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Integrating the Effects of Ocean Acidification across Functional Scales on Tropical Coral Reefs

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There are concerns about the future of coral reefs in the face of ocean acidification and warming, and although studies of these phenomena have advanced quickly, efforts have focused on pieces of the puzzle rather than integrating them to evaluate ecosystem-level effects. The field is now poised to begin this task, but there are information gaps that first must be overcome before progress can be made. Many of these gaps focus on calcification at the levels of cells, organisms, populations, communities, and ecosystem, and their closure will be made difficult by the complexity of the interdependent processes by which coral reefs respond to ocean acidification, with effects scaling from cells to ecosystems and from microns to kilometers. Existing ecological theories provide an important and largely untapped resource for overcoming these difficulties, and they offer great potential for integrating the effects of ocean acidification across scales on coral reefs.

Keywords: ecosystem, theoretical models, coral reefs, scleractinians, ocean acidification, scaling

The history of investigating the effects of ocean acidification on coral reefs is short, with initial studies appearing in the 1990s and the first syntheses appearing in the new millennium (Kleypas et al. 2005, Gattuso and Hansson 2011). Most studies address the effects of ocean acidification on single species of corals and calcified algae in tanks (e.g., Gattuso et al. 1988, Langdon et al. 2000, Ries et al. 2009) and *in situ* (e.g., Kline et al. 2012), with a few addressing reef communities in mesocosms (e.g., Andersson et al. 2009, Dove et al. 2013, Comeau et al. 2015) or *in situ* near carbon dioxide (CO_2) vents (e.g., Fabricius et al. 2011) or other areas of low pH (Barkley et al. 2015). In this article, we consider the challenges of integrating empirical studies conducted at a single functional scale to obtain a broader understanding of the effects of ocean acidification on coral reefs, and we propose experimental and theoretical means by which these challenges can be overcome. Progress in these areas will make it possible to integrate results from lower functional scales (e.g., species) to larger functional scales (e.g., communities and ecosystems) to predict how coral reef ecosystems will respond to ocean acidification. Ultimately, these responses will also be strongly coupled to the effects of rising seawater temperature, but here, we limit our discussion to the analysis of the effects of ocean acidification. Therefore, the themes described below must ultimately be closely integrated with temperature effects, and at least some of the approaches described herein are well suited for this purpose. For ocean acidification, the challenge of integrating studies at multiple scales is a general issue (Andersson et al. 2015, Riebesell and Gattuso 2015), but it has particularly strong implications for coral reefs. For this ecosystem, our capacity to predict whether they will maintain a positive balance between the deposition and dissolution of calcium carbonate ($CaCO_3$; i.e., to persist as a calcified ecosystem) requires a consideration of scaling effects.

A defining feature of biological systems is the way in which multiple functional components sum to emergent properties that are not apparent at lower levels. In mutualistic symbioses, for example, the biology of the holobiont cannot be understood from the biology of the symbiotic partners alone, because it is their metabolic, functional, and structural interactions that change through an association of their individual biological traits (Edson et al. 1981, Brown et al. 2004). Likewise, ecosystems achieve emergent properties through resilience, stability, and metabolic functionality that cannot be determined by summing the effects on the species from which they are built.

The ways by which biological properties vary among spatial, temporal, and functional scales (Levin 1992) have a long history of investigation, with one of the best-known
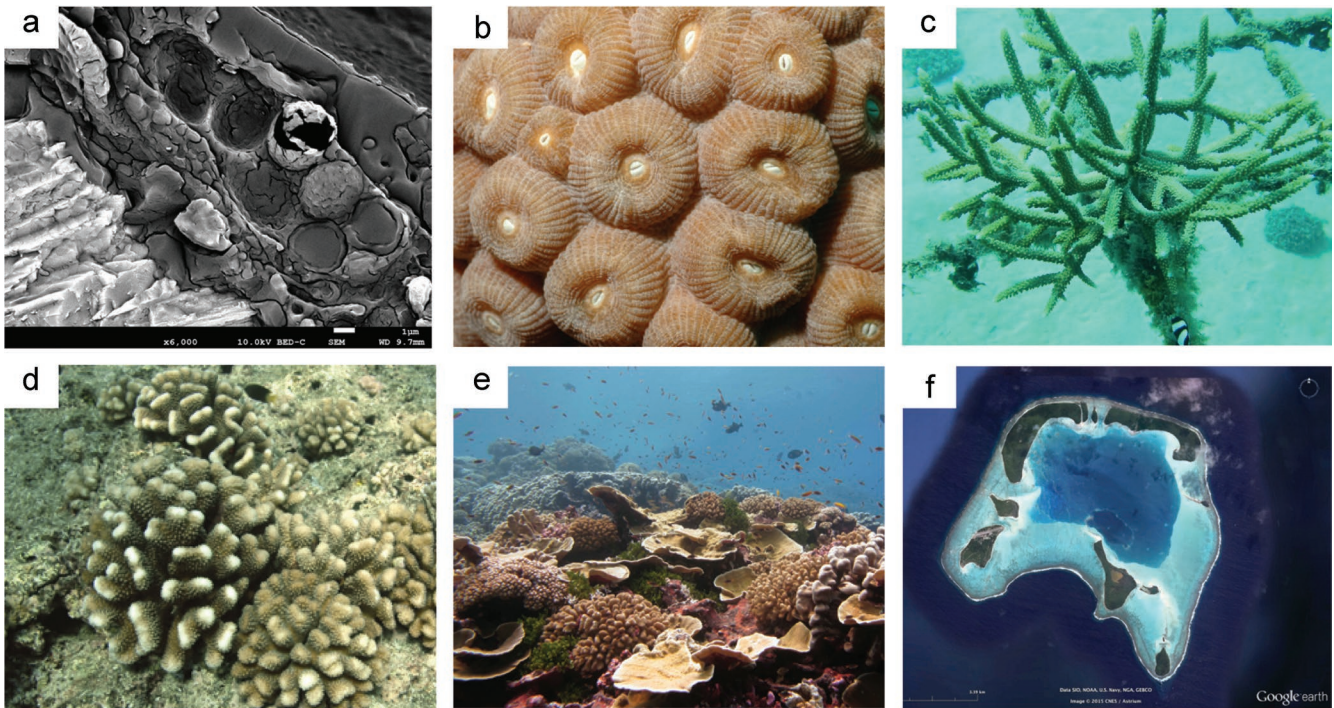
Figure 1. Illustrations of the scales of observations described in the present study and characteristic of contemporary investigations of the effects of ocean acidification on corals, algae, and coral reefs. (a) **Cellular** *level: scanning electron micrograph of a cross section of the aragonite skeleton (left) and body wall (right) of* Acropora cervicornis, *showing* Symbiodinium *nestled in the oral endoderm (1 micrometer, μm, scale bar, lower right). Photograph: J. Ries.* (b) **Organism** *level: polyps of* Montastraea cavernosa *(each approximately 1 centimeter, cm, in width). Photograph: P. Edmunds.* (c) **Organism** *level: a single cultured colony of* A. pulchra *growing in the back reef of Moorea. Photograph: C. Lantz.* (d) **Population** *level: a population of multiple colonies of* Pocillopora verrucosa *on the outer reef of Moorea. Photograph: P. Edmunds.* (e) **Community** *level: a coral reef community composed of a diversity of corals, algae, and other taxa on the outer reef of Millennium Atoll. Photograph: M. Johnson.* (f) **Ecosystem** *level: satellite image of the Tetiaroa Atoll in the south Pacific. Photograph: Google Earth.*

