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Coral Community Composition Linked to Hypoxia Exposure

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ABSTRACT

Tropical reef ecosystems are strongly influenced by the composition of coral species, but the factors influencing coral diversity and distributions are not fully understood. Here we demonstrate that large variations in the relative abundance of three major coral species across adjacent Caribbean reef sites are strongly related to their different low O_2 tolerances. In laboratory experiments designed to mimic reef conditions, the cumulative effect of repeated nightly low O_2 drove coral bleaching and mortality, with limited modulation by temperature. After four nights of repeated low O_2, species responses also varied widely, from > 50% bleaching in *Acropora cervicornis* to no discernable sensitivity of *Porites furcata*. A simple metric of hypoxic pressure that combines these experimentally derived species sensitivities with high-resolution field data accurately predicts the observed relative abundance of species across three reefs. Only the well-oxygenated reef supported the framework-building hypoxia-sensitive *Acropora cervicornis*, while the hypoxia-tolerant weedy species *Porites furcata* was dominant on the most frequently O_2-deplete reef. Physiological exclusion of acroporids from these O_2-deplete reefs underscores the need for hypoxia management to reduce extirpation risk.

1 | Introduction

Large framework building coral species historically dominated shallow coral reef communities, but these species are becoming rare across many Caribbean assemblages (Jackson et al. 2014; Cramer et al. 2021). *Acropora cervicornis* is one of these species, with living branches that grow into large three dimensional frameworks, providing underlying reef matrix space for many fish and invertebrates to hide, feed, reproduce and shelter in (Graham et al. 2015). During the last 50 years, *A. cervicornis* has been extirpated from many reefs, facilitating transitions to communities dominated by short-statured weedy species including *Agaricia tenuifolia* and *Porites furcata*. These changes led to subsequent losses in species richness, reef habitat, and overall biodiversity (Alvarez-Filip et al. 2009, 2011; Graham and Nash 2013). Despite the well-known negative biodiversity effects from increasing dominance of weedy species, there is still uncertainty about what causes these transitions.

Our understanding of the controls on coral distribution are largely based on the environmental conditions preceding community transitions. One of the first documented transitions occurred in the late 1970s and was attributed to white band disease that killed 90% of *A. cervicornis* (Gardner et al. 2003; Pandolfi et al. 2003). Additional losses of *A. cervicornis* in 1998 were attributed to high temperatures (Cramer et al. 2020). Other major *Acropora* declines occurred without obvious disease or temperature stress, alluding to the importance of alternate controls (Alvarez-Filip et al. 2009).

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On the Caribbean coast of Panama, analysis of reef matrix cores using Uranium-Thorium dating and $\delta^{13}C$ implicated low oxygen in reef simplification, via loss of *A. tenuifolia* and increasing dominance of *P. furcata* 1200 years ago (Figuerola et al. 2021). High nutrient loads and herbivory may have also contributed to these changes (Aronson et al. 2005). On nearby reefs, low oxygen was recently implicated in localized mass mortalities and community transitions to less-diverse *P. furcata* dominated reefs in 2017 (Johnson, Scott, et al. 2021). In most of these cases, the environmental conditions were not directly measured during the transition, making it difficult to identify why weedy coral species are able to replace framework building species.

The success of *A. tenuifolia* and *P. furcata* has been attributed to their high environmental stress tolerance (Darling et al. 2012), while the failure of *A. cervicornis* has been attributed to its low environmental stress tolerance (Precht and Aronson 2004). But experimental data quantitatively assessing physiological tolerances of these species is limited. Existing studies on weedy species' congeners have shown high tolerances to temperature (Seemann et al. 2012) and oxygen stress (Altieri et al. 2017), while acroporids have lower tolerances to these same stressors (Alderdice et al. 2021; Johnson, Swaminathan, et al. 2021). No studies have assessed the comparative effects of both oxygen and temperature tolerances on all three species in a laboratory setting. These interacting stressors are particularly relevant as rising ocean temperatures increase the frequency and intensity of episodic low oxygen on some coral reefs (Lucey et al. 2023). Matching species-level tolerances to realistic, co-occurring environmental temperature and oxygen conditions is needed to quantify the importance of oxygen for coral reefs and its potential for driving shifts in the community composition.

