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ARTICLE

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Biodiversity of macroalgae does not differentially suppress coral performance: The other side of a biodiversity issue

Cody S. Clements[1] | **Zoe A. Pratte**[2] | **Frank J. Stewart**[2] | **Mark E. Hay**[1]

[1]School of Biological Sciences and Center for Microbial Dynamics and Infection, Georgia Institute of Technology, Atlanta, Georgia, USA

[2]Department of Microbiology and Cell Biology, Montana State University, Bozeman, Montana, USA

Correspondence
Cody S. Clements
Email: cclements9@gatech.edu

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Abstract

Hundreds of studies now document positive relationships between biodiversity and critical ecosystem processes, but as ecological communities worldwide shift toward new species configurations, less is known regarding how the biodiversity of undesirable species will shape the functioning of ecosystems or foundation species. We manipulated macroalgal species richness in experimental field plots to test whether and how the identity and diversity of competing macroalgae affected the growth, survival, and microbiome of a common coral in Mo'orea, French Polynesia. Compared to controls without algal competitors, coral growth was significantly suppressed across three macroalgal monocultures, a polyculture of the same three macroalgae, and plots containing inert seaweed mimics; coral mortality was limited and did not differ significantly among treatments. One macroalga suppressed coral growth significantly less than the other two, but none differed from the inert mimic in terms of coral suppression. The composition, dispersion, and diversity of coral microbiomes in treatments with live macroalgae or inert plastic mimics did not differ from controls experiencing no competition. Microbiome composition differed between two macroalgal monocultures and a monoculture versus plastic mimics, but no other microbiome differences were observed among macroalgal or mimic treatments. Together, these findings suggest that algal diversity does not alter harmful impacts of macroalgae on coral performance, which could be accounted for by physical structure alone in these field experiments. While enhancing biodiversity is a recognized strategy for promoting desirable species, it would be worrisome if biodiversity also enhanced the negative impacts of undesirable species. We documented no such effects in this investigation.

KEYWORDS
BEF, biodiversity, coral reefs, coral–algal competition, ecosystem function, macroalgae

INTRODUCTION

Studies commonly find a positive effect of biodiversity on ecosystem function across a wide range of experimental and natural systems—ranging from grasslands and forests (Duffy et al., 2017), to seagrass meadows (Williams et al., 2017), to coral reefs (Clements & Hay, 2019, 2021). Greater biodiversity often enhances key processes such as the productivity, stability, and resilience of an ecosystem, and future loss or conservation of biodiversity is expected to be a major determinant of ecosystem change in the Anthropocene (Hooper et al., 2012). While hundreds of studies in recent decades have investigated how biodiversity affects the ways ecosystems function (Cardinale et al., 2012; Duffy et al., 2017; Hooper et al., 2005; Loreau et al., 2001), the vast majority of research to date has focused on how the diversity of "desirable" focal species (e.g., fishes, corals, or terrestrial plants) impacts desirable ecosystem properties and functions. Because declines in biodiversity are often accompanied by rapid ecosystem shifts toward community assemblages of previously underrepresented, or "less desirable," taxa (Estes et al., 2011; Folke et al., 2004; Scheffer et al., 2001), we also need to understand how diversity of these less desirable species affects the ecosystem of interest.

Previous studies have noted that positive interactions can occur among undesired invasive species, promoting feedbacks that intensify negative impacts and create invasional meltdown (Green et al., 2011; Parker et al., 2006; Simberloff & Von Holle, 1999), but the role of biodiversity per se of undesirable taxa has rarely been evaluated in ways typically utilized in other biodiversity studies, such as how monocultures versus polycultures of less desirable species impact critical foundation species. Addressing this question is particularly relevant for ecosystems exhibiting dramatic, disturbance-driven changes in their natural community assemblages, such as tropical coral reefs. Many reefs have shifted from coral to macroalgal dominance, increasing macroalgal–coral interactions (Bonaldo & Hay, 2014) that suppress corals and enhance macroalgal resilience via positive feedbacks (Dell et al., 2016; Hoey & Bellwood, 2011; van de Leemput et al., 2016).