examples involving the scaling of traits with organism size (Schmidt-Nielsen 1984). The principle of size-dependent scaling of multiple traits is foundational to several domains of theory, including the metabolic theory of ecology (MTE; Brown et al. 2004) and dynamic energy budget theory (DEB; Nisbet et al. 2000, Kooijman 2010), of which the latter has been applied to describe the syntrophic relationship between host and symbiont in scleractinian corals (Muller at al. 2009). These theories describe the rates at which organisms acquire resources from the environment and use the nutrients and energy therein for growth, maintenance, and reproduction to create outcomes that propagate among functional levels. Similar principles apply to ecological processes, and since the work of Levin (1992), scale dependence has been engrained deeply in ecological science, with most studies on this topic showing that the scale of investigation affects the results obtained (Chave 2013). Therefore, it is reasonable to expect that the effects of ocean acidification on coral reef communities and ecosystems cannot be estimated simply by summing the rates of carbonate deposition and dissolution derived from organismal and suborganismal studies.

We highlight the scale dependence of deposition and dissolution of $CaCO_3$ on coral reefs with the objectives of stimulating research to (a) predict whether coral reefs will persist as net depositors of $CaCO_3$ under future lower seawater pH and (b) evaluate the effects of changes in benthic community composition (e.g., Roff and Mumby 2012) on the ability of coral reefs to maintain the net deposition of $CaCO_3$ (i.e., calcification exceeding dissolution). We emphasize the importance of these tasks and highlight the areas of potential biological complexity that will require attention in order to make progress in these areas. In the interests of brevity, we devote less attention to the complexity of $CaCO_3$ dissolution while acknowledging that this issue requires increased attention in future acidification studies.

To achieve our objectives, we consider coral reefs at the scales of cells, organisms, populations, communities, and ecosystem (figure 1). At each scale, we describe traits that are likely to be important in determining responses to ocean acidification and identify the means by which their effects cascade among levels of functionality. We present a simple schematic, which illustrates the outcomes that might be

possible through the use of appropriate theory to scale the effects of ocean acidification on coral reef calcification from cells to ecosystems. Although our schematic is contextualized by empirical data from the literature, there is currently neither sufficient data nor the fully developed theory to realize the potential of the theoretical approaches that we advocate. Finally, we note that the ultimate objective of the research we describe is to better understand how coral reef ecosystems will respond to ocean acidification in a real world situation. To achieve this outcome, it will be crucial to extend the multilevel approach that we describe to encompass other global change factors that we have not specifically addressed, including rising temperatures and nutrient concentrations.

The molecular and cellular effects of ocean acidification on coral reefs

An appreciation of the biology of calcification in the Scleractinia requires an understanding of the evolutionary context of mineralization in this taxon. Scleractinians developed the capacity to mineralize approximately 245 million years ago (Ma; Stolarski et al. 2011), when the chemistry of ancient seas was characterized by high concentrations of magnesium (Mg) relative to calcium (Ca), which favored the deposition of the aragonite polymorph of $CaCO_3$ (Stanley and Hardie 1998). Although aragonite deposition by the Scleractinia persisted throughout their evolutionary history, a transition to lower seawater Mg:Ca ratios from 190 Ma–40 Ma that chemically favors the deposition of the calcite polymorph of $CaCO_3$ appears to have caused the scleractinians to relinquish their role as primary reef builders throughout much of this interval (Stanley and Hardie 1998).

Although calcification is a defining feature of scleractinians, it is the presence of chemically and physically favorable conditions for mineralization (i.e., elevated $CaCO_3$ saturation state, seawater Mg:Ca ratios of more than 2 that favor precipitation of aragonite, warm temperatures, and clear seawater) and a mutualistic symbiosis with *Symbiodinium* algae (i.e., "zooxanthellae") that supports the deposition of the large quantities of $CaCO_3$ that are required for the construction of coral reef ecosystems. Symbioses with *Symbiodinium* (Stambler 2011), as well as with a diversity of microbes (Krediet et al. 2013), create some of the greatest challenges to understanding how calcification scales up from cells to scleractinian colonies and ultimately to reef ecosystems. These challenges arise from the complex and intertwined physiologies of the symbiotic partners, any one (or more) of which could mediate calcification through multiple pathways (e.g., directly through biomineralization or indirectly through photosynthesis or nutrient recycling) and determine the mechanisms by which calcification varies among functional scales.

Calcification on coral reefs begins with molecular and cellular events. Therefore, an understanding of the scale dependence of calcification and how it is affected by ocean acidification must embrace explanatory power at these most

reductionist levels (figure 2a). This should be best exploiting theory with sufficient complexity to capture the emergent ecosystem-level features that are the summation of cellular events translated through organisms, populations, communities, and ecosystems (figure 2e). Although gaps remain in understanding cellular mineralization in diverse coral reef taxa, knowledge is most complete for scleractinians (e.g., Cohen and McConnaughey 2003, Allemand et al. 2011) but is growing rapidly for calcified algae (Wizeman et al. 2014, McCoy and Kamenos 2015). We focus on the Scleractinia, but the investigative principles are potentially transferable to analyses of calcifying algae that are important organismic calcifiers on coral reefs. Three areas with the potential to limit the quantity of $CaCO_3$ deposited by scleractinians under conditions of elevated pCO_2 are highlighted: (1) the organic matrix (Tambutté S et al. 2008); (2) the chemical composition of calcifying fluids (Cohen et al. 2009, Ries, 2011, Venn et al. 2013); and (3) the energetics of calcification (Anthony et al. 2002).

