ECOLOGY

Biodiversity has a positive but saturating effect on imperiled coral reefs

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Species loss threatens ecosystems worldwide, but the ecological processes and thresholds that underpin positive biodiversity effects among critically important foundation species, such as corals on tropical reefs, remain inadequately understood. In field experiments, we manipulated coral species richness and intraspecific density to test whether, and how, biodiversity affects coral productivity and survival. Corals performed better in mixed species assemblages. Improved performance was unexplained by competition theory alone, suggesting that positive effects exceeded agonistic interactions during our experiments. Peak coral performance occurred at intermediate species richness and declined thereafter. Positive effects of coral diversity suggest that species' losses on degraded reefs make recovery more difficult and further decline more likely. Harnessing these positive interactions may improve ecosystem conservation and restoration in a changing ocean.

INTRODUCTION

Loss of biodiversity is altering ecosystems worldwide, negatively affecting their ecological function, sustainability, and provision of ecosystem services (*1*, *2*). Although biodiversity's positive influence on ecosystem function has emerged as a general rule in ecosystems ranging from grasslands to forests to seagrass meadows (*3*, *4*), we still have a poor understanding of how it affects some of the world's most biodiverse and vulnerable ecosystems, including tropical reefs. Corals—the foundation species of these ecosystems—are in rapid decline, and coral species loss can trigger negative feedbacks that suppress reef functions and promote further decline (*5*, *6*). Despite the critical importance of coral diversity, it is unclear both (i) how the positive effects of diversity change with increasing coral species richness and (ii) what processes generate this effect (*7*). Understanding these dynamics may allow better prediction of, adaptation to, and mitigation against global change.

Although ecologists often emphasize negative biotic interactions (competition, predation, parasitism, etc.), positive interactions are common and frequently play large roles in regulating community structure and function (*8*, *9*). If positive effects of coral biodiversity are typical, then reef resilience and conservation depend not only on recruitment and growth of corals but also on coral biodiversity and how the effects of this vary among different groupings of species. Despite this, few studies have investigated the impacts of coral species diversity for corals themselves (*10*–*13*), and manipulative experiments are needed to more directly assess community-level measures of ecosystem performance (e.g., production and invasion resistance) in the wild (*14*)—especially for small corals at sensitive life stages that are increasingly the focus of restoration efforts (*15*). Recent field-based manipulations in Fiji found that lower species richness suppressed coral growth and survivorship in monocultures versus a three-species polyculture (*14*), but it is unknown (i) whether this effect occurs for other taxonomic groups or geographic locations, (ii) what mechanisms are involved, and (iii) how this relationship may change across a greater range of species richness.

RESULTS AND DISCUSSION

Corals benefit from biodiversity

To address these questions, we conducted a series of manipulative field experiments in Mo'orea, French Polynesia; first by assembling monocultures and polycultures using three coral species (*Acropora hyacinthus*, *Pocillopora verrucosa*, and *Porites rus*) that are common in French Polynesia (Fig. 1A) and congenerics to species used in previous manipulations in Fiji (*Acropora millepora*, *Pocillopora damicornis*, and *Porites cylindrica*). This entailed creating 40 cm by 40 cm experimental plots that contained each of the three species in isolation or combined in random configurations of equal density (12 plots per treatment, 18 corals per plot, 864 corals total; Fig. 1B) and monitoring coral growth and mortality, as well as macroalgal colonization, for three months within each plot. Coral growth was a significant 33% greater in polycultures than monocultures (Fig. 1C), with one of the three species, *P. verrucosa*, generating much of this effect (+43%, Fig. 1D). *P. verrucosa* monocultures also accumulated a greater abundance of macroalgal competitors compared to polycultures or to monocultures of *P. rus* and *A. hyacinthus* (Fig. 1E). These findings parallel the reduced growth and greater macroalgal colonization—but not tissue mortality—observed among *P. damicornis* monocultures in Fiji (*14*), suggesting that biodiversity effects among corals may be geographically widespread and predictable for certain coral taxa, such as *Pocillopora* spp. that are common on Indo-Pacific reefs. *Pocillopora* has been largely responsible for rapid reef recovery in Mo'orea following large-scale mortality events (e.g., crown-of-thorns, bleaching, and cyclones) (*16*) and may benefit from diversity at early life stages when mortality is high; if corals escape this critical size category, then survivorship rapidly increases with colony size (*17*).

