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Shifts in coral-assemblage composition do not ensure persistence of reef functionality

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Coral communities are changing rapidly worldwide through loss of coral cover and shifts in species composition. Although many reef-building corals are likely to decline, some weedy opportunistic species might increase in abundance. Here we explore whether the reshuffling of species can maintain ecosystem integrity and functioning. Using four common Caribbean reef-building coral genera we modeled rates of reef construction and complexity. We show that shifting coral assemblages result in rapid losses in coral-community calcification and reef rugosity that are independent of changes in the total abundance of reef corals. These losses are considerably higher than those recently attributed to climate change. Dominance patterns of coral assemblages seem to be the most important driver of the functioning of coral reefs and thus, the future of these ecosystems might depend not only on reductions of local and global stressors, but also on the maintenance of keystone coral species.

Coral reefs are biologically diverse ecosystems that provide goods and services, including coastal protection and food security to a large human population. These benefits primarily rely on the ability of reef-building corals to deposit large quantities of calcium carbonate and form complex three-dimensional structures. A wide range of stressors including diseases, overfishing, pollution and climate change are now forcing many of these ecosystems to move away from coral-dominated communities^{1,2}. Probably, the most evident transitions on coral reefs are the ecological shifts from coral to macroalgae-dominated states^{3,4}, which have severe consequences on carbonate budgets and reef complexity^{2,5}. However, ecological shifts may also occur within guilds of foundation species, as observed in tropical forest ecosystems^{6,7}. Reef corals are a diverse group and present a wide range of responses to environmental change, and while the populations of some coral species are likely to decrease, others may remain stable or even increase. In the last few decades, coral communities have experienced unprecedented modifications^{8,9}. The Caribbean, for example, underwent rapid losses of the structurally important acroporid corals from the white band disease epizootic in the late 1970s and early 1980s¹⁰. Since then, the spread of several emergent diseases, combined with recent bleaching events and other biotic disturbances, resulted in high rates of mortality in other major reef-building species, such as *Orbicella* spp.^{11–13} (= *Montastraea*, *sensu* Budd et al.¹⁴). Throughout the Caribbean, the few species responsible for most of the structural complexity^{8,15,16} have been now replaced by opportunistic species^{13,17}. Although we are only beginning to understand the consequences of these ecological shifts, it is likely that they will affect structural complexity and functioning of coral reefs^{1,2,13}.

A key question in this context is whether flexible patterns of dominance in coral communities can maintain reef functionality under future climate change scenarios. Recently, based on the recognition that climate-related pressures such as ocean warming and acidification do not affect all species equally^{9,18}, it has been suggested that ecosystem collapse is not necessarily the fate of coral reefs, because the populations of coral species that remain or increase could maintain ecosystem integrity¹⁹. This interpretation assumes that both species sets have similar functional attributes (e.g., reef-building capacity) despite differences in their physiological thresholds to environmental conditions. There is, however, little support for this assumption, as physiological attributes tend to be strongly linked to ecological functioning, and therefore species reshuffling tends to produce significant changes in ecosystem structure and functioning^{20–22}.

The functioning of coral-reef ecosystems is in large part dependent on the life-history strategies of corals, as they are strongly linked to the morphological and physiological attributes of the species²³. For example, in the Caribbean, coral species with brooding reproduction and high population turnover are generally tolerant to



environmental change, but are predominantly small colonies that contribute little to reef accretion or habitat provisioning. Whereas massive corals that contribute considerably to calcium carbonate accumulation, and serve as refuge substrate to many other species, are expected to be less tolerant to variable environments²³. The composition of species determines how the system responds to environmental change^{6,24} and, in this context, we can expect that the loss of certain species, or the loss of functional groups, severely compromise reef function by reducing calcium carbonate production and decreasing the complexity of reef topography.