Although the organic matrix has long been known to occur within coral skeletons, attention to this facet of skeletogenesis has only recently been considered in effort to understand how corals respond to ocean acidification. The organic matrix is composed of lipids, sugars, and proteins (for a review, see Tambutté S et al. 2007). Among these components, acidic proteins appear to be essential for biomineralization (Drake et al. 2015), and interest in this material has focused on its roles in shaping the ultrastructure of the coral skeleton beyond what is possible through chemical precipitation alone (Mass et al. 2013). The potential for the organic matrix to modulate skeletal structure is attractive to the consideration of scaling in the calcification response of corals to ocean acidification, because this concept bridges chemical and biological controls of skeletal morphology and, ultimately, the emergent properties of corallum shape that dictate how $CaCO_3$ is used to build coral reefs (Tambutté E et al. 2015, Venn et al. 2015).

Recent research in coral calcification has underscored the role of the biology of the coral host in modifying the chemical composition of the fluid beneath the tissue and adjacent to the calcifying surface (Cohen et al. 2009, Ries 2011a, McCulloch et al. 2012, Venn et al. 2013). Understanding the chemistry of this microenvironment is central to understanding how coral calcification occurs and the extent to which it is affected by ocean acidification. The important processes involve the flux of chemical species, notably the export of protons (H^+) from—and the import of Ca^{2+} ions and dissolved inorganic carbon to, the calcifying fluid—in order to maintain the sufficiently elevated saturation state necessary for $CaCO_3$ deposition (Cohen and McConnaughey 2003).

The crystallographic properties of aragonite crystals accreted under ocean acidification conditions (Cohen et al. 2009), the boron isotope composition of those crystals (McCulloch et al. 2012), pH-sensitive dyes (Venn et al. 2013), and pH microelectrodes (Al Horani et al. 2003, Ries 2011a)
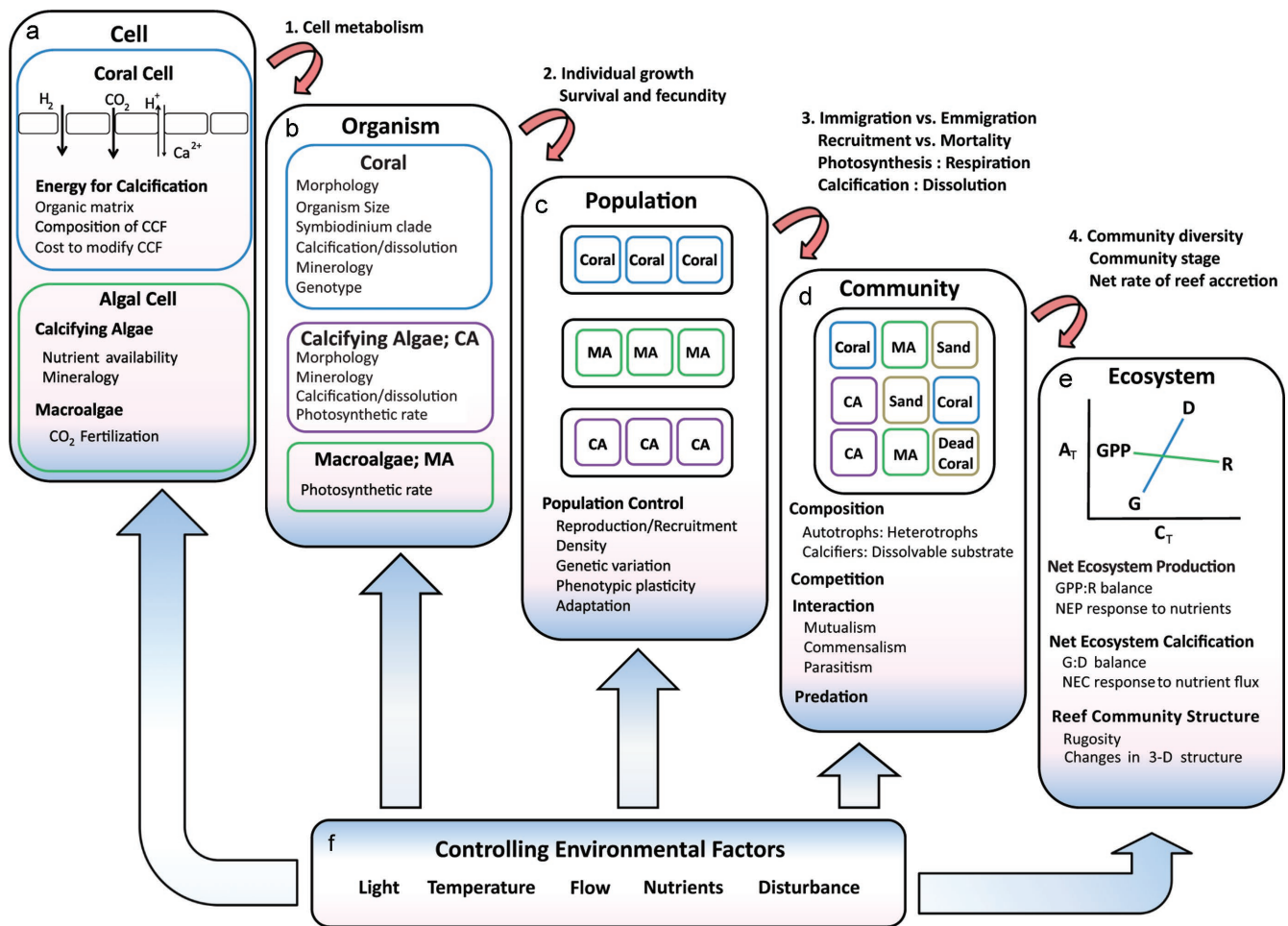
Figure 2. A summary of functional scales at which the effects of ocean acidification on the calcification on coral reef calcifiers is currently being evaluated. An important goal of this research is integrating results across functional scales to better understand the emergent properties of ecosystem-level calcification in a more acidic ocean. This ecosystem-level response is a summation of events at lower functional scales, but we currently lack the empirical and theoretical tools necessary to scale with ecological relevance among these levels. Our construct distinguishes among calcification at the scale of (a) cells, (b) organisms, (c) populations, (d) communities, and (e) ecosystems, all of which are forced to some extent by environmental factors (f); these scales serve as a construct within which the challenges can be articulated and solutions discussed, thereby leading to effective integration. At each scale, traits are described that address the factors modulating calcification, and arrows among the scale describe the direction of scaling effect. At the population (c) and community (d) scales, we emphasize the complexity added through the presence of multiple categories of benthic organisms (corals, macroalgae [MA], and crustose coralline algae [CA]) that vary in abundance through space and time. Ecosystem-level processes (e) represent the highest level of complexity that we seek to understand. At this level, efforts will likely focus on community metabolism and its response to key large-scale responses to ocean acidification. For illustrative purposes, we focus on the interactive effects of dissolved inorganic carbon (C_T) and total alkalinity (A_T) on the balance between gross primary production (GPP) and respiration (R) and $CaCO_3$ deposition (G) and dissolution (D).