The mechanisms generating the positive effects of coral biodiversity observed previously (*14*) and in this experiment are unknown but may result from a number of nonmutually exclusive processes. More diverse coral communities could (i) reduce intraspecific competition (but see the direct test of this below) (*18*), (ii) increase efficiency of resource use (e.g., nutrient uptake) (*10*), (iii) enhance the ability of corals to exclude algal competitors (*19*, *20*), (iv) reduce disease spread due to dilution effects (*21*), (v) reduce predation by coral consumers (*22*, *23*), or (vi) facilitate other physical or chemical interactions (effects of hydrodynamics or interactions of separate coral's chemical defenses,

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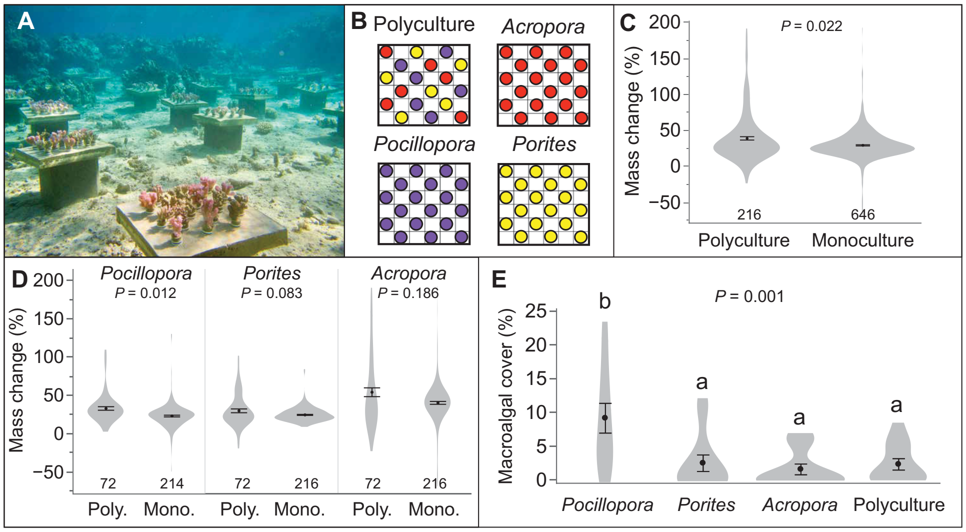

Fig. 1. Biodiversity effects in experimental coral polycultures and monocultures. (**A**) Monoculture and polyculture plots at the beginning of the experiment (month 0) and (**B**) a schematic depicting each treatment. (**C**) The combined percent coral growth (means ± SE) at three months for polycultures versus monocultures. (**D**) Percent coral growth (means ± SE) at three months for *P. verrucosa*, *P. rus, and A. hyacinthus* in polycultures (Poly.) versus monocultures (Mono.). Total numbers of corals assessed per treatment are indicated below each violin plot in (C) and (D). (**E**) Percent cover of upright macroalgae (means ± SE) at three months for monocultures and polycultures (*n* = 12 per treatment). *P* values are from a permutation-based linear mixed-effects (LME) model. Letters indicate significant groupings via a post hoc permutation test for multiple comparisons. Photo credit: Cody Clements, Georgia Institute of Technology.

respectively). These possibilities warrant additional research. We did observe elevated macroalgal abundances in *P. verrucosa* monocultures, and macroalgae predictably suppress coral growth (*24*), but identifying specific mechanism(s) responsible for these increases (e.g., reduced herbivory due to coral density or composition) (*25*) requires further investigation. In Fiji, negative relationships were observed between coral growth and tissue mortality, and we hypothesized that reduced disease transmission may have contributed to the lesser mortality and greater growth of polycultures in that study (*14*); however, we did not observe among treatment differences in tissue mortality in this experiment. Furthermore, evidence for differential predation among treatments was negligible; for example, corallivorous snails (e.g., *Drupella* spp. and *Coralliophila violacea*) were largely absent (only six individuals total) across our 48 plots.

