of sediment production and re-incorporation from bioabraders and quantifying the role of these sediments for longer-term processes, such as reef development and accretion.

Net carbonate sediment production

The net sediment production model comprises 28 variables and 31 relationships. Experts rated 64% of the relationships in the model as high confidence and 26% as low confidence. The high confidence relationships were associated with physical mechanisms (e.g. wave energy) derived from established physics-based principles of fluid mechanics (Brander et al. 2004, Lowe et al. 2005), or relationships between co-dependent environmental variables, such as the influence of seawater turbidity on light at the benthos (Figure 7; Cooper et al. 2007, Fabricius et al. 2016, Morgan et al. 2020). Despite the perceived strength and confidence of the model overall, a paucity of quantitative data that sufficiently characterize rates of sediment production between calcifying taxa, reef settings and geographic regions remains. Relationships classified as low confidence mostly relate to chemical processes (e.g. seawater carbonate chemistry, pore water advection, sediment organic content) involved in the dissolution of existing carbonate sediments (Eyre et al. 2014). The quantitative importance of these relationships to sediment reservoirs remains unclear.

Differences in the temporal variability of sediment production processes on reefs (i.e. minutes to centuries) challenge the incorporation of sediment production into carbonate models and our understanding of how net sediment production will vary with climate change. The challenge arises primarily due to the potential time lags between organism death and the creation of suitably sized sediment for transport, or re-incorporation into the reef framework. For example, physical processes (waves) may create coral rubble instantaneously during a cyclone, but the breakdown of coral rubble into sand-sized particles under normal wave conditions can take decades (Ford & Kench 2012). In contrast, bioerosion processes (e.g. internal boring, grazing) can produce significant quantities of sediment from coral rubble and the reef framework over ecological timescales (Perry & Morgan 2017, Cuttler et al. 2019, Taylor et al. 2020). Similarly, direct sediment producers can rapidly generate sediment on timescales related to their lifecycle (Hallock 1981, Perry et al. 2016, Perry et al. 2019).

Spatial variations in sediment yield observed between reef habitats (e.g. reef crest versus lagoon) and different geographic settings (Smithers 1994, Yamano et al. 2005, Perry et al. 2011, Morgan & Kench 2016b) also influence model confidence. For example, foraminifera species (e.g. *Calcarina*, *Baculogypsina* and *Amphistegina*) often dominate Pacific Ocean reef sediments (Langer & Lipps 2003; Fujita et al. 2009; Dawson et al. 2014), whereas gastropod tests and coral grains provide the bulk of material in the Torres Strait (Hart & Kench 2007), and *Halimeda* grains have high relative abundance on many Caribbean reefs (Folk & Robles 1964). Using spatial interpretations of sediment reservoirs to assess an organism's biological productivity, however, is not straightforward because their relative abundance within sediments may be disproportionately higher to their live cover on reefs (Yamano et al. 2000). This challenge arises because the skeletal properties (e.g. shape, density, porosity) of specific organisms (e.g. foraminifera) may make them more transportable and widespread on reefs (Yamano et al. 2000, Dawson et al. 2014), or more resistant to abrasion enabling higher rates of preservation in the sedimentary record (Ford & Kench 2012). Differences in carbonate composition (e.g. percentage Mg-calcite) also determines how susceptible grains are to chemical dissolution (Eyre et al. 2014, Perry et al. 2016).

In summary, to improve the development of a quantitative carbonate model, areas for future research include (Table 9):

1. The improved understanding of the role of climate change in reef sediment production
2. A deeper understanding of the spatial and temporal dimensions of direct sediment production
3. The quantification of lags between organism mortality and sediment production
4. The examination of the influence of carbonate dissolution on existing sediment reservoirs.

Carbonate sediment transport and depositional sinks

Our carbonate sediment transport and depositional sinks model comprises 21 variables, with 22 relationships (Figure 8). The model describes the main physical drivers (waves, currents, sea level) and mechanisms of sediment transport (mobilisation, transport, deposition) to determine the fate of sediments (landforms, lagoons, off-reef deposits). Within our module, 86% of the relationships were classified with the highest confidence rating. This confidence level reflects the physical basis of the relationships (e.g. reef hydrodynamics; Lowe & Falter 2015) and the wealth of existing knowledge from siliciclastic coastal environments (e.g. sediment transport processes; Aagaard et al. 2013). Three relationships (# 19–21; Figure 8) received more moderate confidence ratings due to the limited quantitative understanding of aeolian (wind-driven) processes across coastal geomorphology, both generally (Houser 2009, Houser & Ellis 2013, Hesp & Smyth 2016) and in reef settings (Hilton et al. 2019).

