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Biodiversity enhances coral growth, tissue survivorship and suppression of macroalgae

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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 the growth and survivorship of multiple species of corals (*Porites cylindrica*, *Pocillopora damicornis* and *Acropora millepora*) under field conditions on a degraded, macroalgae-dominated reef. Our findings highlight the positive role of biodiversity in the function of coral reefs, and suggest that the loss of coral species richness may trigger negative feedback that causes further ecosystem decline.

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[1]. Species loss is now considered among the most serious threats to ecosystem function and integrity[2] 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[1]. Such losses may be especially critical on coral reefs, which are normally complex and biodiverse, but are now becoming degraded and species poor[3,4]. If we are losing both species and critical interactions that depend on biodiversity, species loss in diverse systems such as tropical reefs may initiate negative feedbacks (a biodiversity meltdown) that suppress resilience, suppress recovery and exacerbate losses of both biodiversity and ecosystem function.

The function and maintenance of coral species diversity in reef ecosystems has long intrigued ecologists[5], yet few experimental tests of biodiversity and ecosystem function have been conducted on coral reefs. As coral losses accelerate due to increasing global stressors[6,7], 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[8,9], not the impacts of coral diversity on corals themselves. Studies of the this are limited to assessments of focal coral species' performance for restoration efforts[10,11] or large-scale correlative analyses yielding mixed results[12]. Manipulative experiments assessing community-level measures of ecosystem performance (for example, production and invasion resistance) for coral species in single versus multispecies settings are lacking, despite corals being the foundation taxa on which most reef species depend.

Coral–coral and coral–macroalgae interactions occur on small spatial scales (mm to cm) at colony borders[13,14], so we manipulated coral richness within 36 cm × 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%[15]). Species richness in our manipulations was representative of richness at similar spatial scales in the field (median = 2 species per 36 cm × 36 cm plot; Fig. 1a, inset). Each monoculture plot held 18 implants of a single species (216 of each species total). Each polyculture held 6 implants of each of the 3 species (72 of each species in total; positions randomized on each plot; Fig. 1a,b). The experiment involved 864 corals assessed at 0, 4 and 16 months.

At month 4, we consistently found a richness effect (sensu ref. [16]); growth of all 3 coral species was a significant 21–185% greater in polycultures versus monocultures (Fig. 1b, Supplementary Fig. 1 and Supplementary Table 1). When summed across monocultures, the change in total coral mass was 61% greater in polycultures than in monocultures (Fig. 1c and Supplementary Table 2), and 24% greater than in the best-performing monocultures (*A. millepora*; Fig. 1d and Supplementary Table 3). At 16 months, growths of *P. cylindrica* and *P. damicornis* were a significant 74 and 190% greater, respectively, in polycultures versus monocultures, while growth of *A. millepora* no longer differed significantly in polycultures versus monocultures (Fig. 1e and Supplementary Table 1). Coral growth in polycultures also no longer exceeded that of the best-performing monocultures (*A. millepora*; Fig. 1g and Supplementary Table 3). However, total coral growth in polyculture still exceeded growth averaged across all monocultures by a significant 67% (Fig. 1f and Supplementary Table 2). Differential growth may be attributable to enhanced tissue and colony mortality in monocultures versus polycultures. At 4 months, tissue mortality was 219% greater for *P. damicornis* in monocultures versus polycultures and trended that way for *P. cylindrica* (Fig. 2a), which had significantly greater colony mortality in monocultures versus polycultures (Supplementary Fig. 2). At 16 months, tissue mortalities were a significant 90 and 74% greater for *P. damicornis* and *P. cylindrica*, respectively, when in monocultures versus polycultures (Fig. 2b). Colony mortality was also significantly greater for *P. damicornis* in monocultures versus polycultures, but no longer significantly differed for *P. cylindrica* (Supplementary Fig. 2). *A. millepora* tissue and colony mortality were unaffected by treatment at 4 and 16 months. The rapid and high tissue mortality (40%+) of *P. damicornis* in monocultures was associated with an increased abundance of macroalgal competitors at both 4 and 16 months (Fig. 2c,d). By 16 months, *P. cylindrica* was exhibiting a similar but non-significant trend.