The role of intraspecific competition

Direct tests of the mechanisms generating positive biodiversity effects remain a challenge in many ecosystems (*26*, *27*) and are conspicuously absent for corals. However, an experimentally tractable approach that is grounded in fundamental ecological theory predicts that niche differentiation should reduce competition among species (*18*); thus, a reasonable hypothesis is that elevated intraspecific competition may explain why *P. verrucosa* growth was suppressed in monocultures versus polycultures. To evaluate this hypothesis, we created 60 40 cm by 40 cm experimental plots where we manipulated *Pocillopora* density and coral community composition. Treatments included the following: (i) six *P. verrucosa*; (ii) 12 *P. verrucosa*; (iii) 18 *P. verrucosa*; (iv) six live *P. verrucosa*, *P. rus*, and *A. hyacinthus* (hereafter "live polyculture"); and (v) six live *P. verrucosa* with six dead *P. rus* and six dead *A. hyacinthus* (hereafter "dead polyculture") (576 *P. verrucosa* in total; Fig. 2A). This tested the effects of intraspecific *P. verrucosa* density and the physical presence (but not the biology) of other species in the dead polyculture against the live polyculture.

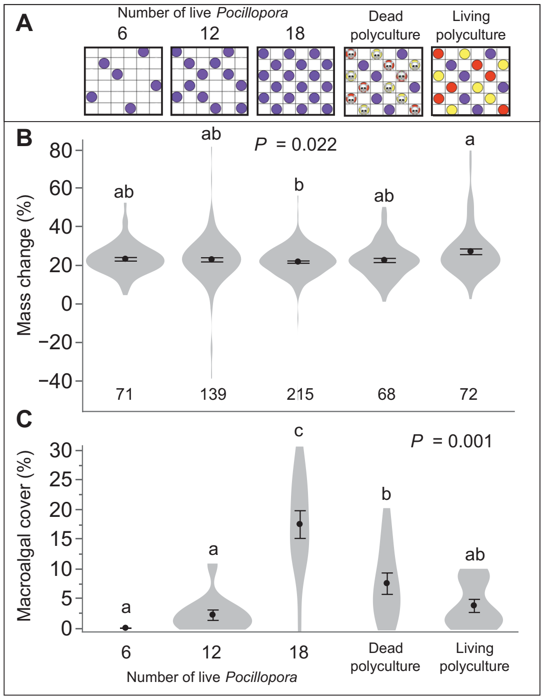

Fig. 2. Effects of intraspecific coral density in generating biodiversity effects on *P. verrucosa* after two months. (**A**) A schematic depicting each treatment. (**B**) Percent *P. verrucosa* growth (means ± SE) and (**C**) percent cover of upright macroalgae (means ± SE) at two months for plots with either six, 12, or 18 living *P. verrucosa*, as well as polycultures containing six *P. verrucosa* and either living or dead heterospecifics (six *A. hyacinthus* and six *P. rus*; *n* = 12 per treatment). Total numbers of corals assessed per treatment are indicated below each violin plot in (B). *P* values are from a permutation-based LME model. Letters indicate significant groupings via a post hoc permutation test for multiple comparisons.

At two months, *P. verrucosa* in live polycultures again outperformed (+25%) the growth of monocultures with 18 *P. verrucosa*. Growth in monocultures with six, 12, or 18 *P. verrucosa* did not differ significantly among density treatments, and they also did not differ from the dead polycultures (Fig. 2B). Macroalgal cover was greater on the *P. verrucosa* monoculture holding 18 individuals than on all other treatments; cover was greater on the dead polyculture than on the six or 12 *P. verrucosa* monocultures, but algal cover did not differ between live and dead polycultures (Fig. 2C).