The direct physical relationships that underlie this model are present across the range of spatio-temporal scales, such that our confidence ratings are likely to be somewhat insensitive to varying spatial or temporal scales. For example, the sediment carrying capacity of a given current is proportional to its speed; this relationship is relevant whether applied over seconds to years, or metres to kilometres. Although we have high confidence in the existence and strength of these relationships across multiple temporal and spatial scales, the ratings do not necessarily reflect our ability to quantify or model these processes in reef environments.

Challenges remain in quantifying carbonate sediment transport rates and linking these processes to the morphodynamics of depositional sinks. Sediment transport formulae are empirical relationships that relate parameters of the overlying flow (i.e. current speed) to sediment characteristics (i.e. grain size, density) to predict sediment entrainment and transport (Soulsby & Whitehouse 1997). These empirical equations have been developed using siliciclastic beach sediment or idealized particles, which tend to be approximately spherical and have a relatively uniform density. Reef-derived sediments, however, are often irregularly shaped and of variable density, thus violating the underlying assumptions of empirical relationships that rely on siliciclastic sediments, and questioning the applicability of these equations to carbonate settings (Kench & McLean 1996, Cuttler et al. 2017, Riazi et al. 2020). Similarly, given the diverse composition of carbonate sediment and the potential for the composition to evolve through time (i.e. as the relative abundance of sediment contributors changes), a need exists to develop quantitative relationships for how individual components are transported (Paphitis et al. 2002, Smith & Cheung 2005, Rieux et al. 2019). Finally, predicting sediment transport in reef environments is further complicated by the presence of the coral canopy, which strongly modifies the near-bed flows (Lowe et al. 2008) and raises questions about the most applicable velocity measurement to use for sediment transport (Pomeroy et al. 2017). Therefore, the complexities of carbonate settings require a new approach to predict sediment entrainment and transport.

In addition to inadequate quantification of relationships for the transport of carbonate sediment, inadequate data exist for disentangling drivers (e.g. storm versus fair-weather conditions) and mechanisms (e.g. bedform migration, transport through complex bathymetry) of sediment transport processes. Previous use of sediment traps enables single point measurements of transport averaged over time (Storlazzi et al. 2009, Browne et al. 2013, Morgan & Kench 2014), but only offers limited insights into the temporal variability of transport (i.e. how transport rates vary based on changes in waves or sea level). To investigate the temporal variability of sediment transport, previous research has relied on acoustic or optical sensors to measure both suspended sediment and bedload transport (Storlazzi et al. 2004, Vila-Concejo et al. 2014, Pomeroy et al. 2015, Cuttler et al. 2017, Pomeroy et al. 2018, Cuttler et al. 2019). Much of this work, however, has been carried out at a small spatial (order 1 m) and temporal (weeks to one year) scales, and it remains a challenge to upscale this knowledge into models that can be applied at an entire reef scale and/or over long timescales (seasonal to decadal).

Similarly, we see a lack of research directly linking sediment supply and transport rates to depositional sink morphodynamics (Harris et al. 2014, Morgan & Kench 2014, Harris et al. 2015a, Cuttler et al. 2019). Most previous work on shoreline dynamics in reef settings has focused on the event scale (Mahabot et al. 2016, Duvat et al. 2017b, Cuttler et al. 2018) or decadal scale (Ford 2013, Kench et al. 2015, Duvat & Pillet 2017, Kench et al. 2018), whereas lagoon infilling or off-reef export has been observed over short-term experiments (weeks to season; Harris et al. 2014, Morgan & Kench 2014). Thus, there is limited understanding of depositional sink morphodynamics over intermediate timescales (seasonal to interannual; Kench & Brander 2006, Cuttler et al. 2020) as well as how the timescales of morphodynamic development relate to temporal variability in sediment supply and transport processes. Finally, for subaerial sinks (islands, beaches), vegetation cover likely plays a significant role in the construction and stabilisation of landforms. Understanding the biophysical feedbacks between vegetation dynamics (species abundance, biomass, density) and aeolian transport processes under changing met-ocean conditions is critical in identifying long-term landform stability and resilience.