Studies in temperate marine systems have demonstrated positive effects of macroalgal diversity on macroalgal growth, biomass, and cover, especially in field studies of longer duration (Bruno et al., 2005; Duffy et al., 2015; Stachowicz, Best, et al., 2008; Stachowicz, Graham, et al., 2008). Furthermore, increasing evidence suggests that both the types of species present and their relative abundances within a system can be the most important determinants of ecosystem function (Winfree et al., 2015). Because different macroalgae have different defensive traits, macroalgal diversity and abundance become harder to control as herbivore diversity declines (Burkepile & Hay, 2008; Rasher et al., 2013)—as has occurred on reefs worldwide (Edwards et al., 2014; Jackson et al., 2001; Mumby & Steneck, 2008). It therefore seems reasonable to hypothesize that macroalgal competitive traits, and impacts, might diversify and increase with species richness, making it harder for corals to tolerate or suppress the effects of diverse assemblages of macroalgae because they may challenge corals via differing competitive mechanisms (Birrell et al., 2008; Clements et al., 2018; Jompa & McCook, 2003; Rasher et al., 2011). Furthermore, the scales at which this "competitor complementarity" manifests may also be diverse—ranging from reductions in coral growth and survival that are apparent at macroscales to alterations in coral microbiomes that could be indicative of dysbiosis or disease (for review, see Clements & Hay, 2023).

The few experimental tests of biodiversity and ecosystem function conducted in coral reef ecosystems have focused on synergistic relationships among desirable species such as corals (Clements & Hay, 2019, 2021) and fishes (Holbrook et al., 2015; Messmer et al., 2011)—not undesirable seaweed species that now commonly dominate tropical reefs and contribute to coral demise. The impacts of increased macroalgal diversity on reef corals (the foundation species of these systems) thus deserve attention, especially given that the frequency and duration of macroalgal–coral contacts are increased and herbivore complementarity is diminished on degraded reefs (Bonaldo & Hay, 2014; Lefcheck et al., 2019; Rasher et al., 2013).

In this field experiment, we manipulated macroalgal species identity and richness in experimental plots to test whether, and how, this undesirable biodiversity affected coral growth and survival. We also investigated the potential roles of physical- and microbially mediated mechanisms in producing macroalgal impacts on corals.

METHODS

Study site and experimental setup

We conducted our manipulative field experiment from 30 May to 7 August 2021 in the back reef lagoon on the north coast of Mo'orea, French Polynesia (17°28′37″ S, 149°50′21″ W), a high volcanic island in the central south Pacific 20 km west of Tahiti. Over the past several decades, coral cover across the back reef of Mo'orea's north coast has declined and stabilized at low levels (<5%), while macroalgal cover consistently increased and remains elevated (20+%) (Adam et al., 2021; Schmitt et al., 2019). To test the impact of macroalgal species richness on coral performance, we manipulated macroalgal assemblages on the upper surface of 25 × 21-cm cement plots that each contained six *Pocillopora verrucosa* coral outplants (six corals per plot, 72 plots, 432 corals total). Each plot was affixed to the substrate and elevated ~30 cm to prevent scour by sand and rubble. The upper surface of each plot contained a 4 × 3 grid space, with upturned soda bottle caps embedded within each space (Figure 1). To create a standardized coral population, 6- to 8-cm-long branches of *P. verrucosa* were fragmented from colonies in situ and individually epoxied (Z-Spar A-788 Splash Zone Epoxy) into the cut-off necks of inverted plastic bottles (following methods of Clements & Hay, 2015). Prior to outplanting, all corals and their epoxy/bottle-top base were wet-weighed in the field using an electronic scale (OHAUS Scout Pro) enclosed within a plastic container mounted to a tripod holding it above the water surface. Before weighing, each coral was gently shaken 30 times to remove excess water and then weighed, immediately placed back in the water, and attached to their designated plot. Six corals that each originated from different *P. verrucosa* colonies were attached to plots by screwing the corals into bottle caps embedded within every other grid space within each plot.

