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## Biodiversity enhances coral growth, tissue survivorship, and suppression of macroalgae

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### Abstract

Coral reefs are declining dramatically and losing species richness, but the impact of declining biodiversity on coral well-being remains inadequately understood. Here, we demonstrate that lower coral species richness alone can suppress growth and survivorship of multiple species of corals (*Porites cylindrica*, *Pocillopora damicornis*, and *Acropora millepora*) under field conditions on a degraded, macroalgal dominated reef. Our findings highlight the positive role of biodiversity in the function of coral reefs, and suggest that loss of coral species richness may trigger a negative feedback that causes further ecosystem decline.

### Keywords

biodiversity; ecosystem function; coral reefs; BEF; species richness; richness effect; transgressive overyielding; selection effect; complementarity

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Understanding the role of biodiversity in ecosystem function becomes increasingly critical as natural communities are simplified or homogenized by extinctions, invasions, and a host of other pressures<sup>1</sup>. Species loss is now considered among the most serious threats to ecosystem function and integrity<sup>2</sup> due to the potential loss of keystone or foundation species, as well as the loss of positive interactions among potential competitors that can improve ecosystem performance<sup>1</sup>. Such losses may be especially critical on coral reefs, which are normally complex and biodiverse, but are now becoming degraded and species poor<sup>3, 4</sup>. If we are losing both species and critical interactions that depend on biodiversity, then species loss in diverse systems like tropical reefs may initiate negative feedbacks (a biodiversity melt-down) that suppress resilience, suppress recovery, and exacerbate losses of both biodiversity and ecosystem function.

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Author Contributions

C.S.C. and M.E.H. conceived the study. C.S.C. conducted the research with minor help from M.E.H. C.S.C. carried out the data analysis, and C.S.C. and M.E.H. wrote the paper.

Competing Interests

The authors declare no competing interests.

Data Availability Statement

Data sets used in this study are available online from the BCO-DMO data system (<http://bco-dmo.org/>).

The function and maintenance of coral species diversity in reef ecosystems has long intrigued ecologists<sup>5</sup>, yet few experimental tests of biodiversity-ecosystem function have been conducted on coral reefs. As coral losses accelerate due to increasing global stressors<sup>6, 7</sup>, there is an urgent need to understand how coral diversity influences ecosystem processes, especially as reefs transition to a new norm often characterized by reduced coral cover and increased cover of algal competitors. Investigations to date have focused mainly on relationships between coral and fish species richness<sup>8, 9</sup> not the impacts of coral diversity on corals themselves. Studies of the latter are limited to assessments of focal coral species performance for restoration efforts<sup>10, 11</sup> or large-scale correlative analyses yielding mixed results<sup>12</sup>. Manipulative experiments assessing community-level measures of ecosystem performance (e.g., production, invasion resistance) for coral species in single vs. multispecies settings are lacking, despite corals being the foundation taxa upon which most reef species depend.

Coral-coral and coral-macroalgal interactions occur on small spatial scales (mm to cm) at colony borders<sup>13, 14</sup>, so we manipulated coral richness within 36 × 36 cm plots in the field. We created experimental monocultures and polycultures of three common Indo-Pacific coral species (*Porites cylindrica*, *Pocillopora damicornis*, and *Acropora millepora*; Fig 1a) to test the effects of coral species richness on coral growth, mortality, and colonization by competing macroalgae – three key measures of reef ecosystem function – on a degraded Fijian reef (coral cover ~4%<sup>15</sup>). Species richness in our manipulations was representative of richness at similar spatial scales in the field (median = 2 species/ 36 × 36 cm plot, Fig. 1a inset). Each monoculture plot held eighteen implants of a single species (216 of each species total); each polyculture held six implants of each of the three species (72 of each species total; positions randomized on each plot; Fig. 1a, b). The experiment involved 864 corals assessed at zero, four, and sixteen months.