Here we present a model of four Caribbean genera, which shows how shifting coral assemblages influence coral community calcification rates and reef rugosity. Considering that climate change is perceived to be the major driver for the rapid decline of coral reefs worldwide¹, we also compare calcification variations derived from changes in the dominance patterns of the coral assemblage, with those attributed to ocean warming and ocean acidification. Although these are simplified models of reef communities, we consider that they provide a robust theoretical framework to assess the effects of species turnover on ecosystem functioning.

Results

In the first model, which assess the effects of species turnover on reef functioning, shifts in the composition and dominance of coral assemblages result in rapid losses in coral community calcification rates and reef rugosity, independent of changes in the total abundance of reef corals (Fig. 1A, 1B). Reef calcification and topographic reef structure were severely affected by the loss of *Acropora* and to a lesser extent by the loss of *Orbicella* in both scenarios (steady coral cover decline, and gradual coral cover increase; Fig. 1C). Even assuming rapid increases in the abundance of other coral species, the loss of *Acropora* was so important for reef development that community calcification rates and reef complexity did not recover, resulting in a reef with limited structural complexity. Only when coral cover shifted from 10% *Acropora* to 45% *Porites* did reef rugosity show signs of stability (Fig. 1C).

To compare community calcification variations resulting from changes in the dominance patterns with those attributed to climate change and ocean acidification, we modeled a theoretical coral community in which coral cover was maintained at a constant 52% (Fig. 2A). Our second model showed that the reductions in