We varied the macroalgal community on the upper surface of each plot by outplanting monocultures holding similar masses of (1) *Sargassum pacificum*, (2) *Turbinaria ornata*, or (3) *Amansia rhodantha*, as well as (4) polycultures containing all three species (12 plots per treatment; Figure 1). These macroalgae are among the most common in back reef habitats of Mo'orea (Poray & Carpenter, 2014; Stiger & Payri, 1999), often co-occur in natural macroalgal assemblages (Bittick et al., 2010; Bulleri et al., 2022), and vary in their allelopathic impacts on *P. verrucosa* (Longo & Hay, 2017). Furthermore, our experimental manipulations with these three species were representative of macroalgal richness occurring at similar spatial scales on degraded back reefs in Mo'orea (three to 15 total algal species per 20 × 20-cm area, including six identified macroalgal spp.; Bittick et al., 2010). There were also two additional treatments: (5) plots with plastic algal mimics to control for effects of shading or abrasion unrelated to the biotic properties of live seaweeds and (6) control plots where corals, but not living algae or physical mimics, were present ($n = 12$ plots per treatment).

To create six standardized units of macroalgae or algal mimics within every other space of the 4 × 3 grid of each plot, cable ties were first individually epoxied into the cut-off necks of inverted plastic bottles that were screwed into bottle caps embedded within the plots. An additional cable tie was then used to attach either *Sargassum* (two ~6- to 8-cm thalli), *Turbinaria* (two ~6- to 8-cm thalli), *Amansia* (two ~6- to 8-cm thalli), or algal mimics (two ~6-cm plastic aquarium plants) to the cable tie embedded in each soda bottle neck. Standardized units used in control plots only had a cable tie attached to the embedded cable tie. In polycultures, units of *Sargassum*, *Turbinaria*, and *Amansia* (two units/species/plot) were distributed to

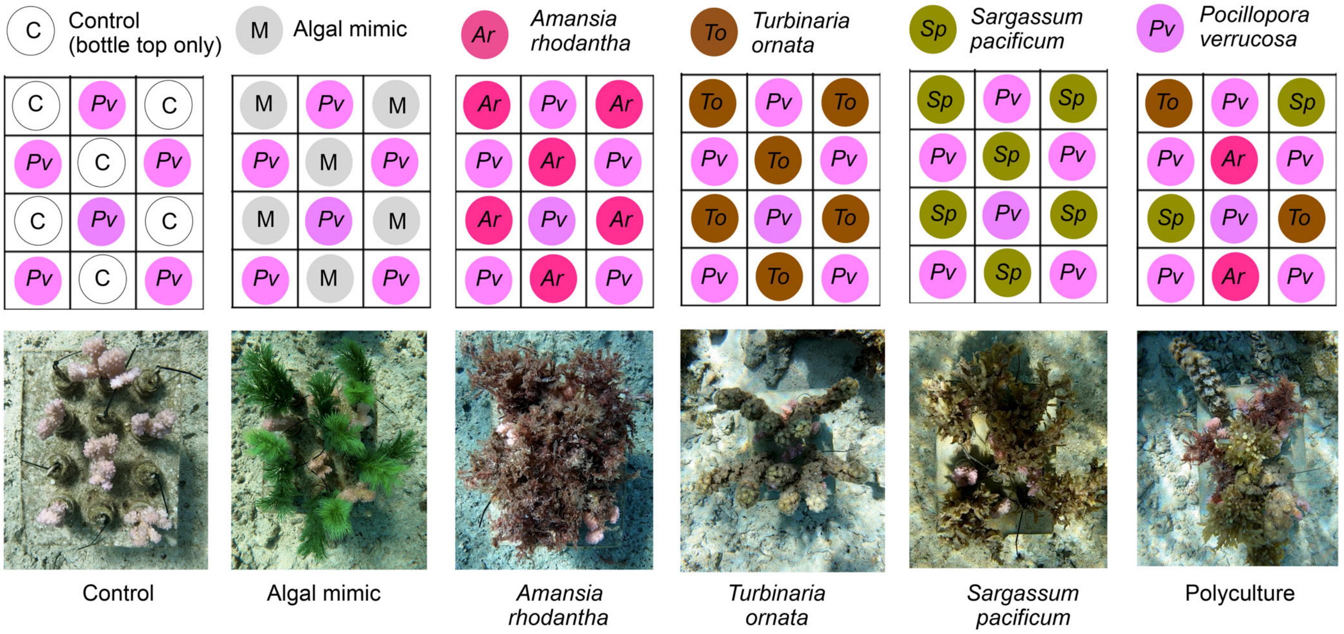

FIGURE 1 Schematic and photographs of one block of treatments of control, mimic, monoculture, and polyculture plots testing effects of macroalgal diversity on *Pocillopora verrucosa* corals. Photo credits: Cody S. Clements.