At month four, we consistently found a *richness effect* (*sensu*<sup>16</sup>); growth of all three coral species was a significant 21–185% greater in polyculture vs. monocultures (Fig. 1b, Supplemental Fig. 1, Supplemental Table 1). When summed across monocultures, change in total coral mass was 61% greater in polyculture than in monocultures (Fig. 1c, Supplemental Table 2), and 24% greater than in the best performing monoculture (*A. millepora*; Fig. 1d, Supplemental Table 3). At sixteen months, growth of *P. cylindrica* and *P. damicornis* was a significant 74% and 190% greater, respectively, in polyculture vs. monocultures, while growth of *A. millepora* no longer differed significantly between polyculture vs. monoculture (Fig. 1e, Supplemental Table 1). Coral growth in polyculture also no longer exceeded that of the best performing monoculture (*A. millepora*; Fig. 1g, Supplemental Table 3). However, total coral growth in polyculture still exceeded growth averaged across all monocultures by a significant 67% (Fig. 1f, Supplemental Table 2). Differential growth may be attributable to enhanced tissue and colony mortality in monoculture vs. polyculture. At four months, tissue mortality was 219% greater for *P. damicornis* in monoculture vs. polyculture and trended that way for *P. cylindrica* (Fig. 2a), which had significantly greater colony mortality in monoculture vs. polyculture (Supplemental Fig. 2). At sixteen months, tissue mortality was a significant 90% and 74% greater for *P. damicornis* and *P. cylindrica*, respectively, when in monoculture vs. polyculture (Fig. 2b). Colony mortality was also significantly greater for *P. damicornis* in monoculture vs. polyculture, but no longer significantly differed for *P.*

*cylindrica* (Supplemental Fig. 2). *A. millepora* tissue and colony mortality were unaffected by treatment at four and sixteen months. The rapid and high tissue (40%+) mortality of *P. damicornis* in monoculture was associated with increased abundance of macroalgal competitors at both four and sixteen months (Fig. 2c, d). By sixteen months, *P. cylindrica* was exhibiting a similar, but non-significant, trend.

Richness effects can occur via (i) complementarity effects among species generated by processes such as resource partitioning or facilitation, or (ii) selection effects involving the inclusion of a species with a disproportionately large impact on the metric of interest<sup>16–17</sup>. We found evidence for both. At four months, growth of all coral species in polyculture exceeded the best performing monoculture (*A. millepora*), an example of transgressive overyielding and indicative of complementarity<sup>17</sup>. However, by sixteen months, growth of *A. millepora* in monoculture no longer differed from the combined growth of all species in polyculture, suggesting that inclusion of the fast-growing acroporid<sup>18</sup> likely contributed to rapid growth of polycultures (i.e. selection effect). Both complementarity and selection effects may occur, but may change with community age.

Differences in coral growth between polyculture vs. monocultures were likely affected by among-treatment differences in tissue mortality. *P. damicornis* experienced significantly greater tissue mortality in monoculture compared to polyculture at both four and sixteen months, while *P. cylindrica* showed a trend at four months that became significant by sixteen months (Fig. 2a, b). All coral species exhibited significant negative relationships between growth and tissue mortality (Supplemental Fig. 3). The strength of these relationships increased across time for *P. damicornis* and *P. cylindrica* but not for *A. millepora*. *P. damicornis* monocultures experienced considerable partial and whole coral mortality within only four months, likely contributing to, or resulting from, enhanced macroalgal colonization within these plots<sup>19</sup>. In contrast, *A. millepora* experienced limited tissue mortality (< 10%) at four months that was statistically indistinguishable between polyculture and monoculture (Fig. 2a). This low rate of *A. millepora* mortality likely contributed to coral growth, rapid monopolization of space (Supplemental Fig. 4), and limited opportunity for macroalgal colonization. At sixteen months, *A. millepora* mortality in polyculture and monoculture had increased to 50% and 59%, respectively, but this appeared to be due to a February 2016 bleaching event<sup>7</sup> after corals had grown considerably (Supplemental Fig. 4). This late stage, heat-generated, mortality likely explains the weak relationship between *A. millepora* growth and tissue mortality (Supplemental Fig. 3).

Increased species diversity often fosters a variety of facilitative interactions, such as reduced consumption<sup>20</sup>, parasitism<sup>21</sup>, and disease<sup>22</sup>, which can limit mortality and enhance overall ecosystem performance. The specific mechanisms contributing to lower *P. cylindrica* and *P. damicornis* tissue mortality in polyculture than monocultures are unknown, but may involve reduced corallivory and disease transmission in more diverse plots<sup>22, 23</sup>. The latter seems more likely because corallivorous snails feeding on *P. damicornis* (*Drupella* spp.), *A. millepora* (*Drupella* spp.) and *P. cylindrica* (*Coralliophila violacea*) at sixteen months were uncommon (0–0.22 snails coral<sup>-1</sup>), highly variable across plots, and predator densities did not differ significantly between conspecifics in monocultures and polyculture (Supplemental Fig. 5). Greater mortality in monocultures might be expected if diseases were transmitted via