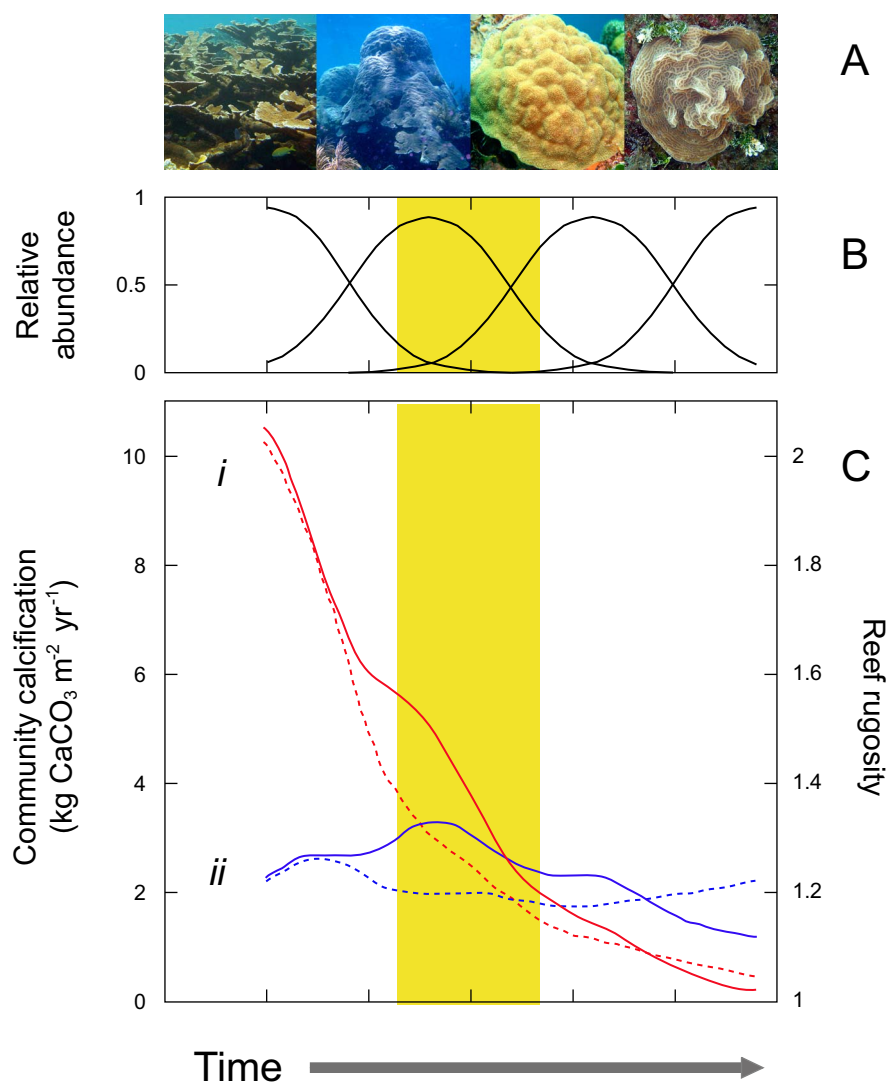


Figure 1 | Shifts in coral assemblages result in rapid losses in coral-community calcification and reef rugosity. Changes in community calcification and reef structure in shifting coral assemblages of four genera ((A); left to right *Acropora*, *Orbicella*, *Porites*, *Agaricia*). (B) Relative abundances over time. (C) Community calcification (continuous lines) and reef rugosity (dotted lines) in two hypothetical scenarios: (i) steady coral cover decline from 45% to 10% (red lines) and (ii) gradual coral cover increase from 10% to 45% (blue lines). Yellow band represents the current state of many Caribbean reefs. Pictures in the figure were taken by R. I.-P. and H. Bahena-Basave.

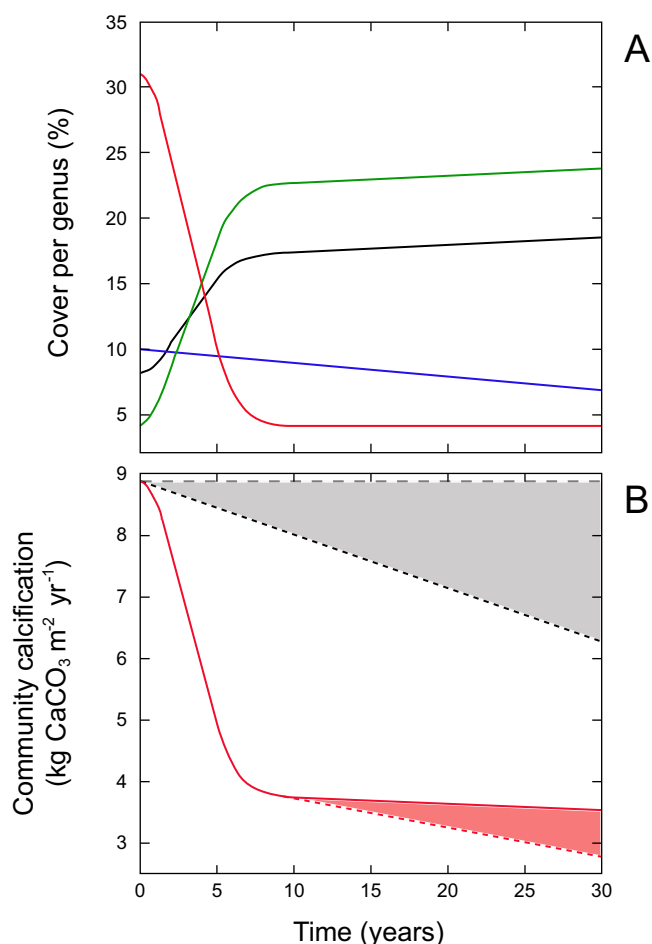


Figure 2 | Shifting dynamics of a theoretical coral assemblage of four genera with constant coral cover (52%). (A) Changes in coral cover per genera through time. *Acropora* (red line) *Orbicella*, (blue line) *Porites*, (black line) and *Agaricia* (green line). (B) Changes in community calcification through time (red line). The shaded area in grey represents the potential negative impacts on community calcification associated with thermal stress and ocean acidification excluding coral bleaching and assuming no changes in the coral assemblage. The red shaded area represents the potential losses in community calcification due to ocean warming and acidification.

calcification attributed to the effects of thermal stress and ocean acidification result in comparatively minor changes, when compared with the effect of changes in the patterns of dominance. These patterns were only detected once the community was dominated by opportunistic species (Fig. 2B). The extraordinary difference in the calcification rates of the four genera employed in the second model explains this difference in community calcification (Table 1). Similar to the results of the first model (Fig. 1), the most dramatic change in community calcification is derived from the rapid replacement of *Acropora* by *Porites* and *Agaricia*, which resulted in a 56% loss of the calcification potential of the community after only seven years (Fig. 2B).