have each been used to show that the pH of the coral calcifying fluid (CCF) is elevated relative to the surrounding seawater pH, and that acidification of the surrounding seawater causes a reduction in pH of the CCF. These observations are significant, because they provide direct evidence of a mechanism by which ocean acidification impairs coral calcification. Proton removal involves active transport across cell membranes (Isa et al. 1980, Zoccola et al. 2004), and this flux

appears to be matched to the supply of dissolved inorganic carbon (DIC) from seawater and host tissue (Zoccola et al. 2004, Allemand et al. 2011, Allison et al. 2014) in order to support the deposition of $CaCO_3$. Understanding the processes determining the chemical composition of the CCF will be pivotal to understanding how calcification scales from cells to ecosystems to support the growth of coral colonies, populations, communities, and ecosystems.

Finally, the modification of the ionic environment of the CCF represents physical work that is supported with metabolic energy. Faced with an increased thermodynamic challenge to precipitating $CaCO_3$ under ocean acidification (Erez et al. 2011, Ries 2011a), it seems reasonable to suggest that ocean acidification depresses calcification because of increased metabolic costs (Cohen and Holcomb 2009, Erez et al. 2011). However, evidence of elevated aerobic respiration in corals exposed to ocean acidification is equivocal (Crawley et al. 2010, Kaniewska et al. 2012), and it is therefore unclear whether energy demands alone can explain why ocean acidification depresses calcification. This outcome, however, does not exclude the possibility that changes in the allocation strategies of energy resources among metabolic sinks within corals could have a similar effect in depressing calcification. Analyses of the energetic costs of calcification (including both absolute costs and allocation strategies for metabolic energy) are, because of the power of the laws of thermodynamics, inherently attractive in considering scaling of physiological processes. This type of approach is already deeply engrained in several theoretical frameworks addressing the flux of energy among multiple scales of biological functionality (Nisbet et al. 2000, Brown et al. 2004, Kooijman 2010), including a recent model relating subcellular and physiological processes to the population-level impacts of ocean acidification on calcification in coccolithophorids (Muller and Nisbet 2014).

The aforementioned areas of complexity governing cellular calcification in scleractinians provide an effective platform for investigating how the products of cellular calcification affect ecosystem-level calcification (figure 2). Moreover, much of this complexity can be explained from the physical and chemical principles governing the deposition of $CaCO_3$, and these same principles can provide pathways through which the effects of ocean acidification in depressing coral reef calcification can be considered.

The organismal effects of ocean acidification on coral reefs

Of the functional scales relevant to coral reefs, organisms have received the most attention in ocean acidification studies (Erez et al. 2011, Kroeker et al. 2013). Most tropical corals and calcifying algae show decreased or parabolic (Castillo et al. 2014) calcification responses to ocean acidification, but results differ among taxa, including species, higher taxonomic levels, and functional groups (Ries et al. 2009, Chan and Connolly 2013, Comeau et al. 2014). Although the effects of ocean acidification on the fleshy macroalgae found on coral reefs have received less attention than the effects on calcified taxa, there is the potential for ocean acidification to "fertilize" macroalgal growth through the stimulatory effects of the high partial pressure of carbon dioxide (pCO_2) in seawater on photosynthesis and growth (Johnson et al. 2014).

Species-specific responses of organisms to elevated pCO_2 on coral reefs are caused by a variety of factors, including differing skeletal mineral solubility (i.e., low-Mg calcite versus high-Mg calcite versus aragonite), the ability to regulate pH of the organism's calcifying fluid, the presence of protective shell layers, nutritional status, and the ability to use CO_2 directly via photosynthesis (Ries et al. 2009). Differences in experimental conditions also are likely to contribute to variable results. For example, the magnitude of the treatment effect for ocean acidification acting on calcification ranges from 0% to 100% for corals (Erez et al. 2011) and from approximately 0% to 50% for algae (Anthony et al. 2008, Comeau et al. 2013) when atmospheric pCO_2 is approximately double that of present-day values. In light of such variation, it is crucial to understand why organisms with apparently similar mechanisms of calcification respond in very different ways to modification of seawater carbonate chemistry. A deeper comprehension of cellular mechanisms of calcification and how they scale up to mediate organismal calcification (section 1 above) is of key importance in understanding the drivers of organismal-scale heterogeneity in calcification responses to ocean acidification and the mechanisms by which this variation cascades upward to determine the rates of calcification at higher functional levels (figure 2).