In this study we determined how temperature and oxygen (O_2) shape coral communities. We first assessed coral community composition and environmental conditions on three shallow reefs. We then performed two experiments to determine the importance of O_2 across (1) temperature and (2) time on three coral species' bleaching and mortality responses. Experiments were based on environmental conditions measured on the reefs and included the three dominant species from these reefs. Lastly, we tested whether species' laboratory tolerance to low O_2 predicted their distributions in the field by quantifying a measure of hypoxic pressure. Pressure sums species' expected bleaching intensity from lab experiments, with the frequency and duration of past *in situ* low O_2 on each reef. We found that low-O_2 regimes on shallow reefs explain the coral community simplification in this system. Only a few hypoxia tolerant weedy species, namely *P. furcata* and to a lesser extent *A. tenuifolia*, persist on the most frequently deoxygenated reefs. The hypoxia-sensitive species *A. cervicornis* was extirpated from these same reefs. These distribution patterns are best explained by species' physiological responses to nightly low O_2, not temperature.

2 | Materials and Methods

2.1 | Does Community Composition Relate to Reefs' Environmental Conditions?

We measured O_2 and temperature on three reefs along a known spatial oxy-thermal gradient in Bahía Almirante, a semi-enclosed bay on the Caribbean coast of Panama. The reefs span ~25 km, extending from the mainland to the open ocean: Inner Bay Reef, Intermediate, and Outer Bay Reef (Figure 1a). Loggers were deployed on each reef at 3 m depth and measured hourly dissolved O_2 and temperature from Sept. 7, 2021, to Oct. 10, 2023. Loggers were mounted ~15 cm above the reef on cement blocks with copper antifouling protectors and were calibrated every 4–6 months. We tested the significance of (1) average daily O_2 minima across sites using Kruskal–Wallis tests, which accounted for violations of homogeneity (Figure 2a), and (2) average daily T maxima across sites (Figure 2c) using ANOVA. Differences between sites were determined using post-hoc Tukey comparisons.(Lucey, Haskett, and Collin 2020; Lucey et al. 2023)

The focal species in this study were *Acropora cervicornis, Agaricia tenuifolia*, and *Porites furcata*. They are all common, fast growing, branching, or plating, stony coral species and they can be found together on shallow Caribbean coral reefs (Aronson et al. 2005). We targeted these species because they can be abundant within the region and they all do, or recently did, live together at each of the three reef sites (*Personal observation*, *NML*).

At each of the three reef sites with loggers, and three additional nearby replicate sites (Figure 1), we surveyed the coral cover and species abundance. At each site, a transect tape was overlaid on the reef from the logger location, following a 3 m depth contour for 25 m. Photographs were taken every 5 m along the transect line. Photographs were taken at a distance 1 m above the transect tape using a fixed height PVC scale bar, so that plot photos were equal in size. After photographing 6 plots per site, we uploaded images to CoralNet and applied the uniform grid method to add 64 points to each plot. In this method, the image is automatically divided into a grid of cells and within each cell, 1 point is placed at the center. We annotated these points by identifying any stony coral present to the species level. When no stony corals were present, we identified the alternative substrate type as sand, dead coral, algae, or soft coral. Soft corals were not taxonomically identified but included zoanthids, rod sponges, encrusting sponges, and *Millipora* (i.e., fire corals). Species' abundance was calculated as the total number of points covered by the living target species divided by all points with any living stony coral species, i.e., # target species divided by total # stony corals, per site. Similarly, we assessed species abundance relative to total coral substrate, which included soft and stony corals. Surveys and photo-quadrat methods were adapted from Reef Life Survey and Marine GEO standard protocols (Harper 2021).

2.2 | Experiment 1: Is Low Oxygen the Primary Driver of Stress, or Is Warming?

In the first experiment, we manipulated O_2 and temperature in laboratory aquaria, in the dark, to mimic one night of low O_2 in the field. Treatments included two different O_2 levels (low $O_2 = 0.3–0.5\,mg\,L^{-1}$ and a well-oxygenated control $> 6.0\,mg\,L^{-1}$) under four different temperatures (25°C, 28°C, 31°C, and 34°C) for each of the three species. For each species, we collected 6 colonies from a reef without a known history of low O_2 (Punta Caracol, Figure 1). Each colony was fragmented to produce 20 growing ramets. Each day we performed a trial at one temperature with both O_2 levels for a given species. Trials ran between May 4 and June 16, 2022 (12 trials in total) and new corals were used in each trial.