In summary, to improve the development of a quantitative carbonate model the future research directions include (Table 9):

1. The development of carbonate-specific sediment transport formulations that account for variable sediment composition and characteristics
2. The increase of observations of sediment transport rates and processes, including transport through complex bathymetries
3. The quantification of depositional sink morphodynamics (especially shorelines) over intermediate timescales
4. The investigation of the role of vegetation in reef-fronted shoreline stability.

Quantitative modelling feasibility

The development of the quantitative reef geo-ecological carbonate reef system model will require considerable effort across several integrating disciplines (e.g. ecology, geology, statistics, data science) as well as computational knowledge and power. The qualitative model presented here represents, to the best of our knowledge, all the known organisms, drivers and relationships that are part of the geo-ecological carbonate reef system, but mathematically accounting for all these relationships might not yet be possible. The main reasons that could limit quantitative model development include (1) a lack of data that describe some of the identified relationships; (2) issues around resolving and integrating processes that operate at different spatial and temporal scales; and (3) compounding errors that result in a non-meaningful output. A complete assessment of how the quantitative model may be developed is beyond the scope of the study, but creating six sub-system models that are targeted (i.e. more discipline specific), incorporate processes that (for the most part) operate at the same timescales and can be run independently allows parts of the model to be developed separately despite possible roadblocks in other areas. When all (or some) of the sub-system models are complete, they could be integrated using a loosely coupled system model (Giri et al. 2019), which also allows for the use of different software (e.g. among the different sub-system models) that work across different spatial and temporal scales.

Summary

Overall, the variables and relationships in the models for each sub-system module of the geo-ecological carbonate reef system model do not necessarily represent single, stable cause–effect relationships. Instead, they represent, to the best of our knowledge, the weight of evidence of carbonate reef system variables and their relationships to one another over the coming decades. As we increase our knowledge of these variables and relationships, the model will evolve and increase in its predictive capacity and accuracy. Importantly, the data in the literature do not necessarily enable reliable quantification of each of the relationships in the qualitative model, for many of the reasons outlined above, limiting immediate opportunities for prediction.

Identifying relationships and associated knowledge gaps is critical in improving our understanding of complex interactions that exist within all facets of the geo-ecological model. Here, we identified common knowledge gaps (among modules) for future research directions that include (1) tracking long-term (interannual to decadal) processes, (2) capturing interactions between ecological components and environmental controls (including interactions of multiple effects), (3) measuring changes in net carbonate production during stressed environmental conditions and (4) developing a deeper understanding of the spatial and temporal dimensions of carbonate production and sediment dynamics. These knowledge gaps exist largely due to methodological constraints (e.g. quantifying direct sediment production) and resource requirements (e.g. long-term studies that capture ecological and geological changes).

A growth in the use of both GIS and earth observation technology provides promise for addressing some of these knowledge gaps. These technologies can generate continuous measurements of critical variables (e.g. turbidity, coral cover, cyclone duration and strength, island vegetation cover), providing high spatial and temporal resolution data during stressed and unstressed environmental conditions. Furthermore, localized rates of carbonate production (i.e. for a patch reef) can be upscaled to geomorphically meaningful units, such as entire coral reefs and, by extension, sedimentary landforms, such as reef-associated landforms (Hamylton 2014). However, a critical part of this approach will be to ensure appropriate ground-truthing at relevant spatial and temporal scales, which could be incorporated into ongoing, local monitoring programs where this level of information can be easily collected.

The wider application of all approaches outlined here may help link the ecological and geological processes that feature in most carbonate budgets and models that attempt to forecast reef response with climate change impacts. No single approach, however, will be capable of addressing all issues associated with describing or forecasting coral reef change on the scale of decades. Improvements can only be made by using multi-disciplinary methods over multiple spatial and temporal scales, which are likely only possible via collaboration and knowledge sharing across disciplines.

