



Original Articles

Calcification of coral assemblages in the eastern Pacific: Reshuffling calcification scenarios under climate change



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ABSTRACT

The rearrangement of coral assemblages may produce significant changes in coral community calcification, yet it is not understood how the modification of community structure in depauperate areas under climate change scenarios may affect reef functionality. Observed coral community calcification (OCC) was calculated using coral cover data from 126 sites across the eastern tropical Pacific (ETP). To assess the effect that species assemblages exert on potential coral community calcification (PCC) of ETP reefs, we implemented a novel permutation approach for this purpose. We contrasted OCC across the ETP against the PCC of hypothetical monospecific and maximum ecological evenness (ME) ETP reefs and monogeneric Indo-Pacific (IP) and Caribbean (C) reefs. Average coral cover ($21 \pm 23\%$; mean \pm SD) and OCC ($8.23 \pm 11.32 \text{ kg m}^{-2} \text{ yr}^{-1}$; mean \pm SD) in the ETP were not related to species richness but to *Pocillopora* abundance and calcification. For any level of coral abundance or species richness, the permutation model indicates that PCC depends on community structure: the PCC of *Pocillopora* monospecific reefs reaches its maximum; PCC drops to half of its potential when ME is attained; and PCC reaches its minimum when slow-growing species turn dominant. A dynamic model with changing community structure based on the differential species tolerance to climate change showed a similar pattern as the permutation model. ETP *Pocillopora* reefs have lower PCC than IP *Acropora*, IP *Pocillopora* and C *Acropora*. Massive taxa are more tolerant to climate change and could replace branching taxa if environmental pressure trends in the ETP continue, meaning an $\sim 85\%$ drop in PCC.

1. Introduction

Coral reefs develop thanks to the ability of scleractinian coral to deposit calcium carbonate to build their skeletons and form complex three-dimensional structures as part of their growth (Carricart-Ganivet et al., 2012; Norzagaray-López et al., 2015). Coral calcification studies (per species, populations or community level) are used to assess the overall resilience, health state, fitness, and ecological success of corals and coral reefs at different spatio-temporal scales (Vecsei, 2004; Calderon-Aguilera et al., 2007; Manzello et al., 2008).

Reef-forming coral assemblages result from the combination of

physiological processes and the thresholds to environmental conditions of each coral species (Sheppard et al., 2009). Every coral species has an ecological functional role in the reef ecosystem (e.g., reef-building capacity, substrate complexity formation, carbonate stocks, tide or water flow protection), which may be redundant or shared by one or more species (Veron 2000; Hughes et al., 2018; McWilliam et al., 2018). Theoretically, coral species composition and community structure determine the benthic substrate architecture, habitat complexity, and coral community calcification of the coral reef ecosystem (Sheppard et al., 2009). Branching fast-growing coral are the main source of carbonates on most reefs around the world; they provide considerable

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habitat complexity for diverse organisms; however, they are more susceptible to environmental disturbance (Darling et al. 2013; Perry et al., 2015; Pratchett et al., 2015; Hughes et al., 2018). On the other hand, slow-growing massive coral have life-history strategies to resist and cope with environmental disturbance, but their growth morphologies provide a lesser degree of habitat complexity (Polunin and Roberts, 1993; Carreiro-Silva and McClanahan, 2012; Carricart-Ganivet et al., 2012).

A rearrangement of the coral assemblage in coral reefs (due to a changing environment for example), may produce significant changes in the coral community calcification (Wellington, 1982; Walther et al., 2002), due to the loss of key-species or functional entities since coral populations have different degrees of resistance and respond differentially to environmental pressures (Glynn et al., 2001; Loya et al., 2014; Pandolfi and Jackson, 2006; Pandolfi et al., 2011). A determining factor regarding this issue is whether the patterns of coral community assemblages (i.e., ecological dominance and evenness, species similarity) are equally successful in maintaining reef structural integrity under various species assemblage scenarios. An increase or drop in coral community calcification is not necessarily the only answer as populations of coral species remaining after a hypothetical reshuffling could maintain the net positive calcification production of a coral community (Hughes et al., 2012).

Considering that climate change is the major driver for the decline of coral community calcification in coral reefs (Kennedy et al., 2013; Alvarez-Filip et al. 2013) modeled the effect that different coral species assemblages and dominance shifts have on overall community calcification and reef rugosity, concluding that the loss and subsequent substitution of key reef-building genera by other opportunistic species with reduced ability to produce and maintain reef framework may compromise reef structural integrity and ecosystem functionality. Alvarez-Filip et al. (2013) propose that highly diverse coral communities (i.e. Indo-Pacific), may retain a certain degree of functionality under a hastily changing environment due to inherent species ecological functional redundancy; in contrast, in less-diverse ecosystems (in terms of coral species), like the Caribbean, coral assemblages may easily be dominated by coral species with a reduced capacity to produce and maintain reef framework (Aronson et al., 2002; Green et al., 2008; Alvarez-Filip et al., 2011; McWilliam et al., 2018). The authors highlighted the need to fully understand how modifying coral community structure in regions with different coral assemblage arrays may affect reef functionality.