There are many physiological characteristics of corals and calcifying algae on tropical reefs that could drive variation in their responses to ocean acidification. For example, the morphology of coral colonies and algal thalli, skeletal mineralogy (Ries 2011b), and organism size have a strong potential to affect the response of reef organisms to ocean acidification (figure 2b). Among corals, the differential sensitivity of calcification to seawater carbonate chemistry also could be driven by tissue thickness (Edmunds et al. 2012), gender, and/or the mechanism of nutrient acquisition (Holcomb et al. 2012). Interestingly, recent work suggests that variation in the *Symbiodinium* types within symbiotic corals does not play a role in determining sensitivity to elevated pCO_2 (Noonan et al. 2013). In coralline red algae, the Mg:Ca ratio of their calcite skeleton (which controls calcite solubility), as well as the abundance of ancillary minerals such as dolomite and brucite, varies among species (Nash et al. 2014). Nutrient availability also is potentially crucial to influencing calcifying algal sensitivity to ocean acidification. For fleshy macroalgae, calcifying algae, and zooxanthellate corals, carbon-acquisition strategies—the ability to use CO_2 directly and the presence of carbon-concentrating mechanisms (CCMs)—are crucial in determining the potential fertilization effect of increasing pCO_2 on photosynthesis and growth (Raven et al. 2011, Castillo et al. 2014). In turn, the effects on photosynthesis and growth ultimately could indirectly favor greater supplies of metabolic energy necessary to meet the costs of calcification. Currently, the combination of features that determines taxon-specific susceptibility to ocean acidification in corals and calcifying algae is unknown, and studies addressing this problem have yet to identify one or more mechanisms that are common among multiple taxa (Chan and Connolly 2012, Comeau et al. 2014).

The scaling of the effects of ocean acidification from organisms to populations to communities to ecosystems is complicated by (a) the coupling of calcification and photosynthesis at the organismal scale, because both are affected directly by environmental parameters such as water flow speed, temperature, and light/nutrient availability (figure 2f; Gattuso et al. 1999); (b) nonlinear relationships between organism growth and population growth; and (c) the complex ways by which organism interactions (e.g., inter- and intraspecific competition, predation, and bioerosion) determine how populations' responses sum to communities and ecosystems. Many of these complications can be addressed with the kinds of theoretical approaches we advocate (box 1), although additional empirical data (e.g., to address the implications of organism size) are still required to fully exploit these approaches. Given the aforementioned challenges, it is surprising that the role of organism size in determining sensitivity to ocean acidification has received little attention for any reef taxon. However, a study on chitons showed that the severity of their metabolic response to ocean acidification was proportional to their body size (Carey and Sigwart 2014). It is likely that the omission of organism size effects will need to be rectified in order to scale responses to ocean acidification across functional scales on coral reefs (Brown et al. 2004).

The population effects of ocean acidification on coral reefs

As we described above, ocean acidification research has focused on quantifying individual-level responses to a lower pH (Gattuso and Hanson 2011, Kroeker et al. 2013). The challenge at the population level is to integrate responses among individuals of the same species to understand how the size, structure, and distribution of individual populations respond to ocean acidification (figure 2). Consideration of population-level responses also requires an understanding of how intraspecific interactions, including density dependence, in turn alters the physiological responses of individuals. In this section, we describe some ideas that are available to achieve this integration while remaining aware that the best approach to this scaling step will vary with respect to the species being considered. Ideally, the scaling of individual-to population-level responses is best done in a manner that allows these effects to be propagated through interactions among multiple species, many of which likely respond in different ways to ocean acidification, because this will ultimately enable scaling up to the community level (figure 2).

Understanding the population-level responses of scleractinians and calcifying algae to ocean acidification requires linking the organismal-level responses of growth, calcification, survival, and fecundity to population structure and demographic properties. Mathematical tools for scaling up from individual performance to single-species population dynamics are well developed and have been widely applied to a diverse group of taxa (Caswell 2000). Structured population models (Caswell 2000), in which individuals are classified according to one (or several) state variable(s) that correlate(s) with demographic inputs, provide one effective tool for this purpose. For scleractinians, colony size is a useful state variable that often is measurable in ecological surveys and is associated directly with demographic rates (Hughes 1984). Therefore, if ocean acidification was found, for example, to reduce *per capita* fecundity (as life-history theory suggests; Mumby and van Woesik 2014) or to weaken colony skeletons by favoring bioerosion and decreasing skeleton density (Andersson and Gledhill 2013, Tambutté E et al. 2015), thereby increasing the vulnerability of larger colonies to breakage, structured population models could translate these colony-level inputs to long-term population growth and structure.

Population projection matrices (Caswell 2000) and integral projection models (Easterling et al. 2000) are types of structured population models that offer fully developed suites of tools for scaling up from individuals to populations. These models can be easily modified to accommodate additional phenomena that may prove essential for understanding the organismic responses of corals and calcifying algae to ocean acidification and, ultimately, for scaling the effects to the population level (Edmunds et al. 2014). For example, mesocosm experiments can be used to define the relationships between pCO_2 and colony growth, which can be integrated into field-based demographic models evaluating change in colony size over time in order to explore directly the effects of ocean acidification on the intrinsic rate of population growth (i.e., λ; Edmunds et al. 2014). A wide spectrum of viable permutations to such models is feasible, and we describe some of the potentially more valuable modifications below.

First, structured population models can be expanded to include dead corals. This would be a valuable expansion of theory if bioerosion or the dissolution of dead or weakened corals modulates the availability of surfaces suitable for settlement of coral larvae or if it affects carbonate chemistry in a way that feeds back on local $CaCO_3$ deposition and colony growth. Recent work highlights the importance of reef dissolution under elevated pCO_2 and depressed seawater saturation with respect to $CaCO_3$ minerals (Andersson and Gledhill 2013, Eyre et al. 2014, Comeau et al. 2015). Second, state variables other than colony size may be worth considering, especially if other individual-level characteristics are important for determining responses to ocean acidification. Genetic structure may prove to be a particularly important individual-level covariate, especially if transgenerational plasticity or adaptation through rapid evolution (Mumby and van Woesik 2014) buffers individual-level demography against environmental change. Third, structured population models can be embedded in a spatial context if, for example, the impacts of ocean acidification are experienced differently across different reef locations (e.g., fore-reef versus back-reef) that are connected by propagule dispersal. Fourth, density dependence or inverse density dependence may be added if population density feeds back onto colony- or individual-level demographic rates (e.g., through self-shading, the competition for nutrients). Finally, structured

Box 1.