Richness effects can occur via (1) complementarity effects among species generated by processes such as resource partitioning or facilitation or (2) selection effects involving the inclusion of a species with a disproportionately large impact on the metric of interest[16,17].

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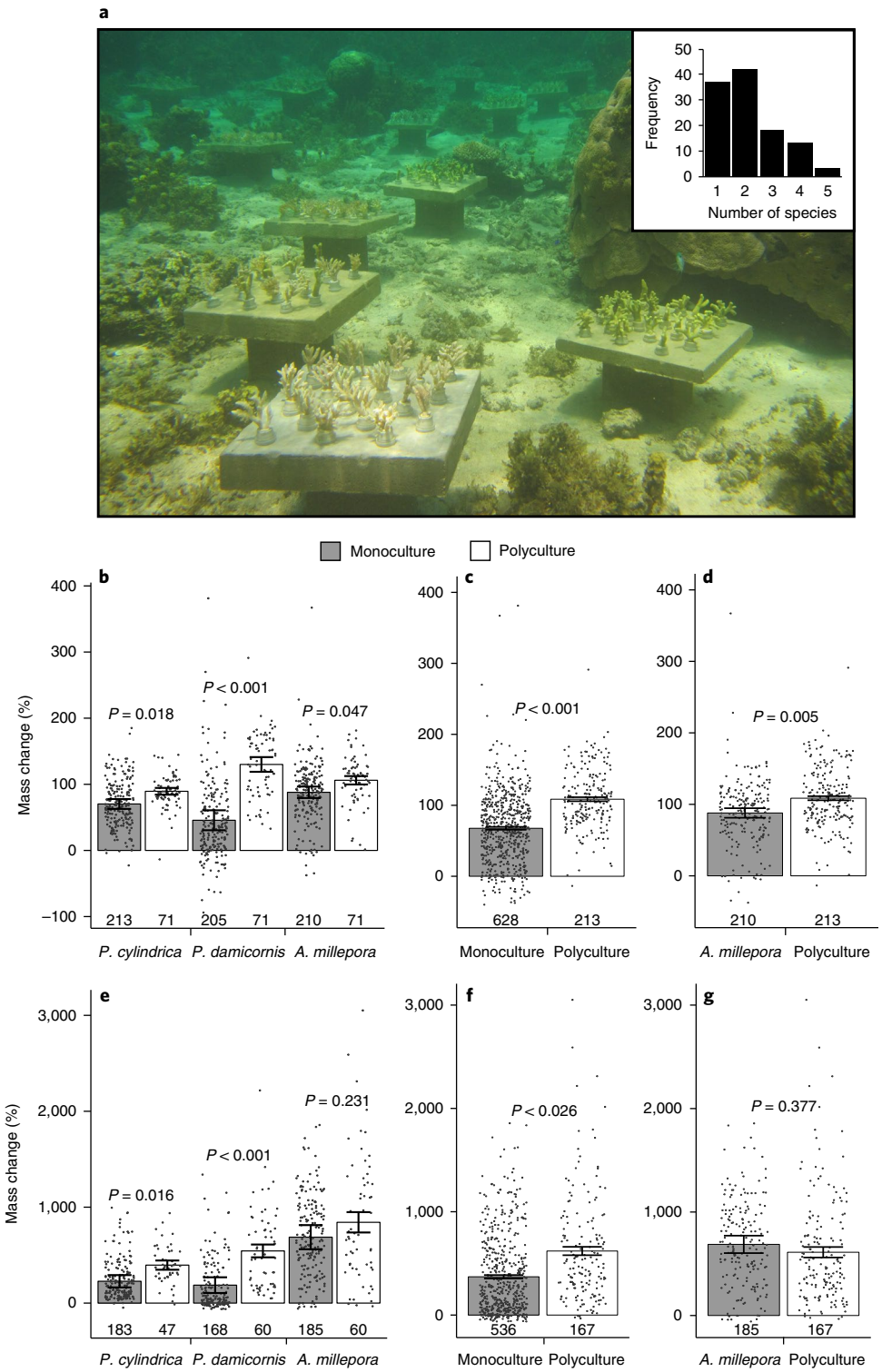