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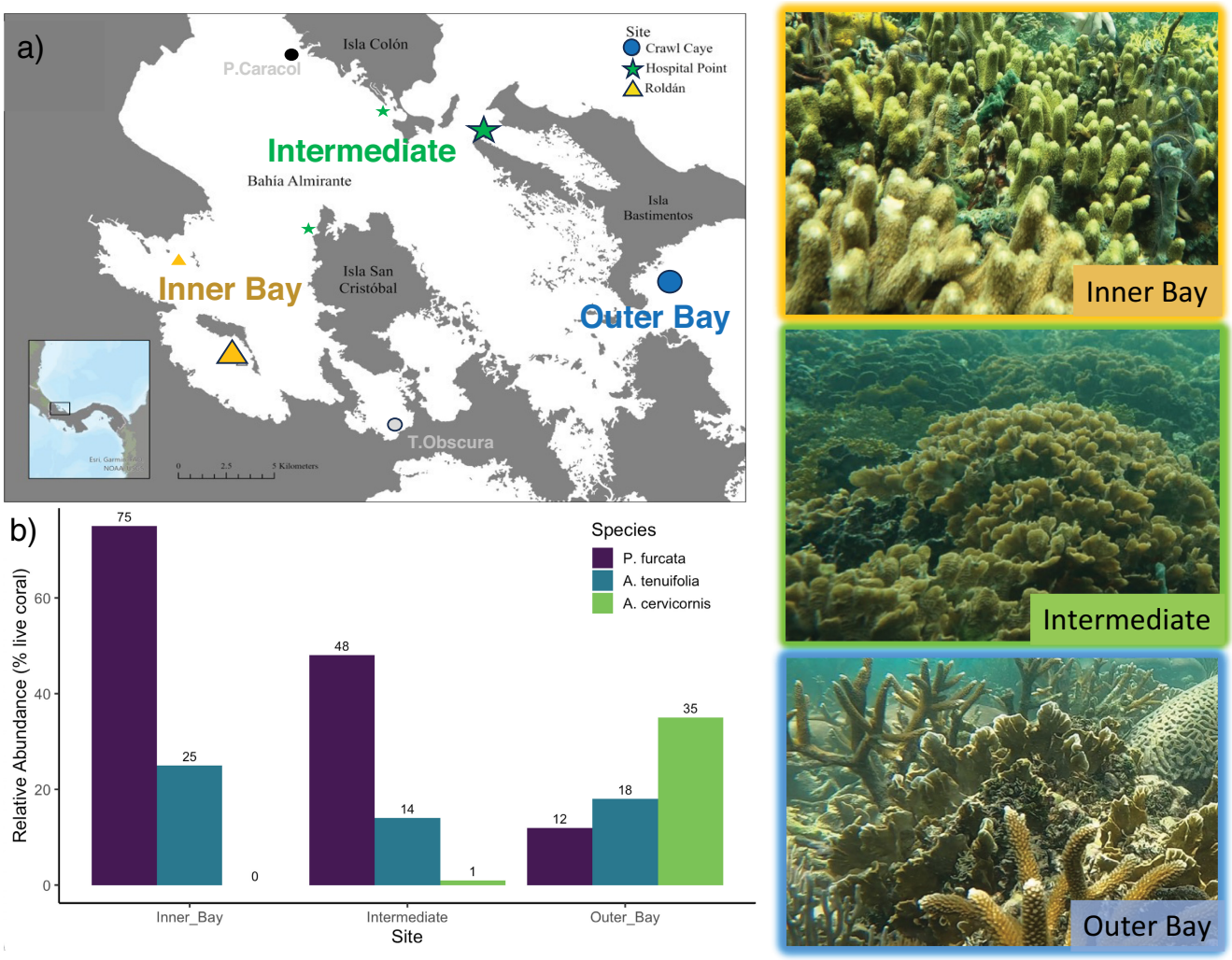

FIGURE 1 | Coral community composition differs across three shallow coral reefs in Bahía Almirante, Panama. (a) Location of the three primary study sites, inner bay, intermediate, and outer bay reefs, with the mainland of Panama on the far left of map. (b) Relative abundance of target species from all living stony coral species on each 3-m deep reef. *Porites furcata* abundance progressively increases towards the inner bay, while *A. cervicornis* abundance becomes absent. Right-side photographs show reefs at each of three study sites. Corals in Experiment 1 were collected from Punta Caracol (black filled circle), while corals in Exp. 2 were collected from two of the three study sites, i.e., inner bay, intermediate, and outer bay sites, see methods. Tierra Obscura (grey circle) shows where reef cores were taken to analyze community composition throughout the last century. Replicate inner and intermediate bay reef sites are identified with smaller colored shapes without black outlines (yellow triangles and green stars, respectively). Map lines delineate study areas and do not necessarily depict accepted national boundaries.