Here are four approaches (A–D) and the potential outcomes (E), on community calcification (figure 3):

(A) **Simple extrapolation** uses empirical data describing the physiological responses of reef calcifiers (differing both by species and higher taxonomic alliance) to differing pCO_2 regimes and extrapolates these responses on the basis of community composition. As an illustration, we show a quadrat recorded at a 17-meter (m) depth on the outer reef of Moorea in 2006 that was used as a basis to create a reef community in a flume for which calcification as a function of pCO_2 was measured. To extrapolate the effects of ocean acidification, the community structure in 2006 was used to evaluate the percentage cover of CCA and the population size structure for scleractinians belonging to branching, mounding, or sheeting functional groups. It is reasonable to expect these functional groups to affect the response to ocean acidification, because each reflects a differential distribution of biomass/skeleton to the benthos versus the water column and each translates the mass deposition of $CaCO_3$ into linear extension in different ways. On the basis of the aforementioned data, community calcification (grams per square meter per day) was calculated under present-day conditions (approximately 400 microatmospheres, µatm, pCO_2) and those expected by the end of the current century (approximately 1000 µatm pCO_2; E). CCA cover was taken as 20%, the mean sizes of corals in the three functional groups were calculated (shown in histograms), and their mean densities were 13.9, 5.0, and 6.9 colonies per square meter for branches, mounds, and plates. Coral surface areas were calculated from the relationship between diameter and area—as determined for *Pocillopora verrucosa* from $y = 2.493. \times 2.312$ where y is area (in square centimeters) and x is diameter (in centimeters)—assuming mounds were hemispheres, and sheets were circles. Organismic rates of calcification at different pCO_2 values were obtained from Comeau et al. 2013, 2014, 2015).
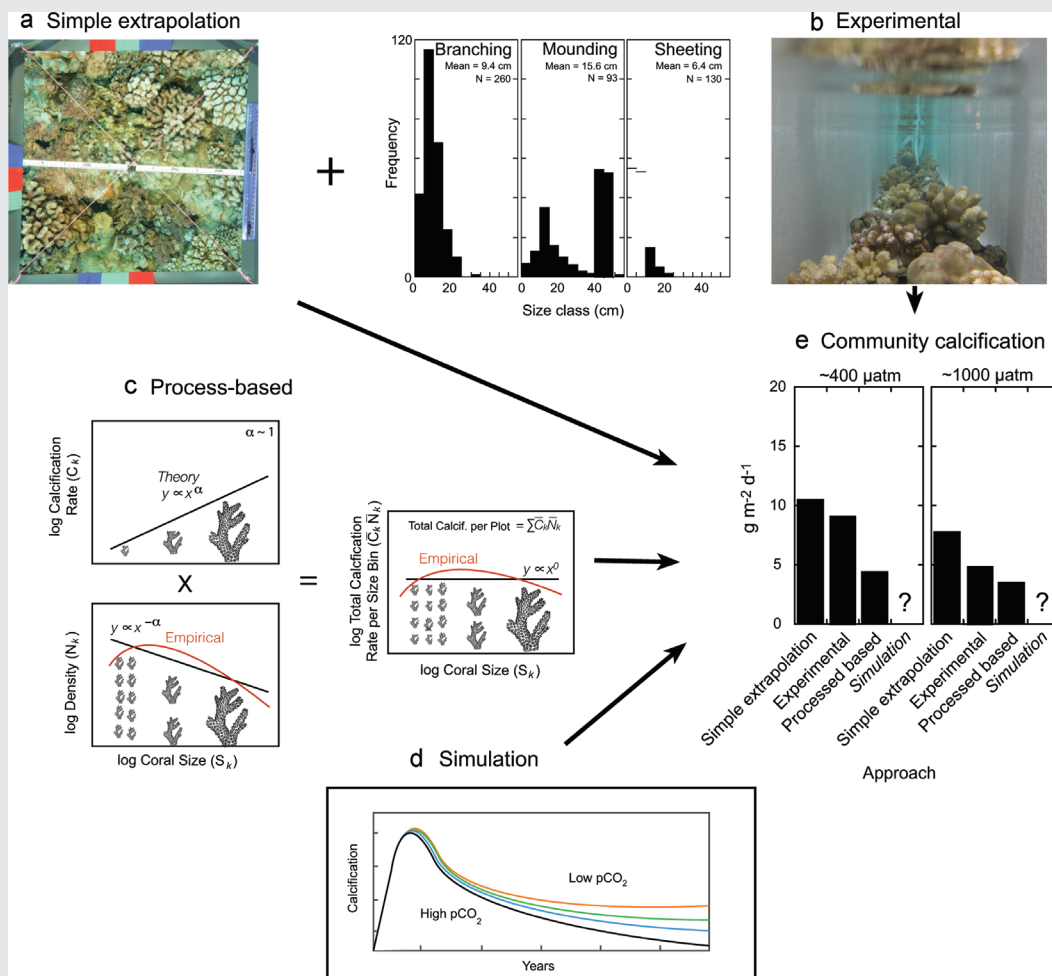

Figure 3. Schematic illustrating the application of four approaches (A–D) to calculating community calcification (E). Refer to Box 1 content for detail.

(Continue)

Box 1. Continued.

(B) The **experimental** approach relies on direct measurements of net community calcification, which in our recent work (Comeau et al. 2015) exploits communities assembled from specimens collected from the outer reef (17-m depth) and assembled at ecologically relevant densities (as assessed from percentage cover) in 5.0 (length) $\times$ 0.3 $\times$ 0.3 m flumes. These communities included carbonate pavement, which was added to capture the effects of dissolution on this aspect of the community.

(C) The **processed-based** approach posits that reef-scale calcification can be understood based on the first principles of biological organization. The metabolic theory of ecology (MTE; Brown et al. 2004), for example, uses allometric scaling to predict the emergent properties of an ecosystem (such as the net calcification rate) using power–law relationships between physiology and colony size and between abundance and colony size. A mature MTE for coral reefs has yet to emerge, so we illustrate the hypothetical scaling relationships inspired by MTE (Enquist et al. 2003, West et al. 2009) and informed by empirical data describing the size–frequency structure of branching, mounding, and sheeting corals (as in 2006 at a 17-m depth in Moorea) and empirical derived calcification rates at the organismic level (both as in A above). Here, coral area is the measure of body size, and the densities of colonies (N) are observed for each body size bin k. The product of the scaling relationships (with exponents α) for calcification (y, by size class, C_k) rate and density (y, by size class N_k) with mean size (x) yields the total calcification rate for each size bin. The integration of these values provides an estimate of the community calcification rate under ambient and elevated pCO$_2$. Although power laws provide good fits for observed organismic calcification scaling (*black*), as was predicted by theory, quadratic functions fit better to our observed patterns of coral density (*red*).