ensure that conspecifics were not located adjacent to one another within the grid space of the plot and so that the mass of each species was approximately the same (Figure 1). Any macroalgae or algal mimics displaced from their cable tie (e.g., because of wave action or herbivory) were replaced every 1–2 days, and all mimics were replaced weekly to minimize the influence of fouling organisms (e.g., diatoms, cyanobacteria) that might produce chemical or biological interactions confounding the physical effects these biologically inert “controls” are meant to produce. The different treatments were interspersed randomly to prevent confounding spatial effects with treatment effects.

Assessment of coral growth, tissue mortality, and coral microbiomes

The percentage growth and tissue mortality of individual corals in each plot were assessed at 9 weeks (experiment initiated on 30 May with treatment effects assessed on 7 August 2021). Each coral was visually examined from all sides, and the percentage tissue mortality was estimated and assigned in 10% classes (e.g., 0%, 10%, 20% … up to 100%). Twenty-four to 48 h before the second weighing session, each coral’s epoxy/bottle-top base was brushed clean of fouling organisms. To assess growth, corals were detached from the substratum, reweighed in the field as previously described to determine percentage change in mass, and immediately placed back in the water and reattached to their respective bottle caps. Corals were exposed to air for less than 1 min during the weighing process—a timeframe unlikely to impact population or DNA turnover in the microbiome. Following coral weighing, we collected clippings (approximately 1 g) from three corals in each plot (216 total), which were preserved separately in RNAlater (Thermo Fisher Scientific) and stored at −20°C for analyses evaluating treatment effects on coral microbiomes (see analysis procedures below). Following sample collection, the remaining corals were then outplanted back to the reef.

We used permutation-based, linear mixed-effects (LME) models in the R package predictmeans (Luo et al., 2020) to compare differences in the percentage mass change and tissue mortality of corals among treatments. In each analysis, plot treatment (*Sargassum*, *Turbinaria*, or *Amansia* monoculture, polyculture, control, or mimic plots) was treated as a fixed factor, with coral colony treated as a random effect and individual replicate plots treated as a random effect nested within treatment. When appropriate, subsequent comparisons were conducted using a post hoc permutation test for multiple comparisons using the R package predictmeans.

Microbial 16S rRNA gene amplicon sequencing and analysis

Coral clippings (approximately 1 g) were thawed on ice and transferred to the bead beating tube of Qiagen’s DNeasy PowerSoil Pro DNA extraction kit. DNA was extracted according to the manufacturer’s protocol. For quality control, four blanks were carried out through extraction, polymerase chain reaction (PCR) and sequencing steps. The V4 region of the 16S rRNA gene was amplified from all samples using the updated primers described by the updated Earth Microbiome Project (515F:GTG**Y**CAGCMGCCGCGGTAA; 806R:GGACTAC**N**VGGGTWTCTAAT) (Gilbert et al., 2014) with universal overhangs to attach Illumina-compatible barcodes and adapters in a second PCR. The first PCR contained 12.5 µL of Promega’s GoTaq Green Mastermix, 0.5 µL of each primer (10 µM), 0.5 µL of BSA (20 µM, New England BioLabs), and 1 µL of genomic DNA, and each reaction was brought up to 25 µL total with sterile molecular-grade water. The reactions were heated to 95°C for 3 min, then subjected to 30 cycles of 95°C for 45 s, 55°C for 45 s, and 72°C for 90 s, followed by a final elongation step at 72° for 10 min. The second PCR to add duel index barcodes and Illumina adapters was conducted according to the Illumina amplicon protocol (Illumina, 2019) at the Georgia Genomics and Bioinformatics Core. Barcoded amplicons were then randomly pooled into two pools, one with 201 samples and the other with 17 samples, in equimolar concentration and sequenced on Illumina’s MiSeq using one 250 × 250 chips regular chip (for the large pool) and one 250 × 250 nano chip (for the small pool), V2 chemistry, and 20% PhiX to increase read diversity.