Each fragment was approximately 6 cm long and included a growing tip or edge. *Porites furcata* and *A. cervicornis* fragments were glued to stands and allowed to recover for 1 week prior to starting experiments. Each trial, i.e., day, had three tanks in each O_2 treatment, distributed between two water baths at the same temperature. There were 48 fragments in each temperature trial, with 24 fragments distributed into each of the two O_2 treatments, from 6 colonies, with 4 clonal fragments (ramets) randomly placed into each of the 3 tanks in each treatment (Figure S1). A total of 192 fragments were used per species, with 48 per temperature treatment. Plexiglass tanks were filled with 8 L of seawater. Temperature was regulated using submersible heaters (Sous Vide, accuracy: 0.2°C). Tubing supplied either air or N_2 gas to the seawater in each tank, and was constantly bubbling. Submersible aquarium circulation pumps were also added to each tank to ensure water circulated within tanks at a rate of ~6 L m^{-1} (PULACO 95 GPH). O_2 was monitored every minute and adjustments to gas mixtures were made to maintain levels between 0.3–0.5 mg L^{-1} during the 6 h dark trial (PreSens O_2 dipping probe). Following each trial, fragments were moved to fully oxygenated recovery tanks with flowing seawater at ambient temperature (28.5°C ± 0.5°C).

Coral fragments from Experiment 1 were photographed the day before trials in a blacked-out container under fluorescent lights with a Nikon camera using automatic settings with flash to attain a baseline to determine bleaching intensity. The camera was mounted above a shallow white bin filled with seawater and corals were photographed while submerged alongside their ID tags and a white reference standard. Fragments were photographed in the same setup again 24 h after the 6 h experimental exposure (following day with 24 h recovery). Pre-exposure and post-exposure photos of fragments were analyzed in ImageJ using

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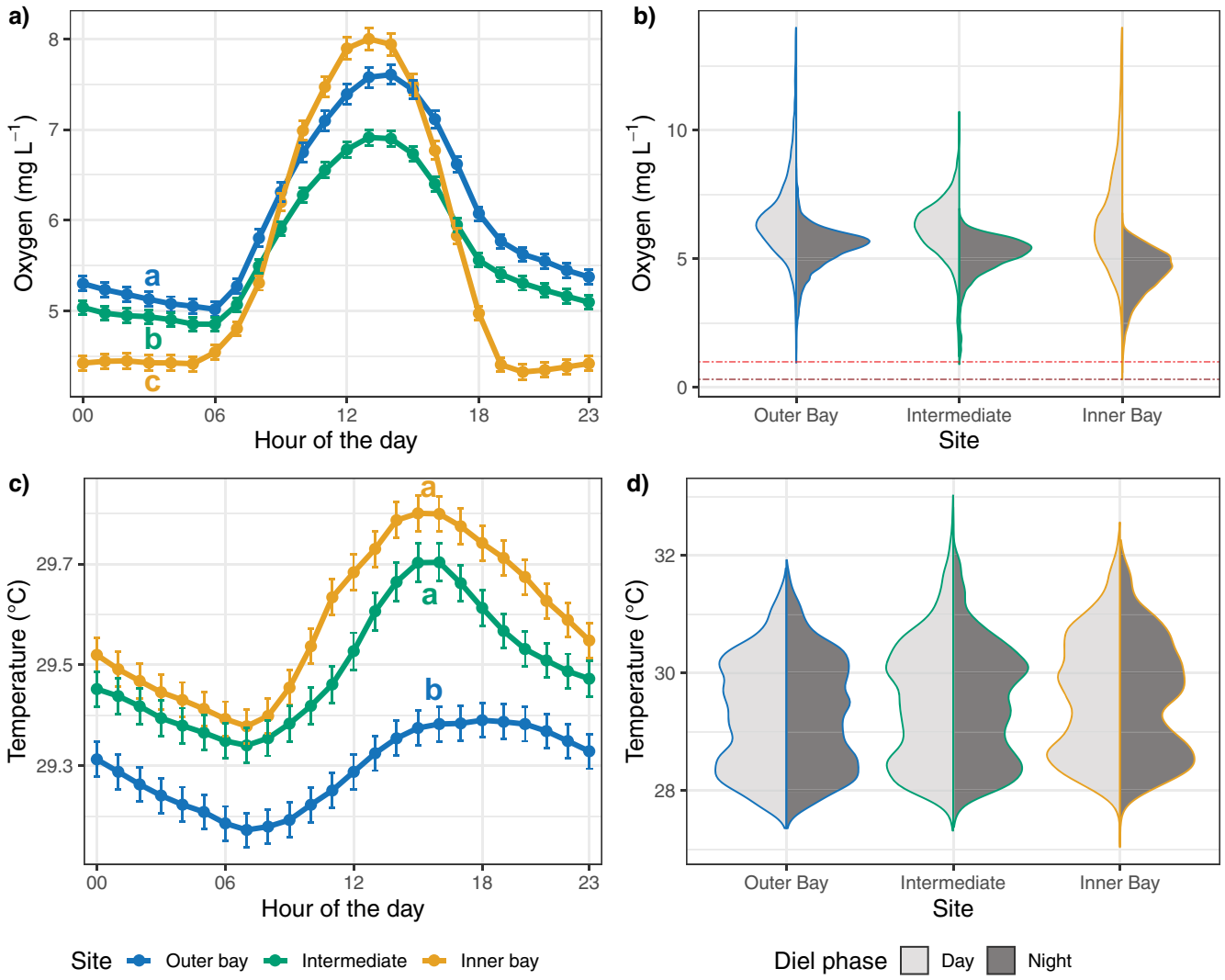