(D) The **simulation** approach builds an *in silico* replica of an ecosystem that incorporates all known rules of how individuals in a complex system behave and interact and then explores emergent ecosystem behavior through simulation under various environmental scenarios. This approach is exemplified by individual-based models (IBMs; Grimm and Railsback 2005) and is illustrated by Harfoot and colleagues (2014). The difference between analytical theory and computer simulation often is one of dimensionality, although computer simulations require intricate knowledge of the entities (e.g., the extent of intra- and interspecific variation) in the simulation and how they behave and interact. Such knowledge is provided by experimental evidence and first-principles theory (Harfoot et al. 2014); therefore, computer simulations rely on the advances provided by other approaches to scientific discovery. IBMs for coral reef ecosystems have yet to emerge, so we illustrate the approach with a schematic.

(E) **Community calcification** was calculated using the approaches described above (A–D) to reveal the differences in rates depending on the scaling technique; it is not yet possible to evaluate calcification rates from first principles using simulation techniques (shown as "?"). The research challenge faced by the coral reef ocean acidification community is the expansion of existing theory to capitalize on the strengths of each domain while understanding the sources of mismatches in predictions and uncertainties in the properties of the predictions. The theoretical estimates shown here reflect the quadratic fits for the scaling of coral abundance.

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population models can be integrated into multispecies models to capture ecological interactions with other benthic taxa (e.g., the inhibition of larval recruitment by fleshy macroalgae) that can mediate changes in community structure (Gaylord et al. 2014). Conceptually, multispecies models often are associated with the community scale (discussed below), although the mathematical distinction between single- and multispecies models often is small.

The tools of population ecology, including structured population models, frequently are developed to focus on long-term responses, such as a population's eventual growth rate and structure in terms of distributions of individuals varying in age or size. In the context of an environmental covariate such as ocean acidification that is likely to change slowly over decades to centuries (Gattuso and Hansson 2011), it may be valuable to analyze short-term "transient" biological responses to these conditions, as well as the potential for the acclimatization of coral and other reef calcifiers. The analysis of short-term responses (i.e., transients as defined by the timescale of changes affecting ecological systems) to changing environmental conditions is a mathematical frontier in population ecology (Hastings 2004), but short-term responses also can be quantified through simulations instead

of through empirical approaches. Understanding short-term population responses of coral reef calcifiers exposed to chronic pCO$_2$ exposure may be important, especially for interfacing models with management timetables and for validating models on human timescales. Importantly, the outputs (projections) from population-level models of how species and species interactions will respond to ocean acidification must provide compatible inputs to community and ecosystem scale modeling efforts.

The community and ecosystem effects of ocean acidification on coral reefs

The processes of interest for understanding the impact of ocean acidification at the scale of coral reef communities and ecosystems are inter- and intraspecific interactions, net ecosystem production (NEP = primary production − total respiration), and net ecosystem calcification (NEC = gross calcification − gross CaCO$_3$ dissolution; figures 2d and 2e). The chief emergent properties arising from populations that influence these processes are species composition, including the functional capabilities of each taxon and the likelihood that they will not all be affected equally by ocean acidification; the abundance of soft and hard substrata;

diversity; richness; and the community assemblage at a particular point in time (figure 2). Multiple communities that differ in these features contribute to ecosystem-level responses to ocean acidification observed at the ecosystem level. Characterizing the response of coral reef ecosystems to ocean acidification can be achieved through direct measurements, but these efforts need to be matched with theoretical approaches that can be used to reveal how effects at lower functional levels affect the ecosystem-level processes. Significantly, the combination of empirical and theoretical approaches will be necessary to evaluate the implications of shifts in benthic community composition on the ability of coral reef ecosystems to maintain the net deposition of $CaCO_3$ and therefore persist under different ocean acidification regimes.

The differential effects of ocean acidification on the population growth rates of corals and calcifying algae will lead to shifts in their relative abundance, as mediated by changes in the ability of these species to persist and maintain calcified structures. Changes in the relative abundance of these taxa have important implications, because corals and calcifying algae are unequal functionally, with some serving as primary reef builders and some as secondary reef builders, cementers, and/or consolidators. Resource competition among coral taxa (e.g., for space) potentially will modulate changes in coral species abundance, because the ability of corals to compete by overgrowth is likely to be impaired as their ability to rapidly grow will be impaired by ocean acidification. This mechanism of change in coral community structure will only be important in reefs where coral cover remains high enough to ensure colonies encounter one another as they grow. The implications of ocean acidification for competition for space are likely to extend to interactions among corals and other members of the community, notably macroalgae, and could have strongly nonlinear or threshold effects. For instance, ocean acidification could accentuate the rate at which phase shifts from a coral- to a macroalgal-dominated state occur if ocean acidification negatively affects corals while enhancing the growth of macroalgae.

Coral reefs growing in naturally acidified seawater offer unique and valuable opportunities to evaluate community-level responses to ocean acidification, largely because they are composed of organisms that have been subject to elevated pCO_2 over evolutionary timescales. To date, several such locations have been identified in tropical coral reef locations, and the biological features of their benthic communities—as well as the physical and chemical conditions under which they occur—have started to be characterized (Barkley et al. 2015). The diverse outcomes of these nascent investigations highlight the challenges of understanding the responses of coral reef ecosystems to elevated pCO_2 under ecologically relevant conditions. For example, one naturally acidified reef off Iwotorishima Island in the Ryukyu Islands, Japan, displayed a transition to soft corals (Inoue et al. 2013), whereas another naturally acidified reef off D'Entrecastraux Island, Papua New Guinea, hosted

scleractinian communities that retained coral cover but experienced reduced net calcification and dramatically modified scleractinian community structure (Fabricius et al. 2011). At another naturally acidified reef in Palau, scleractinian community structure changed but maintained coral richness, skeletal density, and rates of calcification (Barkley et al. 2015). None of these sites are perfect analogues of the conditions expected under future ocean acidification, and all bring the burdens of large temporal variability and the confounding factors (e.g., varying temperature, nutrients, and varying supplies of coral larvae) inherent in "natural experiments" that probably contributed to the lack of common community responses to apparently similar conditions (Barkley et al. 2015). Interestingly, however, increases in macrobioerosion with declining pH was the only common community response to naturally acidified conditions (Barkley et al. 2015), which underscores the potential importance of ultimately considering such effects in the approaches we advocate herein.