To evaluate whether this pattern changed with duration, we continued the experiment for five additional months. At seven months, growth was again greater (+29%) in live polycultures than monocultures with 18 corals, but dead polycultures and six or 12 density monocultures did not differ from any other treatments (fig. S1). At this time period, macroalgal cover was absent across all treatments. Nonsignificant trends in *P. verrucosa* growth with increasing density (Fig. 2B and fig. S1) suggest that reduced intraspecific competition might contribute slightly to increased growth, but a positive effect of heterospecifics is more consistent with our data because there was never a detectable effect of *P. verrucosa* density on its growth (Fig. 2 and fig S1). This indicates that simple niche theory alone cannot account for the enhanced polyculture performance we observed and highlights the potential for positive interactions that overwhelm negative effects of competition (*8*, *28*) among these foundation species.

As with our initial experiment, lower growth of *P. verrucosa* at the highest density likely involved competitive suppression by macroalgal colonizers that were most abundant in the *P. verrucosa* monocultures holding 18 individuals (Fig. 2C). Greater community resistance to colonization is a commonly observed benefit of biodiversity in other systems (*8*, *29*) and may explain differences in algal abundances we observed among treatments. For example, both coral density and composition (e.g., different coral growth forms) can affect the ease with which herbivores can access and remove macroalgae (*25*), and lower density (six and 12 *P. verrucosa*) monocultures and live polycultures exhibited the least macroalgae in our manipulations.

Do biodiversity effects saturate?

As reefs are increasingly threatened, it is critical to determine desirable targets of coral species richness that can maximize ecological functions and slow or avert ecosystem collapse. Our experimental manipulations with three species were representative of richness occurring at similar spatial scales on degraded reefs in Mo'orea (mean = ~two species per 40 cm by 40 cm plot; fig. S2) and elsewhere (*14*) but may miss richness optima on less degraded reefs, or in early stages of reef recovery, that could inform management goals. Biodiversity effects on ecosystem function are generally saturating in other ecosystems (*30*), but this has not been evaluated for corals. If saturation occurs on coral reefs, biodiversity loss could initially have a weak effect but could accelerate unexpectedly with further loss. Such a relationship might help explain why the species-poor Caribbean has declined faster and more markedly than the species-rich Pacific (*6*).

To address these issues, we conducted an experiment to assess changes in coral community performance across a greater range of coral species richness; this also lessened the potentially confounding effects of species identity instead of diversity per se. We erected 48 experimental plots supporting equal densities of either one, three, six, or nine coral species, drawn at random for each replicate plot from a pool of nine species: *P. rus*, *Porites lobata*, *Stylophora pistillata*, *P. damicornis*, *P. verrucosa*, *Pavona cactus*, *A. hyacinthus*, *Acropora pulchra*, and *Acropora cytherea* (12 plots per treatment; 864 corals total; Fig. 3A). These corals are among the most common in lagoons of French Polynesia and span a variety of morphologies (e.g., digitate, branching, massive, and tabular) and reproductive strategies (e.g., brooding, spawning, and fragmentation).

At three months, coral growth saturated in plots with three to six species and exceeded growth in monocultures by a significant 62 to 67%. Coral growth in nine-species plots was statistically indistinguishable from plots with one, three, or six species (Fig. 3B). Tissue mortality, which exhibited a significant negative relationship with coral growth ($r^2 = 0.298$, $P < 0.001$), was significantly less in plots with three or six species (~19 to 20%) versus monocultures (~45%), while nine species plots did not differ significantly from any other treatment (Fig. 3C). Macroalgal cover was absent across all treatments in this experiment. This contrasts with our initial experiment where macroalgal cover, but not tissue mortality, differed among treatments and suggests that multiple, context-dependent mechanisms (e.g., suppression of macroalgal competitors or disease) may be responsible for producing positive biodiversity effects.