coral-to-coral contact<sup>24</sup> or via water- or vector-mediated pathways<sup>25</sup>. Disease spread may be hindered by diversity-mediated dilution effects<sup>26</sup>. Analogous dilution effects have been documented in other ecosystems<sup>22</sup>, and correlative analyses suggest that coral disease is less prevalent in geographic regions with greater coral diversity<sup>24</sup>. Other studies have also found that corals surrounded by heterospecifics experience reduced predation by corallivores implicated in the spread of coral pathogens<sup>27, 28</sup>. Future experiments with increased temporal resolution may help identify the biodiversity-mediated mechanisms involved in the patterns we documented.

Our findings add to a growing body of research that biodiversity can enhance important measures of ecosystem function<sup>29</sup>. Similar positive biodiversity effects have been implicated in the recovery of foundation species in other marine ecosystems<sup>30, 31</sup>, suggesting that our findings may have important implications for coral reef conservation and restoration. If the biodiversity effects we document for these three common corals are typical, then reef recovery following major disturbances depends not only on coral recruitment and growth, but also on the diversity of remaining or recruiting corals and how richness interacts to create synergies that enhance growth and survivorship while suppressing damaging competitors<sup>32, 33</sup>. As coral diversity declines on modern reefs, they may experience a diversity-meltdown where critical, positive interactions are lost and the system fails to recover. It is possible that this may have played a role in the larger losses of corals in the low-diversity Caribbean versus the higher diversity tropical Pacific.

## Methods

### Study site and organisms

Our study was conducted from December 2014 to April 2016 on a ~1–3 m deep back-reef lagoon (at Votua Village, Viti Levu, Fiji; 18°12'46.13"S, 177°42'15.61"E) that is subjected to artisanal fishing and exhibits low coral cover (~4%) and high macroalgal cover (~91%)<sup>15</sup>. We focused on this degraded reef because such reefs are becoming increasingly common, and we wanted to understand factors possibly suppressing the recovery of degraded reefs. Our manipulative experiment used the corals *Porites cylindrica*, *Pocillopora damicornis*, and *Acropora millepora*; three species common on reefs throughout the Indo-Pacific and on the reef where we conducted our study<sup>34</sup>. These species were chosen due to their local abundance and because they are representative of coral families that differ in their reproductive strategies<sup>35</sup>, growth rates<sup>36</sup>, and vulnerability to disturbances such as macroalgal allelopathy<sup>34, 37, 38</sup>, bleaching<sup>34, 39</sup>, and *Acanthaster* spp. predation<sup>40, 41</sup>. To determine whether coral species richness in our manipulations was representative of species richness in the field, we surveyed coral species richness on hard substrates within a ~1 km section of fringing reef neighboring our study site (–18° 12' 20.52" S, 177° 40' 14.16" W). A 36 × 36 cm quadrat was placed at 15 randomly-chosen intervals along twenty, 30 m transects that were nonoverlapping and located haphazardly across the reef. We counted coral species richness in each quadrat, focusing exclusively on quadrats located on 100% hard substratum (113 quadrats total) – so as to mirror our experimental plots.

## Coral performance in monocultures vs. polycultures

To manipulate coral species composition and richness, we created  $36 \times 36 \times 6$  cm cement plots to serve as the substrate for replicate monoculture and polyculture coral communities. Each plot was attached to a concrete block ( $19 \times 9 \times 19$  cm) affixed to the reef bottom near the center of the shallow (1–3 m) back-reef lagoon. This elevated plots 25 cm above the bottom and minimized damage associated with the benthos during storms (e.g., sand scour, burial by unconsolidated rubble, crushing by dislodged coral heads, etc.). This elevation mimicked positioning of many natural coral colonies, which often occurred on small bommies that elevated them above the reef pavement to which our plots were anchored. The upper surface of each plot consisted of a  $6 \times 6$  cm grid, and in every other grid space, an upturned soda bottle cap was embedded flush with the plot's upper surface (18 bottle caps per plot). Similar sized-branches (6–8 cm in length) of *P. cylindrica*, *P. damicornis*, and *A. millepora* corals were collected from colonies across the lagoon (18 colonies per species) and were individually epoxied (Emerkit epoxy) into the cut-off necks of plastic soda bottles during late December 2014. These inverted soda bottle necks and corals could then be anchored into the plot by screwing each into its designated bottle cap embedded within the plot. To assemble monocultures of each species, eighteen conspecifics collected from different colonies were randomly embedded within each plot ( $N=12$  plots per monoculture, 216 corals per species in monoculture plots). To assemble polycultures, six individuals of each species from different colonies were embedded in the same manner at randomized locations within each plot ( $N=12$  plots, 72 corals per species) (Fig. 1).