Fundamentally, the growth of coral reefs is dependent on $CaCO_3$ deposition exceeding dissolution and destruction as defined by simple mass balance (Eyre et al. 2014): Net $CaCO_3$ accumulation = Gross calcification – Gross $CaCO_3$ dissolution – $CaCO_3$ export (Equation 1). Whereas the calcification and dissolution terms in this relationship ultimately are the products of events occurring at lower functional levels (e.g., as we discussed above), the products of their action (i.e., reef-wide $CaCO_3$ dissolution and export) feature prominently at the community level (figure 2). There are biogeochemical techniques with the potential to quantify the performance and function of coral reefs at the ecosystem scale that effectively incorporate $CaCO_3$ dissolution and export into predictive models of coral reef ecosystem accretion while embracing the need to integrate the contributions of lower functional levels to ecosystem function. For example, simultaneous measurements of seawater-dissolved inorganic carbon and total alkalinity (TA) over space and time can be used to quantify the relative levels of net ecosystem calcification and net ecosystem organic carbon production (figure 2; Gattuso et al. 1996, Suzuki and Kawahata 2003, Watanabe et al. 2006, Lantz et al. 2014). Evaluating TA anomalies relative to offshore conditions also indicates whether a reef is net calcifying (depletion of TA) or net dissolving (augmentation of TA). These ecosystem properties are a function of performances at lower functional levels, but we have a poor quantitative understanding of the relative importance of community members within a given functional level to ecosystem-level processes. There is a significant need to develop the means to contextualize organism performance under ocean acidification within the response of the broader ecosystem, and this task serves as a case history of the value of combining emergent theory with empirical observations.

Combining theory and observation

Half a century ago, Levins (1966) argued that models in ecology can be organized by the balance they strike among

the countervailing axes of realism, precision, and generality. He further suggested that although models may enjoy two of these desirable characteristics simultaneously, no model can be realistic, precise, and general all at once. Although the virtues of Levins's scheme are debatable, the core observation that models are subject to trade-offs is indisputable. No model or modeling approach is suited uniformly for all scientific purposes, in the same way that no single empirical approach renders all other approaches inferior. Therefore, we should not expect a "grand unifying theory" of the effects of ocean acidification on coral reefs to emerge that simultaneously unites all the scales of biological organization at which ocean acidification and its impacts can be described (figure 2). Instead, the study of ocean acidification on coral reefs will advance by embracing a suite of complementary modeling approaches and their associated strengths.

The preceding sections have suggested several theoretical tools that may be useful for the study of ocean acidification and which take different approaches to understanding complex, multiscale behavior (box 1). For example, both DEB and MTE are rooted in the philosophy that much of the variation observed in the natural world can be explained by appealing to a fundamental collection of first principles—such as the allometric scaling of metabolic rates and the allocation of assimilated energy. Although these approaches do not strive for pinpoint predictions for any particular time and place, they can inform a conceptual framework that unites disparate observations of the effects of ocean acidification. In contrast, contemporary computing power has enabled detail-rich computer simulations of highly specific and complex systems. Such computing power can be deployed to study complex systems as varied as the different genetic pathways within a single cell (so-called systems biology; Kitano 2002) or the interactions among thousands to millions of individuals in an ecosystem (often called individual- or agent-based models; Grimm et al. 2005). These approaches emerged from the philosophy that a detailed understanding of the rules that govern behavior within a complex system can enable profitable exploration of the emergent properties of that system through computer simulation. Lying somewhere between these two extremes are compartmental models (including stage-structured models) that have featured prominently in population and community ecology. Compartmental models do not strive for the same broad universality as DEB or MTE but also require strategic assumptions about which sources of biological variation must be incorporated into a model and which sources can be ignored.

Finally, just as theory and empiricism benefit from a diverse collection of approaches, theory and empiricism themselves provide complementary routes to scientific progress, and therefore, both benefit from a vigorous exchange of ideas. Indeed, both theory and experimentation can inspire new hypotheses that motivate evaluation from a complementary perspective. The learning that ensues may suggest refinement of the hypothesis, wholesale rejection of hypotheses, and/or generation of new hypotheses.

Future directions

Given the rapid changes in seawater carbonate chemistry that are being driven by the anthropogenic emission of CO_2 and the long time necessary to reverse these changes once CO_2 emissions are reduced (Ciais et al. 2013), there are compelling reasons to be concerned about the impacts of ocean acidification on coral reefs (Gattuso et al. 2014). We still lack a basic understanding of the time required for a coral reef to transition from net deposition to net dissolution and how such a process would reduce the structural complexity of the reef and impair its ecological function (e.g., habitat provisioning, Fabricius et al. 2014; wave buffering). It is clear that theoretical approaches, in addition to the multi-scale approaches outlined above, will be needed to evaluate the impact of a reef transitioning from net deposition to net dissolution (and the reverse). Such approaches have the capacity to model the effect of ocean acidification on emergent properties (species composition, diversity, richness) that influence the functionality (species interactions, NEP, NEC) of coral reef ecosystems. Against this backdrop, there are several research priorities that should be addressed to improve the synthetic capacity of ocean acidification studies on coral reefs that may ultimately help mitigate the deleterious impacts of CO_2-induced ocean acidification.

A massive number of empirical studies designed to document the effects of ocean acidification on organisms has accrued since the threat became apparent. Future progress will depend on the integration of these observed effects and the application of theory to these massive data sets. Powerful and appropriate theory is already available for this task, and significant effort should be allocated to adapting and expanding this theory to coral reef applications.

Although integrating the effects of ocean acidification across multiple functional scales (figure 2) will advance the field, there are still many pieces missing from the puzzle. Major needs include (a) greater attention to the effects of ocean acidification on the processes (e.g., recruitment, competition, predation, bioerosion, $CaCO_3$ dissolution) that mediate the connections between functional scales on coral reefs; (b) an improved understanding of the ways in which the physical and chemical aspects of the environment modulate biological responses to ocean acidification; (c) the expansion of the taxonomic breadth of ocean-acidification experiments; (d) an improved understanding of the population-level impacts of ocean acidification; and (e) an improved understanding of how the population-level impacts of ocean acidification sum to community- and ecosystem-level impacts.

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