Contributions and conclusion

We have provided the first comprehensive method and model for understanding geo-ecological carbonate reef systems. This work provides three major contributions to the field. First, we have provided a novel method for individual elicitation of mental models and shared development of a qualitative complex system model. Second, we have generated a qualitative geo-ecological carbonate reef system model. Third, we have identified a number of critical future research pathways. We briefly touch on each of these contributions, before providing some concluding thoughts.

A novel method for developing a shared qualitative model of a complex system

The novel elicitation modelling method was developed specifically for modelling complex systems, such as carbonate reef systems that are governed by complex and interacting biological, physical and chemical processes. Method development enabled a structured approach in identifying variables and their relationships to one another, which form the geo-ecological carbonate reef system model. Relationships were evaluated by considering our confidence in the existence of the relationship, as well as the relative strength of that relationship. The method supported a modular approach to model development, providing opportunities to explore both similarities and differences within expert-generated models. The extensive literature review that accompanied and followed model development led to the identification of knowledge gaps within the model. This information is critical in working towards the development of a quantitative model.

A qualitative geo-ecological carbonate reef system model

The most significant contribution of this work is a complex system model that links the carbonate reef system (the focus of previous carbonate budgets) to carbonate sediment production (sediment budgets) and associated landforms. As such, we have moved beyond carbonate budgets to provide the first qualitative model that crosses the geo-ecological divide. Census-based carbonate budgets provided the framework on which to build the geo-ecological carbonate system model. By evaluating previous field-based studies that quantified (part of) the carbonate reef budget, with additional related literature that focused on specific aspects of carbonate sediment systems, we were able to identify strengths and limitations within carbonate budgets. The model partly addresses these limitations through accommodating system complexity, assessing model reliability and accounting for environmental influences. We also highlight where additional data, knowledge and methodological testing are required to further address these limitations and improve our capacity to estimate carbonate production. Furthermore, by developing our qualitative model using a modular approach, the model provides flexibility for future researchers working on part (or all) of the carbonate reef to landform system.

Pathways for carbonate reef system research

This review provides a number of critical resources for researchers working within (and across) a number of disciplines related to carbonate reef systems (e.g. ecology, sedimentology, biogeochemistry, oceanography, coastal morphology, conservation). These resources can be classified into three broad areas: (1) planning new research projects (1–5), (2) planning *in situ* data collection (6–8) and (3) developing quantitative models (9–11; Table 10). New research projects (e.g. PhD or post-doctoral project) require an extensive literature review (knowledge and associated methods), which are provided here together with a list of targeted research questions and related research requirements

Table 10 A summary of resources provided through the extensive literature review and model development

No.	Resource
1	Extensive reference list
2	Summary of past census-based carbonate budget studies
3	A comprehensive list of variables and definitions
4	Reliable understanding that underpins management actions
5	Future research questions/directions
6	Overview of current methods for census-based studies
7	Assessment of associated limitations per sub-system module
8	Identification of critical variables
9	Individual conceptual sub-system modules
10	Reef-system carbonate model high-level overview
11	Semi-quantitative evaluation of model confidence

Note: Resources are grouped into three categories that include planning new research projects (white), planning *in situ* data collection (light grey) and developing quantitative models (dark grey).

(Table 9). The overview of methods used in carbonate budget studies, with their related limitations and the identification of critical variables, provides a solid foundation from which to design a well-considered data collection plan. For those researchers focused on developing predictive models, we anticipate that the conceptual sub-system models (together with our assessment of model confidence) will provide a blueprint for a quantitative model that incorporates one or more of the sub-system models.

Concluding comments

We need to improve our capacity to predict coral reef and associated landform responses to future climate change. More reliable predictions of ecological response to physiochemical changes are critical for developing appropriate management and mitigation strategies that seek to protect and preserve these complex systems. Importantly, a multi-disciplinary approach is required to assess and resolve differences in the spatial and temporal scales over which ecological, physical and chemical processes operate. Quantitative models that capture system complexity and bridge the geological-ecological divide will play an increasingly important role for predicting future changes. Our qualitative geo-ecological carbonate reef system model provides an important first step towards the development of these predictive models. As such, we anticipate that this qualitative model will be of significant value to both the scientific and conservation communities.

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