Percent growth and tissue mortality of individual corals in each plot, as well as colonization of each plot by benthic macroalgae, were assessed at four and sixteen months (April 2015 and 2016, respectively). During assessments, each coral was visually examined from all sides and percent tissue mortality was estimated and assigned in 10% classes (0%, 10%, 20%, etc. up to 100%). To assess coral growth, corals and their epoxy/bottle top base were unscrewed from their respective bottle cap and 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. Twenty-four to forty-eight hrs before weighing, each coral's bottle-top/epoxy base was brushed clean of fouling organisms. Before weighing, each coral was gently shaken thirty times to remove excess water, weighed, immediately placed back into the water, and reattached to its respective bottle cap. At the end of the experiment (16 months), each coral was separated from its bottle-top/epoxy base, and each coral and base were weighed separately. We could then determine, via subtraction, coral mass and thus percent growth throughout the experimental period. To assess plot colonization by benthic macroalgae at 4 months, photographs of each plot were analyzed for the percentage cover of macroalgae using ImageJ (v. 1.8.0\_121). At 16 months, we assessed macroalgal abundance by manually collecting all upright macroalgae from the upper surface of each plot, separating to genus, and wet-weighing after removing excess water using a salad spinner (15 revolutions per sample).

## Statistical analyses

We used linear mixed effects (LME) models in the R (v. 3.3.2) package nlme (v. 3.1–130) to assess differences in percent mass change at both four and sixteen months between

conspecific corals in monocultures and polycultures. We also used LME models to compare the combined percent mass change of all species in polyculture to that of all species in monoculture, as well as percent mass change of corals in polycultures compared to the most productive monoculture (i.e., *Acropora millepora*). Individual corals within plots that had been completely broken off from their bottle top base were excluded from analyses; this occurred to only 23 of our 864 corals (2.6%) at four months and 143 corals at sixteen months (16.6%), did not vary significantly with treatment ( $P = 0.478$ ; permutation ANOVA (5000 permutations)), and in some observed instances was due to human trampling. Models were fitted using restricted maximum likelihood with plot type (i.e., monoculture & polyculture) as a fixed factor and individual replicate plots treated as a random effect nested within plot type. When individual models did not meet assumptions of homogenous variance and normally distributed errors, we reran the analysis and specified the variance structure using the `varIdent` function in `nlme`.

To assess differences in percent tissue and whole colony mortality at four and sixteen months between conspecific corals in monocultures vs. polycultures, we first separately averaged percent tissue and mortality of individual corals in each plot. Mean tissue and colony mortality of conspecifics in monoculture and polyculture plots at each time point were then compared separately with Fisher-Pitman permutation tests (10000 permutations) in the R (v. 3.3.2) package “`coin`” (v. 1.2–2). Macroalgal colonization of polycultures and monocultures of each species at four and sixteen months were compared separately with ANOVA and Tukey post-hoc tests using a permutation approach (5000 permutations) in the R (v. 3.3.2) package `lmPerm` (v. 2.1.0).

## Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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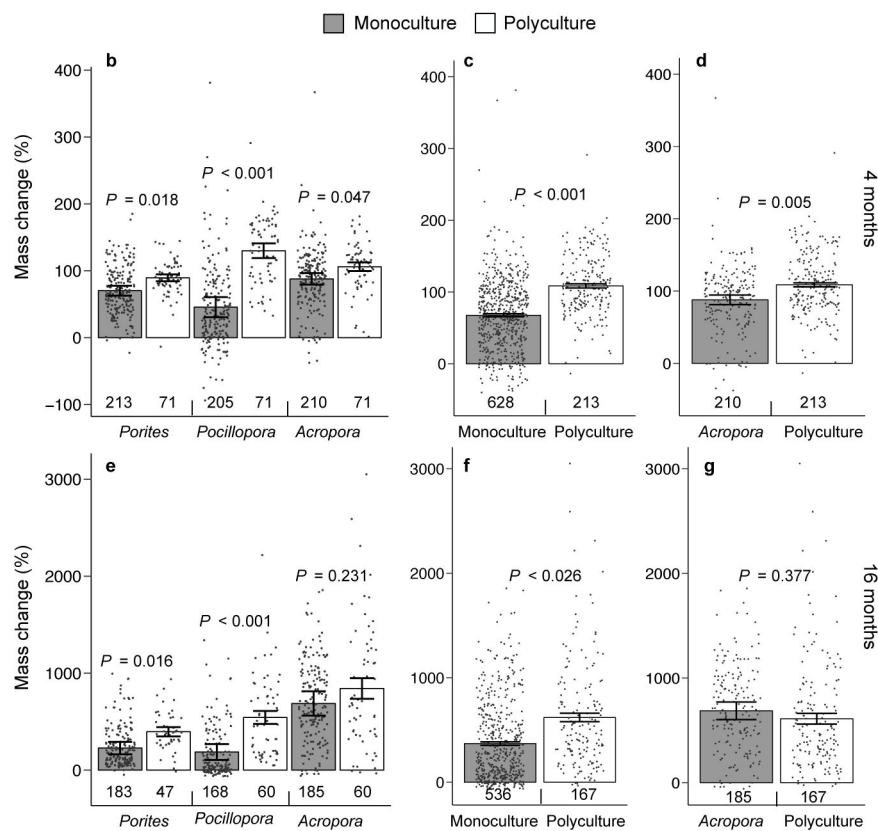
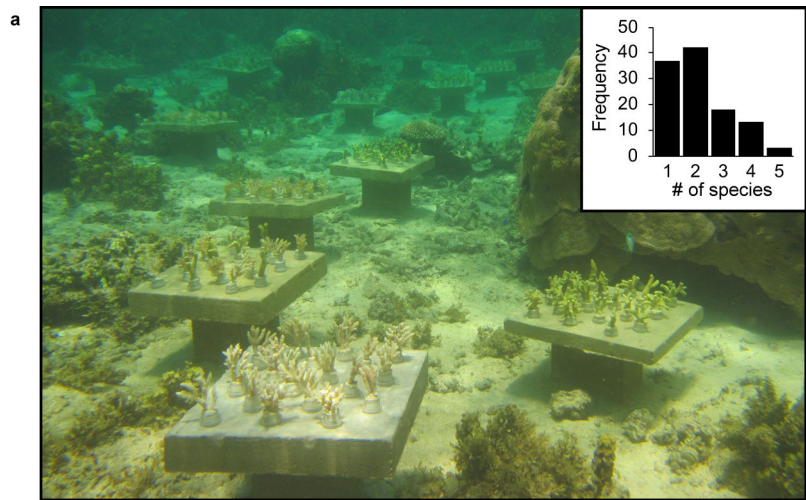
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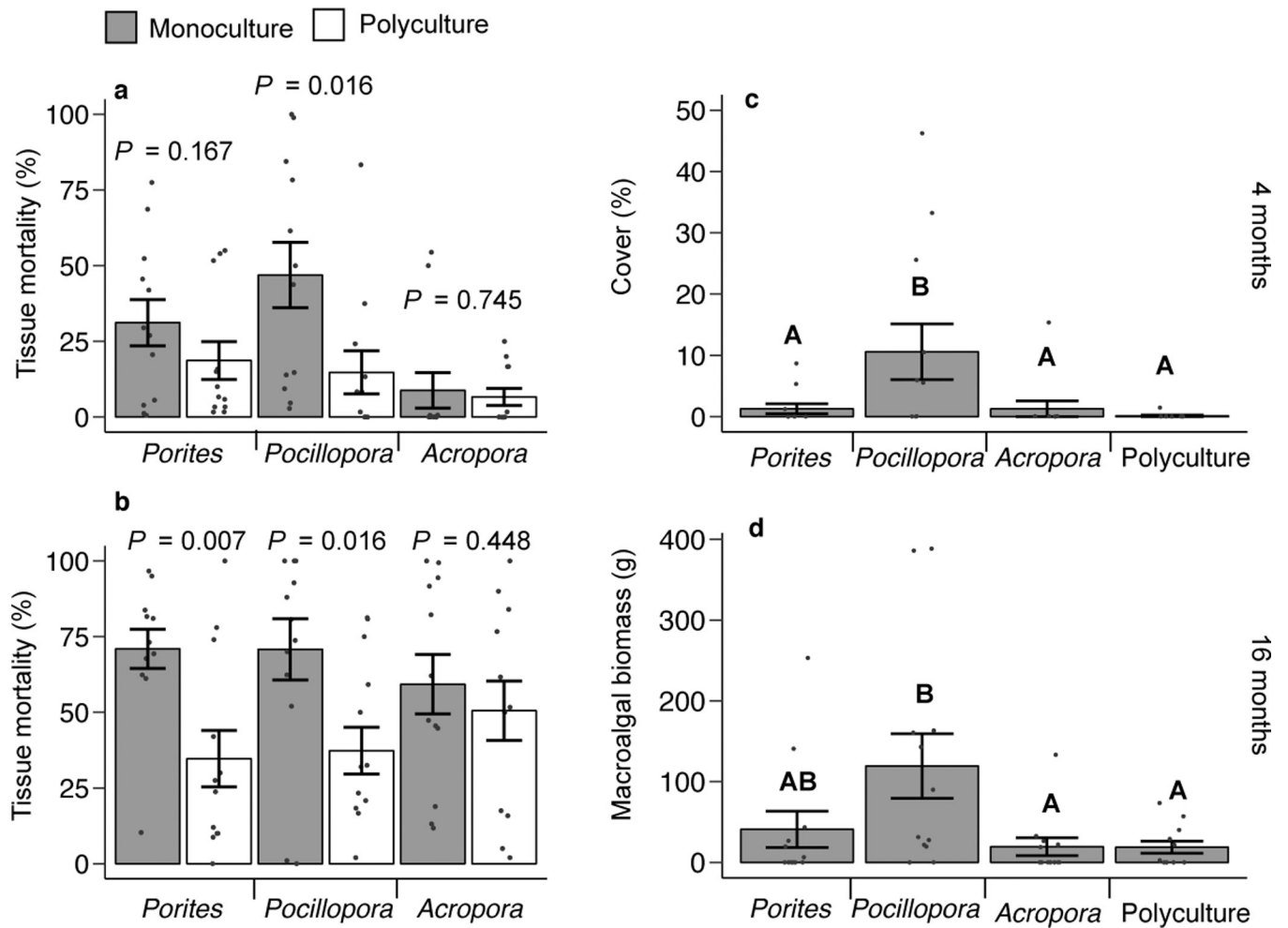