Discussion

In the Caribbean, the loss of a key reef-building species has substantially reduced the structural and functional integrity of the reef. Collectively, our models indicate that the reshuffling of coral species, by itself, does not ensure coral-reef function. On the contrary, the replacement of major reef-building coral species (*i.e.*, losers) by opportunistic forms (*i.e.*, winners) drastically reduce the capacity

A

Table 1 | Mean extension rate (cm year^{-1}), mean density (g cm^{-3}), estimated calcification rate ($\text{kg m}^{-2} \text{ year}^{-1}$) and mean colony rugosity of the four genera used to construct the modeled hypothetical scenarios presented in figures 1 and 2. *Acropora* = *A. palmata* + *A. cervicornis*, *Orbicella* = *O. annularis* + *O. faveolata*, *Porites* = *P. astreoides*, and *Agaricia* = *A. agaricites*. In parenthesis the number of colonies used to calculate mean colony rugosity per genus

Genus	Extension rate	Density	Calcification rate	Colony rugosity
<i>Acropora</i>	8.84 ± 4.33	1.88 ± 0.26	22.30	3.33 ± 1.31 ($n = 13$)
<i>Orbicella</i>	0.85 ± 0.32	1.59 ± 0.25	13.80	1.87 ± 0.44 ($n = 46$)
<i>Porites</i>	0.41 ± 0.13	1.48 ± 0.16	6.12	1.49 ± 0.40 ($n = 51$)
<i>Agaricia</i>	0.25 ± 0.04	1.92 ± 0.05	2.43	1.52 ± 0.43 ($n = 73$)

B

of the coral assemblages to deposit calcium carbonate at rates higher than the rate of erosion. These changes will therefore compromise the structural complexity of the ecosystem and the long-term stability of reef-associated biodiversity²⁵. Our first model shows that only reef rugosity remains stable when coral cover shifts from 10% of *Acropora* to 45% of *Porites*. Although reaching this scenario is possible with effective management policies²⁶, the reef will still have low structural complexity—similar to a degraded reef, and therefore the ecosystem's structure and functioning would still be compromised⁵. The magnitude of the structural and functional losses portrayed by our models may represent a *de facto* state transition, similar to the transition from forest to grassland in terrestrial systems.

Shifts in the structure and composition of Caribbean coral communities produced substantial changes in reef accretion and rugosity beyond any recent effect attributed to climate change. Our second model suggests that the loss of acroporids from many Caribbean reefs represented a major loss in coral community calcification, and that any recent effect attributed to thermal stress and ocean acidification is comparatively minor. However, changes in the composition of species are in part driven by changes in the temperature and chemistry of the oceans¹⁸, and thus the two effects shown in figure 2 could synergistically influence the rates of calcification on coral reefs. To increase our understanding of the possible trajectories that reefs will follow under rapid climate change and ocean acidification, it will be necessary to explore possible trade-offs between the abilities of corals to deposit calcium carbonate and their capacity to tolerate thermal stress and ocean acidification. It has been shown that corals harboring thermally tolerant symbiotic algae exhibit reduced calcification rates when compared with specimens containing temperature-sensitive symbionts²⁷. This trait appears to be related to the greater capacity of temperature-sensitive symbionts to provide the host with the photosynthates required for calcification^{28,29}. In this context, acclimation to higher temperatures by acquiring thermally tolerant symbiotic algae will further compromise the calcification potential of the species.