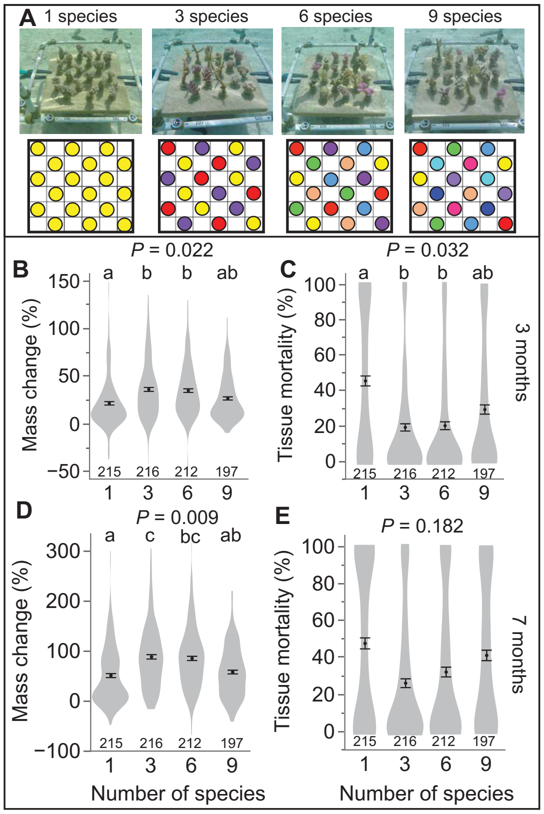

Fig. 3. Positive biodiversity effects peak at intermediate coral species richness. (**A**) Plots at the beginning of the experiment (month 0) and a corresponding schematic representing each treatment. (**B**) Percent coral growth (means ± SE) and (**C**) tissue mortality at three months for plots with either one, three, six, or nine coral species. (**D**) Percent coral growth (means ± SE) and (**E**) tissue mortality at seven months for plots with either one, three, six, or nine coral species. Total numbers of corals assessed per treatment are indicated below each violin plot in (B) to (E). *P* values were obtained from a permutation-based LME model. Letters indicate significant groupings via a post hoc permutation test for multiple comparisons. Photo credit: Cody Clements, Georgia Institute of Technology.

A follow-up assessment at seven months revealed that growth was still saturating in plots with three to six species; however, differences in tissue mortality among treatments were no longer detectable ($P = 0.183$; Fig. 3E). Growth in three-species plots significantly exceeded (by 53 to 74%) growth in one- or nine-species, but not six-species, plots (Fig. 3D). Growth in six-species plots exceeded (by 68%) that in monocultures, but not nine-species plots, which, in turn, were indistinguishable from monocultures (Fig. 3D). Hump-shaped relationships between species richness and productivity are commonly observed in nature (*31*) and, in this case, may arise from community assembly effects coupled with the traits of the nine species used in our manipulations (*32*).

We also evaluated species-specific patterns of growth and tissue death at both three and seven months. At three months, growth of three species (*P. verrucosa*, *P. damicornis*, and *P. rus*) exhibited significant hump-shaped relationships that peaked in plots with intermediate richness; five of the remaining six species exhibited similar trends, but these were not statistically significant (Fig. 4A). At seven months, *A. cytherea*, *P. verrucosa*, and *P. cactus* exhibited significant hump-shaped relationships between richness and coral growth; four of the remaining six species again showed similar but nonsignificant trends (Fig. 4B). Tissue mortality of each species was statistically indistinguishable among treatments at both three months ($P = 0.066$ to 0.848) and seven months ($P = 0.169$ to 0.740).