**Figure 1: Coral monoculture and polyculture plots in the field (a) where growth was commonly enhanced in polyculture vs. monocultures.**

**a**, Monoculture and polyculture plots at the beginning of the experiment (month zero; Image Credit: C.S. Clements). **a inset**, Histogram of the frequency of coral species richness in 36 × 36 cm quadrats ( $N = 113$ ) from field surveys. Coral growth (mean % ± SE;  $N = 12$  plots treatment<sup>-1</sup>) at four months for: **b**, *Porites cylindrica*, *Pocillopora damicornis*, and *Acropora millepora* in monocultures vs. polycultures, **c**, the combined growth of *Porites*, *Pocillopora*, and *Acropora* in monocultures vs. polycultures, **d**, *Acropora millepora* (the best performing monoculture) vs. the combined change of *Porites*, *Pocillopora*, and *Acropora* in polycultures.

**e**, **f**, and **g** mirror **b**, **c**, and **d**, but at sixteen months. *P*-values from linear mixed effect models. Dots show values for individual data points, with the total number of corals assessed per treatment indicated below each bar.



**Figure 2: Coral tissue mortality and macroalgal cover in polyculture vs. monoculture.**  
**a,** Percent tissue mortality (mean %  $\pm$  SE) at four months for *Porites cylindrica*, *Pocillopora damicornis*, and *Acropora millepora* in monocultures vs. polycultures. **b,** As above, but at sixteen months. *P*-values from Fisher-Pitman permutation tests (10000 permutations). Dots represent mean values for each independent plot ( $N = 12$  plots treatment<sup>-1</sup>). **c,** Percent cover of upright macroalgae (mean  $\pm$  SE) at four months and **d,** biomass of upright macroalgae at sixteen months for monocultures of *Porites cylindrica*, *Pocillopora damicornis*, and *Acropora millepora* and polycultures containing all three species. Letters indicate significant groupings ( $P < 0.05$ ) via ANOVA and Tukey post-hoc tests using a permutation approach (5000 permutations). Dots represent mean values per plot ( $N = 12$  plots<sup>-1</sup> treatment<sup>-1</sup>).