Coral community shifts have also been reported in other regions of the world, highlighting the need to fully understand how global change is modifying reef structure in regions with a more diverse and different array of coral assemblages²³. Species richness may prevent or delay ecosystem collapse in diverse ecosystems, as the probability that at least some species continue to function under changing environments increases^{19,30}. However, this only applies if the increased number of species also increases the species responses to environmental fluctuations (*i.e.*, functional redundancy), and species with different functional properties are maintained under the new environmental conditions^{30–32}. Because of inherent redundancy, it is possible that the highly diverse coral reefs in the Indo-Pacific could partially retain a degree of functionality under rapid changing environmental conditions, however, the evidence from the less-diverse



Caribbean indicates that new coral assemblages are becoming dominated by species with substantially reduced capacity to produce and maintain reef framework^{13,15,17}.

Total coral cover has been commonly used to assess changes in coral-reef ecosystem condition or *health*^{33,34}. However, our findings imply that opportunistic coral species, although highly competitive in impacted environments, will probably not have the capacity to maintain reef development, even in communities with high coral cover. Thus, important information regarding the current state and recovery potential of coral reefs might be missing if all coral species are clustered in one single category (*i.e.*, coral cover). Local-scale and regional assessment of the state of world's coral reefs should therefore aim to evaluate changes in composition and dominance patterns of reef-building corals. Our models provide a simplified view of the effects of the changing dominance patterns on the potential of community calcification. Future analyses should incorporate information about changes in the susceptibility of different coral communities to the destructive forces of erosion. Recent analyses of the carbonate budget trajectories in Caribbean reefs under several future scenarios, indicate that maintenance of positive reef-carbonate budgets requires a combination of local conservation measurements, effective fisheries management, and significant global reductions in the emissions of greenhouse gases¹. The future of coral reefs will ultimately depend not only on the reduction of local and global stressors, but also on management actions that guarantee the survival and propagation of keystone reef-building coral species and not just on those actions that focus on maintaining high coral cover.

Methods

Models. We generated two simple theoretical models that include four coral genera: two important Caribbean reef-building corals, *Acropora* (*A. palmata* + *A. cervicornis*) and *Orbicella* (*O. annularis* + *O. faveolata*), and two highly competitive weedy corals that form smaller and less-complex colonies, *Porites astreoides* and *Agaricia agaricites*. First, to assess the effects of species turnover on reef functioning, we modeled changes in the relative abundance of these genera over time by simulating species dominance turnovers. Identical Gaussian curves were used to model the change in the relative abundance of *Acropora*, *Orbicella*, *Porites* and *Agaricia* (Fig. 1A). Curves were lagged along the temporal axis following a successional order in such a way that, at any point in time, the sum of all relative abundances was one (Fig. 1B). Species succession was constructed following a hierarchical order in calcification rates (Table 1), but it also resembled recent shifts in the composition of coral species in the Caribbean. Community calcification and reef rugosity were calculated at each point in time by weighing the mean calcification rate and colony rugosity (see below for mean calcification rates and rugosity calculations) with the relative abundance of each genus for two hypothetical scenarios: steady coral cover decline from 45% to 10%, and increase from 10% to 45%. With this method we only simulate the reef rugosity of these four genera, assuming that the rest of the reef is flat (rugosity index = 1).

Second, to compare community calcification variations derived from changes in the dominance patterns of the coral assemblage with those attributed to climate change and ocean acidification, we modeled a theoretical coral community in which coral cover was maintained at a constant 52%, which is the mean coral cover for the Caribbean in the late-1970s³³ (Fig. 2). In this model we simulated an exponential loss of *Acropora* with a rate constant of 3.5% year⁻¹, a reciprocal increase in the relative abundance of *Porites* and *Agaricia*, and a linear reduction in the relative abundance of *Orbicella*. The species turnover employed in the simulation is consistent with the community changes observed during the last 30 years in the Caribbean, as it captures the widespread mortality of acroporids in the 1980s, the recent decline of *Orbicella*, and the increase in the relative abundance of opportunistic and weedy corals^{13,15,17}. Reductions in community calcification derived from climate change and/or ocean acidification were assumed at 10% per decade, an estimation that incorporated inter-specific variability reported in the literature^{9,35–39}.