Raw microbiome data were imported into QIIME2 version 2023.2 (Bolyen et al., 2019). Reads were quality controlled, trimmed, merged, checked for chimeras, and sorted into sequence variants (SVs) using the DADA2 plugin (Callahan et al., 2016) with the following parameters: -p-trim-left-f 30, -p-trim-left-r 30, -p-trunc-len-f 200, -p-trunc-len-r 200. Each sequencing run was processed through DADA2 independently with identical parameters, and then the data were merged after processing. Each sample was then run through a rigorous quality control check. Potential contaminants were identified by comparing the average abundance of SVs found in samples versus blanks ($n = 4$). Those SVs that were more abundant, on average, in the blank samples were identified as contaminants and removed from the SV table. The table was then rarefied to 4439 sequences for diversity analysis. None of the four blanks made this quality control and rarefaction cutoff, nor were there any significant differences among the two sequencing runs (data not shown). Taxonomy was then assigned to the SVs using the SILVA database (version 138).

Analyses of microbiome data were conducted to compare differences in microbial community metrics among treatments (*Sargassum*, *Turbinaria*, or *Amansia* monoculture, polyculture, control, or mimic plots). Principal coordinate analysis (PCoA) and corresponding tests for differences in microbiome composition (permutational multivariate analysis of variance [PERMANOVA]) and variability (PERMADISP) were implemented in Primer E (Clarke, 1993) using a Bray–Curtis dissimilarity matrix of square-root-transformed data. Alpha diversity (SV richness, Shannon diversity) of relevant data sets was calculated using QIIME2 (Callahan et al., 2016), and differences among treatments were analyzed using permutation-based, LME models in the R (R Core Team, 2020) package predictmeans (Luo et al., 2020). In each analysis, treatment was treated as a fixed factor, with coral colony and sequence run treated as random effects and individual replicate plots treated as a random effect nested within treatment.

RESULTS

After 9 weeks, the growth of control corals (+16%) was 118%–276% greater than the growth of all other treatments (+4%–7%), with the effects of all live algae treatments being statistically indistinguishable from the effects of plastic mimics (Figure 2a). Coral growth was 65%–72% greater for corals in monocultures of *Turbinaria* than monocultures of *Amansia* or *Sargassum*, but these were the only pairwise comparisons where growth significantly differed among live algae treatments. No treatments differed significantly in either mean percentage tissue mortality, which varied from 1% to 10% among treatments (Figure 2b), or in the frequency of total mortality. Only 17 of the 432 total corals in our manipulations exhibited 100% mortality, and these were dispersed among all treatments (1–7 corals per treatment).

Composition of coral microbiomes differed significantly among some treatments (PERMANOVA, $p = 0.012$, Figure 3), but not variability (PERMDISP, $p = 0.069$) or diversity (LME, exact suquence variant richness, $p = 0.592$; Shannon diversity, $p = 0.248$, Pielou evenness, $p = 0.114$; Faith's phylogenetic diversity, $p = 0.186$). Pairwise comparisons between treatments revealed that microbiome composition of corals embedded in monocultures of *Sargassum* differed significantly from corals embedded in monocultures of *Amansia* ($p = 0.002$) or plastic mimics ($p = 0.002$; Figure 3), but other pairwise comparisons did not differ significantly.