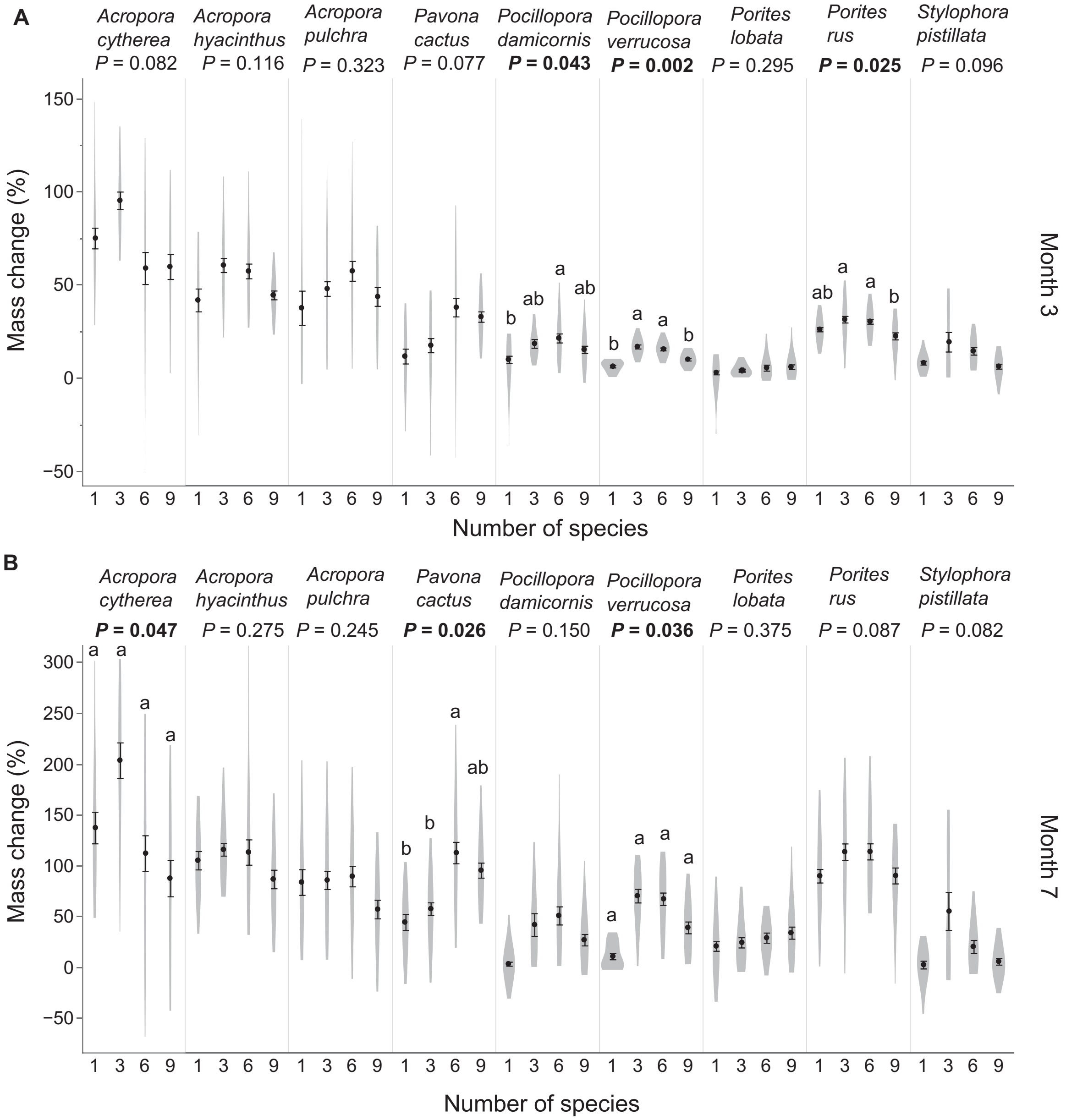

Fig. 4. Positive biodiversity effects are species specific. Percent coral growth (means ± SE) at three (**A**) and seven (**B**) months for each coral species used in plots with either one, three, six, or nine coral species. *P* values were obtained from a permutation-based LME model. Significant values are denoted in bold font. Letters indicate significant groupings via a post hoc permutation test for multiple comparisons.

Our study encompassed three manipulative experiments involving more than 2300 corals and consistently demonstrated the importance of biodiversity for coral productivity, which is critical to reef functions such as $CaCO_3$ accretion and the creation of reef structure and habitat for other species. Positive biodiversity effects were not generated by a greater impact of intraspecific versus interspecific competition in our three-species experiment; we found no effect of intraspecific density alone (Fig. 2). At the scale of our experiment, biodiversity benefits saturated at intermediate levels of three to six species and appeared to begin a decline above this level (Fig. 3). How biodiversity effects may vary at temporal or spatial scales exceeding those of our manipulations deserves investigation.