Fig. 1 | Coral monoculture and polyculture plots in the field, where growth was commonly enhanced in polycultures versus monocultures. **a**, Monoculture and polyculture plots at the beginning of the experiment (month 0). Inset, histogram of the frequency of coral species richness in 36 cm × 36 cm quadrats ($n = 113$) from field surveys. **b**–**d**, Coral growth (mean ± s.e.m.; $n = 12$ plots per treatment) at 4 months for: *P. cylindrica*, *P. damicornis* and *A. millepora* in monocultures versus polycultures (**b**); the combined growth of *P. cylindrica*, *P. damicornis* and *A. millepora* in monocultures versus polycultures (**c**); and *A. millepora* (the best-performing monocultures) versus the combined change of *P. cylindrica*, *P. damicornis* and *A. millepora* in polycultures (**d**). **e**–**g**, As in **b**–**d**, respectively, but at 16 months. *P* values were obtained from LME models. Dots show values for individual data points, with the total number of corals assessed per treatment indicated below each bar. Photo credit: C. S. Clements.

We found evidence for both. At four months, the growth of all coral species in polycultures exceeded the best-performing monocultures (*A. millepora*)—an example of transgressive overyielding, and indicative of complementarity[17]. However, by 16 months, the growth of *A. millepora* in monocultures no longer differed from the combined growth of all species in polycultures, suggesting that inclusion of the