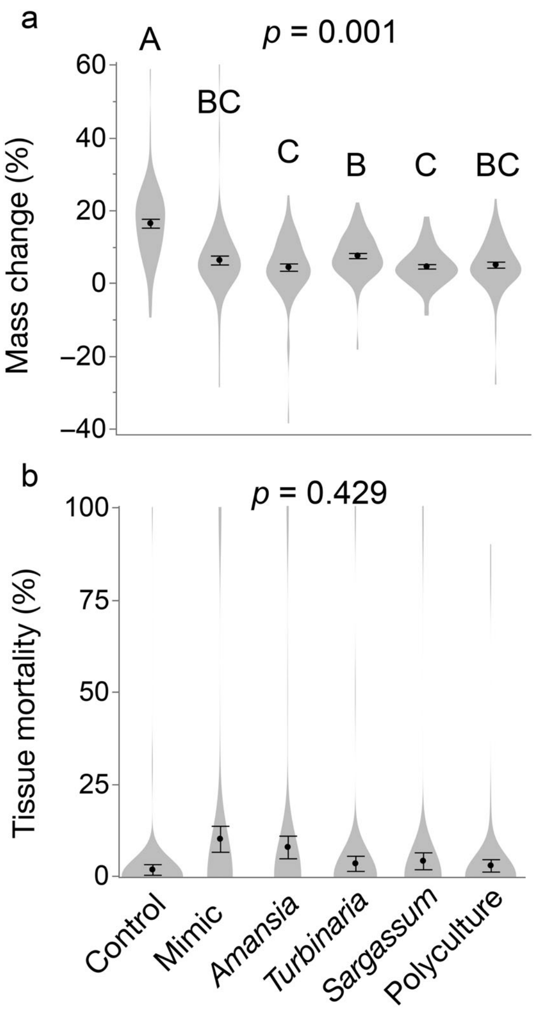

FIGURE 2 Coral (a) growth and (b) tissue mortality at 9 weeks for plots with no algae (control), plastic algal mimics, monocultures of *Amansia rhodantha*, *Turbinaria ornata*, or *Sargassum pacificum*, and polycultures containing all three algal species.

DISCUSSION

Resolving relationships between biodiversity and ecosystem function are increasingly critical as ecosystems experience disturbance-induced shifts in species richness, composition, and abundance (Hooper et al., 2012; Naeem et al., 2012). The beneficial effects of biodiversity have been documented extensively, but less is known about how the diversity of less desirable species affects trajectories of ecosystem structure and function, especially when they impact foundation species. On many tropical reefs, benthic communities have transitioned from dominance of corals—the foundation species of these ecosystems—to less desirable macroalgae that compete with corals and promote further coral decline (Hughes et al., 2010; Mumby & Steneck, 2008). While evidence suggests that loss of coral species can suppress reef functions and promote further

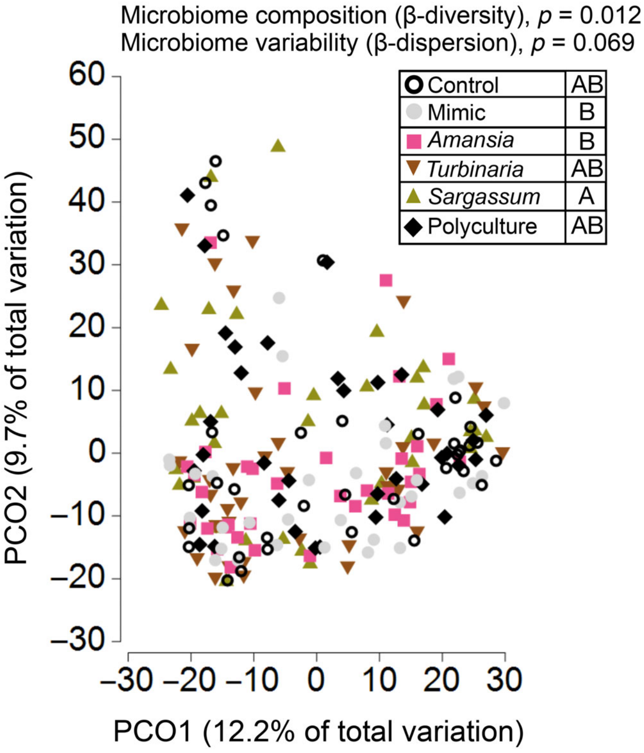

FIGURE 3 Microbiome composition (β-diversity) of coral samples from plots with no algae (control), plastic algal mimics, monocultures of *Amansia rhodantha*, *Turbinaria ornata*, or *Sargassum pacificum*, and polycultures containing all three algal species. Letters in legend denote significant groupings.

coral decline (Clements & Hay, 2019, 2021), the role that macroalgal diversity plays in affecting coral–macroalgal competition had not been tested previously.