Our findings suggest that increased coral richness may facilitate corals at early stages of community recovery and may disproportionately benefit certain taxa, such as *Pocillipora* spp., that can drive reef recovery following disturbance (*16*). Harnessing these positive interactions could improve coral conservation and restoration efforts in a similar manner to that observed for foundation species in other marine ecosystems (*4*, *33*). Conversely, continued loss of synergies among species could lead to a "biodiversity meltdown" that compromises coral community resilience in ways that further hasten reef decline.

MATERIALS AND METHODS

Experiment 1: Biodiversity effects in three-species polycultures versus monocultures of each species

We conducted a manipulative experiment in the back reef lagoon of Mo′orea, French Polynesia (17°28′37″S 149°50′21″W) comparing monocultures of the corals *A. hyacinthus*, *P. rus*, and *P. verrucosa* to polycultures composed of all three species. We constructed 48 40 cm by 40 cm cement slabs affixed to the benthos and elevated on cinder blocks to prevent scour by sand or unconsolidated rubble (Fig. 1A); this elevation mimics the coral presence on raised bommies around our manipulation site. The upper surface of each slab contained a six by six grid space in which we embedded 18 upturned bottle caps per plot within every other space (Fig. 1A). Approximately eight-cm length branches of *A. hyacinthus*, *P. rus*, and *P. verrucosa* were fragmented from colonies in situ and epoxied individually into the cutoff neck of soda bottles, which were then attached to plots at randomized locations by screwing the bottle necks into the upturned caps within each plot (18 corals per plot, 864 corals in total). This produced $n = 12$ for each of the three monocultures and the polyculture, with treatments assigned to plots at random to assure interspersion of treatments. At the initiation of the experiment, 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. This provided a wet mass starting value for each individual coral and its base. At three months, we assessed the percentage growth and tissue mortality of individual corals in each plot, as well as the colonization of each plot by benthic macroalgae. Each coral was visually examined from all sides, and the percentage tissue mortality was estimated and assigned in 10% classes (0, 10, and 20%, etc., up to 100%). To assess coral growth, corals and their epoxy/bottle-top base were unscrewed from their treatment plot and wet-weighed in the field as described above. Twenty-four to 48 hours before this second weighing, each coral's epoxy/bottle-top base was brushed clean of fouling organisms. Before all weighings, 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, each coral was separated from its epoxy/bottle-top base, and each coral and base were weighed separately to assess change in mass of the coral alone. Previously, we have used this method to determine, via subtraction, the coral mass and thus the percentage growth throughout the experimental period (*14*, *24*, *34*); however, in many cases, the epoxy/bottle tops used in this experiment did not exhibit clean breaks from their coral outplant. Thus, we decided to calculate the mean weight of all bottle tops and epoxy with visually clean breaks (326 of 864 bottle tops; mean = 21.76 g ± 0.08 g SE) and subtracted this value from each coral replicate to calculate percent coral mass change. To assess plot colonization by benthic macroalgae, photographs of each plot were analyzed for the percentage cover of macroalgae using ImageJ (version 1.8.0_121).

We used permutation-based, linear mixed-effects (LME) models in the R (*35*) package predictmeans (*36*) to compare differences in the percentage mass change and tissue mortality of conspecific corals in monocultures versus polyculture, as well as the combined percentage mass change of all species in polycultures with that of all species in monocultures. In each analysis, plot type (monoculture or polyculture) was treated as a fixed factor, and individual replicate plots were treated as a random effect nested within plot type. Two individual corals that became dislodged from their epoxy base were excluded from the analyses. Macroalgal colonization of polycultures and monocultures of each species were compared with permutation analysis of variance (ANOVA) and a post hoc permutation test for multiple comparisons using the R package predictmeans (*36*).