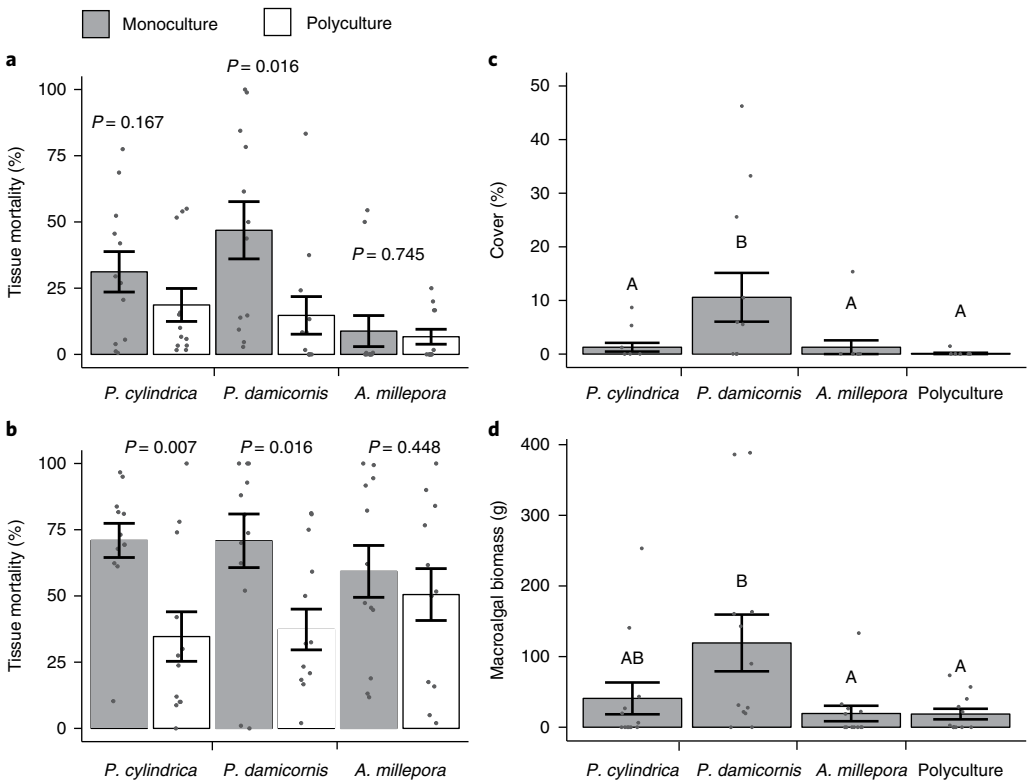

Fig. 2 | Coral tissue mortality and macroalgal cover in polycultures versus monocultures. a, Percentage tissue mortality (mean ± s.e.m.) at 4 months for *P. cylindrica*, *P. damicornis* and *A. millepora* in monocultures versus polycultures. **b**, As in **a**, but at 16 months. *P* values were obtained from Fisher–Pitman permutation tests (10,000 permutations). Dots represent mean values for each independent plot ($n = 12$ plots per treatment). **c**,**d**, Percentage cover of upright macroalgae (mean ± s.e.m.) at 4 months (**c**) and biomass of upright macroalgae at 16 months (**d**) for monocultures of *P. cylindrica*, *P. damicornis* and *A. millepora*, and polycultures containing all 3 species. Letters indicate significant groupings ($P < 0.05$) via ANOVA and Tukey's post-hoc tests using a permutation approach (5,000 permutations). Dots represent mean values per plot ($n = 12$ plots per treatment).

fast-growing acroporid[18] probably contributed to the rapid growth of polycultures (that is, selection effect). Both complementarity and selection effects may occur, but may change with community age.

Differences in coral growth between polycultures and monocultures were probably affected by among-treatment differences in tissue mortality. *P. damicornis* experienced significantly greater tissue mortality in monocultures compared with polycultures at both 4 and 16 months, while *P. cylindrica* showed a trend at 4 months that became significant by 16 months (Fig. 2a,b). All coral species exhibited significant negative relationships between growth and tissue mortality (Supplementary 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, probably contributing to (or resulting from) enhanced macroalgal colonization within these plots[19]. In contrast, *A. millepora* experienced limited tissue mortality (<10%) at 4 months that was statistically indistinguishable between polycultures and monocultures (Fig. 2a). This low rate of *A. millepora* mortality probably contributed to coral growth, rapid monopolization of space (Supplementary Fig. 4) and limited opportunity for macroalgal colonization. At 16 months, *A. millepora* mortality in polycultures and monocultures had increased to 50 and 59%, respectively, but this appeared to be due to a February 2016 bleaching event[7] after corals had grown considerably (Supplementary Fig. 4). This late-stage, heat-generated mortality probably explains the weak relationship between *A. millepora* growth and tissue mortality (Supplementary Fig. 3).

Increased species diversity often fosters a variety of facilitative interactions, such as reduced consumption[20], parasitism[21] and disease[22], which can limit mortality and enhance overall ecosystem performance. The specific mechanisms contributing to lower *P. cylindrica* and *P. damicornis* tissue mortality in polycultures than monocultures are unknown, but may involve reduced corallivory and disease transmission in more diverse plots[22,23]. Disease transmission seems more likely because corallivorous snails feeding on *P. damicornis* (*Drupella* species), *A. millepora* (*Drupella* species) and *P. cylindrica* (*Coralliophila violacea*) at 16 months were uncommon (0–0.22 snails per coral) and highly variable across plots, and predator densities did not differ significantly between conspecifics in monocultures and polycultures (Supplementary Fig. 5). Greater mortality in monocultures might be expected if diseases were transmitted via coral-to-coral contact[24] or via water- or vector-mediated pathways[25]. Disease spread may be hindered by diversity-mediated dilution effects[26]. Analogous dilution effects have been documented in other ecosystems[22], and correlative analyses suggest that coral disease is less prevalent in geographic regions with greater coral diversity[24]. Other studies have also found that corals surrounded by heterospecifics experience reduced predation by corallivores implicated in the spread of coral pathogens[27,28]. 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 suggesting that biodiversity can enhance important measures of ecosystem function[29]. Similar positive biodiversity effects have been implicated in the recovery of foundation species in other marine ecosystems[30,31], 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, reef recovery

following major disturbances depends not only on coral recruitment and growth, but also the diversity of remaining or recruiting corals and how richness interacts to create synergies that enhance growth and survivorship while suppressing damaging competitors[32,33]. 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 an approximately 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%)[15]. We focused on this degraded reef because such reefs are becoming increasingly common and we wanted to understand the factors possibly suppressing the recovery of degraded reefs. Our manipulative experiment used the corals *P. cylindrica*, *P. damicornis* and *A. millepora*—three species common on reefs throughout the Indo-Pacific and on the reef where we conducted our study[34]. These species were chosen due to their local abundance and because they are representative of coral families that differ in their reproductive strategies[35], growth rates[36], and vulnerability to disturbances such as macroalgal allelopathy[34,37,38], bleaching[34,39] and *Acanthaster* species predation[40,41]. 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 neighbouring our study site (−18° 12′ 20.52′′ S, 177° 40′ 14.16′′ W). A 36 cm × 36 cm quadrat was placed at 15 randomly chosen intervals along 20 30 m transects that were non-overlapping 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) to mirror our experimental plots.