Here, we manipulated macroalgal species identity and richness in the field to test how macroalgal diversity impacted a dominant coral's performance relative to each macroalga in a monoculture and to a physical mimic. We found that coral growth was suppressed in plots hosting monocultures of three common macroalgal species, polycultures containing all three of these macroalgae, or plastic macroalgal mimics compared to controls. All of the macroalgal treatments and the mimic suppressed coral growth relative to a control lacking these competitors, but none of the treatments of live macroalgae differed in impact from the inert plastic mimics. *Turbinaria* suppressed coral growth less than either of the other macroalgae, but no effects of the monocultures differed from the effects of the polyculture. Thus, diversity per se—at least for the macroalgal species tested—did not exacerbate harmful effects on coral performance, and physical structure alone (i.e., the plastic macroalgal mimic) produced effects similar to those of living macroalgae despite the fact that one of the macroalgae (*Amansia*) had been reported in previous assays as allelopathic (Longo & Hay, 2017).

The effect of physical structure alone is consistent with previous studies where inert mimics produced harmful effects on coral physiology (e.g., growth, photosynthetic efficiency) that are comparable to live seaweeds (Clements et al., 2020; Fong et al., 2020) and suggests that physical processes such as shading or abrasion alone can account for the negative effects on coral growth that we observed in this experiment. Additionally, numerous correlative studies have suggested that macroalgae damage corals via the release of dissolved organic carbon that destabilizes coral microbiomes (overview by Clements & Hay, 2023); the similar effects we detected for inert plastic mimics versus live macroalgae indicate that such effects need not be involved here. It is possible that the effects of plastic mimics were generated by epiphytes that colonized both living and plastic plants so rapidly that their effects occurred even on mimics that were changed out at weekly intervals, but (1) mimics never accumulated more than a slight "fuzz" of what might have been diatoms or detritus, (2) the biomass (and, thus, leaked organics) of this "fuzz" would have been trivial compared to that of the macroalgal treatments, and (3) longer-term (3-week) use of plastic and polyethylene mimics in other studies failed to generate such effects (Rasher & Hay, 2010) despite there being more time for epiphyte colonization. Thus, the effects on both coral growth and microbiome composition that we documented were most likely due to shading and abrasion.

Coral tissue mortality did not differ across treatments, and overall coral survivorship was high (90.2%–98.6%), as has been observed among coral–algal pairings of similar timescales (e.g., 3 months; Clements et al., 2018). It is possible that different species assemblages, densities, or timescales could produce outcomes different from those we observed (Clements et al., 2018). However, the macroalgae used in our manipulations are among the most common in the lagoon on the north coast of Mo'orea (Poray & Carpenter, 2014; Stiger & Payri, 1999), vary in their physical structures and allelopathic impacts (Longo & Hay, 2017), and thus represent ecologically realistic, and common, coral-algal pairings for our study site.

Negative algal effects on corals that are apparent at macroscales (e.g., reduced growth, photosynthetic efficiency, or survivorship) often coincide with changes to coral microbiomes that are considered indicative of dysbiosis (i.e., increases in harmful or loss of beneficial microbes; Vega Thurber et al., 2012; Zaneveld et al., 2017) that contributes to coral harm. However, despite consistent suppression of coral growth in seaweed and mimic treatments relative to controls, shifts in coral microbiomes were relatively limited and inconsistent across treatments. The composition, dispersion, and diversity of coral microbiomes in treatments with live macroalgae or inert plastic mimics did not differ from control corals experiencing no competition. The only microbiome differences observed were between *Sargassum* versus *Amansia* and *Sargassum* versus mimic treatments, and these were limited to altered community composition (i.e., beta diversity) and did not result in differential growth of the test coral. No other seaweed or mimic treatments differed in the microbial metrics assessed, despite coral exposure to markedly different biotic and inert macroalgae assemblages. This could indicate that (1) coarse-resolution microbial metrics (e.g., microbiome composition or dispersion) are inadequate for assessing relevant seaweed effects on coral microbiomes, (2) corals can regulate their microbiomes despite exposure to some seaweed/mimic assemblages, or (3) that microbiome changes can be an adaptive—rather than dysbiotic—response to stress (Clements & Hay, 2023). That said, microbially mediated competition is commonly considered an important process involved in coral–macroalgal interactions and a potential driver of coral decline (Barott & Rohwer, 2012; McDevitt-Irwin et al., 2017), while it has sometimes been argued that physical mechanisms play only a minor role (Barott & Rohwer, 2012; but see Box & Mumby, 2007). The disparate microbial findings among treatments in our experiment highlight the relative impact of physical mechanisms (e.g., shading, abrasion) and complicate the assumed role of microbiome changes in impacting coral fitness due to coral–seaweed interactions (see also Clements et al., 2018, 2020).