Experiment 2: The role of intraspecific coral competition in producing biodiversity effects

P. verrucosa was most strongly facilitated by polycultures in the experiment described above—this paralleled similar findings for *P. damicornis* in our initial experiment in Fiji (*14*). To evaluate the potential role of intraspecific competition in suppressing *P. verrucosa* growth in monocultures versus interspecific competition in polycultures, we conducted a subsequent experiment at the same backreef location (17°28′37″S 149°50′21″W) using a similar experimental approach to that described above. We assembled 60 plots (six by six grid space, 18 soda bottle caps embedded) that contained one of five treatment configurations ($n = 12$ plots per treatment, 576 *P. verrucosa* total; Fig. 2A):

1) six live *P. verrucosa*; 12 bottle tops with epoxy but lacking coral
2) 12 live *P. verrucosa*; six bottle tops with epoxy but lacking coral
3) 18 live *P. verrucosa*
4) six live *P. verrucosa*, six *P. rus*, and six *A. hyacinthus* (hereafter live polyculture)
5) six live *P. verrucosa*; six dead *P. rus* and six dead *A. hyacinthus* (hereafter dead polyculture)

Corals were attached to plots at randomized locations by screwing the corals into the bottle caps embedded within each plot. At two and seven months, we assessed the percentage growth and tissue mortality of individual corals in each plot as described above. At seven months, four plots were excluded from our analyses where corals had been heavily predated by the pin cushion star *Culcita novaeguineae*. We observed this event in the field, it occurred for only four of our 60 plots, and it occurred only on these adjacent plots, so we considered it to be a nontreatment-related disturbance that should be excluded. Colonization of each plot by benthic macroalgae was assessed at two months but not at seven months, due to macroalgae absence among plots at that time. As above, percent cover of macroalgae was determined via photographs using ImageJ (version 1.8.0_121), coral tissue mortality was estimated visually, and corals and their epoxy/bottle-top base were wet-weighed in the field to determine changes in mass. At the end of the experiment, corals were successfully separated from their respective epoxy/bottle-top base and were used to determine, via subtraction, the percent coral mass change throughout the experimental period.

We again used permutation-based, LME models in the R (*35*) package predictmeans (*36*) to compare differences in the percentage mass change and tissue mortality of *P. verrucosa* corals in each treatment. In each analysis, plot type (e.g., 18 live *P. verrucosa*) was treated as a fixed factor, and individual replicate plots were treated as a random effect nested within plot type. Ten coral replicates that became dislodged from their epoxy base were excluded from the analyses. Macroalgal colonization of each plot type was compared with permutation ANOVA and a post hoc permutation test for multiple comparisons using the R package predictmeans (*36*).

Experiment 3: Do biodiversity effects saturate?

We conducted an additional experiment that incorporated a greater range of coral species richness to better assess the role of coral diversity per se, evaluate changes in the shape of this relationship with increasing species richness, and lessen the potentially confounding effects of species identity when evaluated across only three species. Forty-eight experimental plots were deployed within a back reef lagoon on Mo'orea (17°29′19″S 149°52′54″W) as described above. Treatments consisted of one, three, six, or nine common coral species drawn at random for each plot from a pool of nine coral species: *P. rus*, *P. lobata*, *S. pistillata*, *P. damicornis*, *P. verrucosa*, *P. cactus*, *A. hyacinthus*, *A. pulchra*, and *A. cytherea* (12 plots per treatment; 864 corals total; Fig. 3A). Individual corals were randomly embedded within each plot, and differences in growth and tissue mortality were assessed at three and seven months with permutation ANOVA and a post hoc permutation test for multiple comparisons using the R (*35*) package predictmeans (*36*). Six and 27 coral replicates that became dislodged from their epoxy base were excluded from our analyses at three and seven months (0.7 and 3.1% of replicates), respectively. At both time points, we also excluded 18 corals from a nine-species plot that was colonized by damselfish (the only plot where this occurred). In instances where significant differences among treatments were detected (i.e., growth at three and seven months and tissue mortality at three months), we also conducted separate analyses comparing growth and tissue mortality among treatments for each of the nine species used in our manipulations. Macroalgal cover was absent among plots across all treatments.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at https://science.org/doi/10.1126/sciadv.abi8592

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