Coral performance in monocultures versus polycultures. To manipulate coral species composition and richness, we created 36 cm × 36 cm × 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 cm × 9 cm × 19 cm) affixed to the reef bottom near the centre 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 (for example, sand scour, burial by unconsolidated rubble, crushing by dislodged coral heads, and so on). This elevation mimicked the 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 cm × 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). Similarly 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 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, 18 conspecifics collected from different colonies were randomly embedded within each plot ($n = 12$ plots per monoculture and 216 corals per species in monoculture plots). To assemble polycultures, 6 individuals of each species from different colonies were embedded in the same manner at randomized locations within each plot ($n = 12$ plots and 72 corals per species) (Fig. 1).

The percentage growth and tissue mortality of individual corals in each plot, as well as the colonization of each plot by benthic macroalgae, were assessed at 4 and 16 months (April 2015 and 2016, respectively). During assessments, each coral was visually examined from all sides and the percentage tissue mortality was estimated and assigned in 10% classes (0, 10 and 20% and so on, 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. Some 24–48 h before weighing, each coral's epoxy/bottle-top base was brushed clean of fouling organisms. Before weighing, each coral was gently shaken 30 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 epoxy/bottle-top base, and each coral and base were weighed separately. We could then determine, via subtraction, the coral mass and thus the percentage growth throughout the experimental period. To assess plot colonization by benthic macroalgae at 4 months, photographs of each plot were analysed for the percentage cover of macroalgae using ImageJ (version 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 (version 3.3.2) package nlme (version 3.1–130) to assess differences in the percentage mass change at both 4 and 16 months between conspecific corals in monocultures and polycultures. We also used LME models to compare the combined percentage mass change of all species in polycultures with that of all species in monocultures, as well as the percentage mass change of corals in polycultures compared with the most productive monocultures (that is, *A. millepora*). Individual corals within plots that had been completely broken off from their bottle-top base were excluded from the analyses; this occurred for only 23 of our 864 corals (2.6%) at 4 months and 143 corals at 16 months (16.6%), did not vary significantly with treatment ($P \geq 0.478$; permutation analysis of variance (ANOVA); 5,000 permutations) and in some observed instances was due to human trampling. Models were fitted using restricted maximum likelihood, with plot type (that is, monoculture and 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 homogeneous variance and normally distributed errors, we re-ran the analysis and specified the variance structure using the varIdent function in nlme.

To assess differences in percentage-tissue and whole-colony mortality at 4 and 16 months between conspecific corals in monocultures versus polycultures, we first separately averaged the percentage tissue and mortality of individual corals in each plot. Mean tissue and colony mortalities of conspecifics in monoculture and polyculture plots at each time point were then compared separately using Fisher–Pitman permutation tests (10,000 permutations) in the R (version 3.3.2) package 'coin' (version 1.2–2). Macroalgal colonization of polycultures and monocultures of each species at 4 and 16 months were compared separately with ANOVA and Tukey's post-hoc tests using a permutation approach (5,000 permutations) in the R (version 3.3.2) package lmPerm (version 2.1.0).

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

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

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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. C.S.C. and M.E.H. wrote the paper.

Competing interests

The authors declare no competing interests.

Additional information

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☐	☒	The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement
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☐	☒	The statistical test(s) used AND whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
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☐	☒	Clearly defined error bars *State explicitly what error bars represent (e.g. SD, SE, CI)*

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Software and code

Policy information about availability of computer code

Data collection	No software was used.
Data analysis	We used linear mixed effects (LME) models in the R (v. 3.3.2) package nlme (v. 3.1-130), as well as Fisher-Pitman permutation tests (10000 permutations) in the R (v. 3.3.2) package "coin" (v. 1.2-2) and ANOVA using a permutation approach (5000 permutations) in the R (v. 3.3.2) package lmPerm (v. 2.1.0).