The lack of biodiversity effects among macroalgae in our experiments has implications for our fundamental understanding of how biodiversity affects reef ecosystem function and the management of these systems as corals and key ecosystem processes (e.g., herbivory) continue to degrade. If the biodiversity effects we document are typical across taxonomic and spatial scales, then relative seaweed abundances and increased frequencies of coral–seaweed interactions—rather than diversity per se—may be overriding factors that determine impacts on resident coral communities (Winfree et al., 2015). This is consistent with previous studies that found coral growth was dependent on the density and proximity of macroalgal competitors (Clements et al., 2018, 2020; River & Edmunds, 2001) and that adverse growth effects among corals transplanted into natural macroalgal assemblages could be remediated via removal of macroalgae within the coral's immediate vicinity (≥15 cm; Clements et al., 2018). Conserving or restoring stocks of herbivorous fishes that target numerically dominant algal species may be prioritized over herbivore complementarity needed to control a broader suite of less-abundant algal species (Rasher et al., 2013). For example, Rasher et al. (2013) found that brown seaweeds of the genera *Sargassum*, *Turbinaria*, *Hormophysa*, and *Dictyota* accounted for the vast majority (87%–94%) of seaweed cover on fished reefs in Fiji and that these were predominantly consumed by two herbivorous fish species (*Naso lituratus* and *Naso unicornis*).

Determining the ecosystem impacts, or lack thereof, of biodiversity is increasingly critical as ecosystems are subject to degradation, invasion, and reconfiguration of natural community assemblages. Our study represents the first experimental investigation into how increased diversity of less desirable macroalgal species, which have become and are becoming more prevalent on tropical reefs worldwide (Bellwood et al., 2004; Mumby & Steneck, 2008), impact the performance of a prominent coral. We did not find evidence that greater macroalgal diversity was more harmful to corals; coral growth was suppressed to a similar degree regardless of macroalgal species, an assemblage of the three species, or an inert plastic mimic. Furthermore, coral microbiomes were similar across macroalgal treatments and nonbiotic mimics, suggesting that physical, rather than microbially mediated biotic, mechanisms produced the effects we documented. We manipulated three macroalgal species that are among the most abundant on these reefs, but more evaluations across a broader range of species would be welcome. That said, if our results are typical, then managers need not consider the "nuances" of macroalgal identities as much as simply macroalgal abundance in attempts to conserve and manage coral reefs. Similar investigations in other vulnerable ecosystems could provide insights for safeguarding their ecological function in the Anthropocene.

AUTHOR CONTRIBUTIONS

Cody S. Clements and Mark E. Hay conceived the ideas and designed the experiment. Cody S. Clements, Mark E. Hay, and Zoe A. Pratte collected the data. Cody S. Clements and Zoe A. Pratte analyzed the data. Cody S. Clements led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Coral growth and tissue mortality data (Hay et al., 2024) are available from the Biological and Chemical Oceanography Data Management Office (BCO-DMO) at https://doi.org/10.26008/1912/bco-dmo.925751.1. Raw microbiome sequence data are available in the National Center for Biotechnology Information Sequence Read Archive database under BioProject PRJNA1015657 at https://www.ncbi.nlm.nih.gov/bioproject/1015657.

ORCID

Cody S. Clements https://orcid.org/0000-0002-0637-1625

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