Calcification rates. Mean annual extension rates (cm year⁻¹) and mean skeletal densities (g cm⁻³) per genus were calculated by averaging the values in locations where previous reports existed in the Caribbean for colonies of these genera growing between 2- and 10-m depths (see references in Supplementary Online Material; Table 1).

Acropora mean annual calcification rate was calculated with the help of field data. In 2012, sixteen 1 × 1 m quadrats were surveyed in a reef portion dominated by *A. palmata* in Puerto Morelos, Mexican Caribbean. At each quadrat the number of all branch tips was counted. Then, in ten randomly selected branches of each quadrat, branch thickness in the apical zone and at 8.8 cm from the tip (*i.e.*, the mean annual extension rate for the genus; Table 1), and branch width, were measured. For each branch, annual calcification rate was then calculated as

$$CR = (((TH1 + TH2)/2) \times BW \times ER \times D)/1000$$

Where:

CR = annual calcification rate (kg cm⁻² year⁻¹),

TH1 = thickness in the apical zone (cm),

TH2 = thickness at 8.8 cm from the branch tip (cm),

BW = branch width (cm),

ER = mean annual extension rate for the genus (cm year⁻¹; Table 1),

D = mean density for the genus (g cm⁻³; Table 1)

Mean annual calcification rate for *Acropora* (kg m⁻² year⁻¹; Table 1) was then calculated as the product of the average annual calcification rate of all measured branches by the mean number of branch tips in the sixteen 1 × 1 m quadrats (43.2 ± 19.3 SD).

Considering the mean annual extension rate and mean skeletal density of *Orbicella* and *Porites* (Table 1), the mean annual calcification rates (kg m⁻² year⁻¹; Table 1) of these genera were calculated as the CaCO₃ increment of a hemisphere with a basal area of 1 m². *Agaricia agaricites* has several colony growth forms including dome-shaped and plate-like⁴⁰. Thus, for dome-shaped *Agaricia* colonies, the mean annual calcification rate was calculated using its mean annual extension rate and mean skeletal density (Table 1) in the same manner as for *Orbicella* and *Porites*. However, for plate-like *Agaricia* colonies, the CaCO₃ increment was calculated considering the mean annual extension rate and mean skeletal density (Table 1) of the growth margin of a 0.5-cm-thick disc with an area of 1 m². It was assumed that the contribution of each of these two growth forms of *Agaricia* was equal; therefore the mean annual calcification rate (kg m⁻² year⁻¹; Table 1) was calculated as an average of the two.

Colony level rugosity. Colony level rugosity for *A. palmata*, *A. cervicornis*, *O. annularis*, *O. faveolata*, *A. agaricites* and *P. astreoides* was measured following a standard methodology commonly used to measure reef rugosity. This consisted of calculating the ratio of the contour to the linear distance between the start and end point of the colony's longest axis. A perfectly flat colony would have a rugosity index of one with larger indices indicating more complex colonies. Coral colony rugosity of 183 colonies was measured in Cozumel (2009) and Puerto Morelos (2012), Mexico in a depth range between 2 and 12 m. The mean rugosity of the genus was obtained by averaging all the colonies of each genus (Table 1). It is important to note we did not include colony size in the index. However, the inclusion of this variable would only make more evident the pattern depicted by Figure 1 because the more structurally complex corals are also the ones with the largest colonies in our model (*i.e.*, *Acropora* and *Orbicella*). Although, colony morphology and size can vary in relation to environmental conditions, we do consider that our estimates of colony-level rugosity are representative and informative because the morphological variability within species (*e.g.*, platy vs massive agaricids) will be less than the morphological variability between species (*e.g.*, *Agaricia* vs *Orbicella*).

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Author contributions

L.A.F., J.P.C.-G., G.H.-P. and R.I.-P. contributed equally to the development of the models and to the preparation of the manuscript. L.A.F. and J.P.C.-G. performed the field measurements. All authors reviewed the manuscript.

Additional information

Supplementary information accompanies this paper at <http://www.nature.com/scientificreports>

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