In accordance with the hypothesis established by Alvarez-Filip et al. (2013), the scenario for the coral reefs of the eastern tropical Pacific Ocean (ETP) is not very encouraging. Coral reefs of the ETP have low coral species richness and coral community calcification compared to both the Caribbean and Indo-Pacific reefs (Manzello et al., 2017; McWilliam et al., 2018), due to the influence of environmental conditions (believed to limit or inhibit coral growth), such as fluctuations in sea temperature, seasonal upwelling events, El Niño/La Niña, low and variable pH, nutrient pulses and increased sedimentation (Manzello et al., 2008; Manzello, 2010a,b).

In the ETP region, coral reefs are mostly constructed by near-monogeneric communities of branching *Pocillopora* and massive *Porites* or *Pavona* (Guzmán and Cortés 1989a,b; Macintyre et al., 1993). Most of the reefs throughout the ETP share a typical zonation pattern: the shallow zone is dominated by *Pocillopora* spp., while massive species dominance increases with depth (Glynn et al., 2017). Although coral diversity increases in the deeper reef zones, coral cover and calcification declines and is minimal in the deepest zones; therefore, coral species assemblages in the ETP strongly rely on reef architecture and environmental factors (Glynn and Ault, 2000). Given that coral reefs in the ETP have low coral species richness, they are expected to have low ecological functional species redundancy; thus, a shift in coral species dominance driven by environmental variability as previously reported (Manzello et al. 2008; Manzello 2010b) may cause coral community

calcification, structural integrity, and overall reef functionality to drop.

The study aims to address the overall dependence of the coral community calcification to changes in coral community structure and composition, but not to quantify or describe detailed CaCO_3 budgets along the ETP. By using coral community calcification estimates for 126 coral reefs across the ETP, from the Gulf of California to Panama, a novel permutation model and theoretical modeled reefs, we evaluated the effect that coral community structure and composition has on the coral community calcification of ETP coral reefs. Also, we used a dynamic model with changing community structure based on the differential species tolerance to climate change to make predictions about the potential coral community calcification (PCC) of the ETP reefs. Finally, our findings in the ETP are contrasted against hypothetical Indo-Pacific (IP) and Caribbean (C) coral assemblages to envision a worldwide coral carbonate production scenario.

2. Materials and methods

2.1. Coral cover data

Datasets of per species coral cover of 126 reef sites across the ETP, from the Gulf of California to Panama (Table S1), were compiled. Data were gathered from different sources. Overall, coral communities and reefs were surveyed using 25-m-long point-intersect transects, and data were recorded every 25 cm. Additionally, we searched the online sources ISI Web of Science, Google Scholar and other relevant databases for peer-reviewed literature. Finally, we directly contacted scientists asking for any available data pertaining to their study sites. Since coral cover per species were addressed using a variety of methods that differ in the scale of measurement, degree of subjectivity, and sample size, we standardized data to coral cover m^{-2} .

2.2. Analyses

Previously published (Wellington, 1982; Guzmán and Cortés 1989a,b; Glynn et al., 1996; Eakin, 1996; Maté, 1997; Jiménez and Cortés, 2003; Manzello, 2010b; Cabral-Tena et al., 2013; Norzagaray-López et al., 2015; Medellín-Maldonado et al., 2016; Norzagaray-López et al., 2017; Tortolero-Langarica et al., 2016, 2017a,b) annual extension rates (cm yr^{-1}) and mean skeletal density (g cm^{-3}) of each species as close and comparable as possible to each reef site in the ETP was used to calculate the observed coral community calcification OCC ($\text{kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$). When data was not available to any species or site, the average of the closest published growth and density data for each coral genus was used (Table S2).

Massive colonies were considered dome-shaped with similar growth rates across their surface (Eq. (1)). Meanwhile, per species mean branch diameter (cm) and branch density (branches m^{-2}) published data (Veron, 2000; Paz-García et al., 2015) were used for calcification rate calculations of *Pocillopora* spp. (Eq. (2)).

$$OCC_M = \sum_{i=0}^n (gr_i \times sd_i \times cc_i) / 10 \quad (1)$$

Where OCC_M is the observed CaCO_3 production of the massive coral community ($\text{kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$), gr_i is the growth rate (cm yr^{-1}) of the species i , sd_i is the skeletal density ($\text{g CaCO}_3 \text{ cm}^{-3}$) of the species i and cc_i is the cover of the species i , 10 was inserted in the model as an adjustment coefficient to set the units as $\text{kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$ (Hubbard et al., 1990; Perry et al., 2012; Alvarez-Filip et al., 2013; Mallela, 2013).

$$OCC_B = \sum_{i=0}^n (((bdia_i \times (gr_i \times sd_i)) \times bden_i) / 1000) \times cc_i \quad (2)$$

Where OCC_B is the observed CaCO_3 production of the branching coral community ($\text{kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$), $bdia_i$ is the mean branch diameter (cm) of species i , gr_i is the growth rate (cm yr^{-1}) of the species i , sd_i is the skeletal density ($\text{g CaCO}_3 \text{ cm}^{-3}$) of the species i , $bden_i$ is the mean branch density (branches m^{-2}) and cc_i is the cover of the species i

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