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

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Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	We manipulated coral species richness in field experiments to assess the role of coral diversity in affecting coral growth and survival. To manipulate coral species composition and richness, we created replicate monoculture and polyculture coral communities with three coral species (Porites cylindrica, Pocillopora damicornis, and Acropora millepora). To assemble monocultures of each species, eighteen conspecifics collected from different colonies were randomly embedded within each experimental 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 experimental plot (N = 12 plots, 72 corals per species).
Research sample	We manipulated coral species composition and richness in experimental monoculture and polyculture coral communities with three coral species (Porites cylindrica, Pocillopora damicornis, and Acropora millepora). To assemble monocultures of each species, eighteen conspecifics collected from different colonies were randomly embedded within each experimental 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 experimental plot (N = 12 plots, 72 corals per species).
Sampling strategy	To assemble monocultures of each coral species, eighteen conspecifics collected from different colonies were randomly embedded within each experimental 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 experimental plot (N = 12 plots, 72 corals per species). Sample size was not predetermined statistically, but was based on what was logistically feasible given field conditions.
Data collection	C.S. Clements collected the data. Percent tissue mortality of each coral fragment was estimated visually in the field. To assess coral growth, 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. 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). We surveyed coral species richness on hard substrates using 36 x 36 cm quadrats that were placed at 15 randomly-chosen intervals along twenty, 30 m transects. 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.
Timing and spatial scale	Percent growth and tissue mortality of individual corals in each 36 x 36 cm plot, as well as colonization of each plot by benthic macroalgae, were assessed at zero, four, and sixteen months (April 2015 and 2016, respectively).
Data exclusions	Individual corals within experimental 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 ($P \geq 0.478$; permutation ANOVA (5000 permutations)), and in some observed instances was due to human trampling.
Reproducibility	Given the number of corals (864 total) and time (≤16 months) involved with our manipualtions, there were no attempts to repeat this experiment.
Randomization	To manipulate coral species composition and richness, we created replicate monoculture and polyculture coral communities with three coral species (Porites cylindrica, Pocillopora damicornis, and Acropora millepora). To assemble monocultures of each species, eighteen conspecifics collected from different colonies were randomly embedded within each experimental 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 experimental plot (N = 12 plots, 72 corals per species).
Blinding	Blinding was not feasible because most of the fieldwork was conducted by one person (C.S. Clements) in challenging field conditions (e.g. data collection was dependent on favorable tide and swell conditions).

Did the study involve field work? ☒ Yes ☐ No

Field work, collection and transport

Field conditions	Our study was 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%). Oceanic water flows over the reef crest at high tide and washes out through deep neighboring channels at low tide.
Location	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).
Access and import/export	To access our sites, we obtained a standard research visa from the Fijian government and were granted oral permissions from the Korolevu-i-wai district elders (the area where this study was conducted) to collect corals and conduct our experiment.
Disturbance	Similar sized-branches (6-8 cm in length) of Porites cylindrica, Pocillopora damicornis, and Acropora millepora corals were collected from colonies across the lagoon at Votua Reef (288 branches per species) and embedded within 36 x 36 cm experimental plots. At the end of the experiment, all surviving corals were outplanted back to the reef, and all plots were removed from the reef.

Reporting for specific materials, systems and methods

Materials & experimental systems

n/a	Involved in the study
☒	☐ Unique biological materials
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology
☐	☒ Animals and other organisms
☒	☐ Human research participants

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging

Animals and other organisms

Policy information about studies involving animals; ARRIVE guidelines recommended for reporting animal research

Laboratory animals	The study did not involve laboratory animals.
Wild animals	Similar sized-branches (6-8 cm in length) of Porites cylindrica, Pocillopora damicornis, and Acropora millepora corals were collected from colonies across the lagoon at Votua Reef (288 branches per species) and embedded within 36 x 36 cm experimental plots. At the end of the experiment, all surviving corals were outplanted back to the reef.
Field-collected samples	The study did not involve samples collected from the field.