FIGURE 2 | A clear oxy-thermal gradient spans the reef sites, with the warmest reefs also having the lowest persistent O_2 at night. (a, c) Hourly averaged dissolved O_2 and temperature show persistent diel patterns over 2 years. The inner bay reef experienced the highest average hourly (±SE) temperatures and lowest average O_2 ($mg\,L^{-1}$) during the night (orange). The intermediate reef experienced less extreme O_2 and was slightly cooler (green). On the outer bay reef, temperatures were cooler throughout the day, and nightly O_2 was higher on average, compared to the other reefs (blue). Differences in average daily temperature maximum and O_2 minimum values between sites are indicated by different colored letters over the parameters ($p < 0.5$). (b, d) Violin plots show the distribution and extreme values of O_2 and temperature at each site. These distributions are parsed into diel phases, with day-time values including measurements made between 06:00 and 18:00 h (light gray), and night-time values calling the remainder of hours (dark gray). Red lines in (b) represent the O_2 limits used in experiments. The lower dark dashed red line identifies the O_2 value used in Experiment 1 ($0.3\,mg\,L^{-1}$), while the upper dashed red line shows the value used in Experiment 2 ($1.0\,mg\,L^{-1}$). Experimental values match measured minima in the inner bay and the outer bay, dark red and red horizontal dashed lines respecitivey.

Mean Intensity Grey (MIG) protocol (McLachlan et al. 2021). Mean Intensity Grey (MIG), or percent whiteness, has been shown to be highly correlated with Symbiodiniacaeae algal density and chlorophyll A concentrations (Amid et al. 2018; Chow et al. 2016) and can give robust estimates of bleaching intensity. Bleaching intensity was then determined by the change in the percent whiteness between pre-and post-exposure images. Fragments with > 50% tissue loss were considered dead during the 24 h post exposure observations.

Pulse-amplitude-modulated fluorometry (PAM) measurements were taken to assess the maximum quantum yield of PSII (Fv/Fm) after trials (DIVING PAM II Underwater Fluorometer). This is a photosynthetic parameter used to describe the condition of the Symbiodiniaceae algae (Warner, Fitt, and Schmidt 1999). Fv/Fm ratio values range from 0 to 1 with values closer to 1 indicating higher photosynthetic performance. Corals were dark acclimated for 30 min prior to readings. Measurements were taken immediately before the trials commenced, and 24 h post-trial. Fv/Fm measurements were taken 1 cm below the growing tip of each coral fragment and spacing was as set to 7 mm. The specific settings for each species were: *Acropora cervicornis* (gain = 1, damping = 1, light = 10, saturation = 7); *Porites porites* (gain = 1, damping = 1, light = 10, saturation = 7); *Agaricia tenuifolia* (gain = 2, damping = 1, light = 10, saturation = 7). We determined the loss of photosynthetic performance from the trials by determining the difference in Fv/Fm of each individual fragment before and after trials.

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We determined if (1) bleaching intensity (MIG), (2) photosynthetic performance (Fv:Fm), and (3) mortality differed between temperature and oxygen treatment using generalized linear mixed models. Initially, *temperature*, O_2 *treatment*, their interaction, and *colony* were set as fixed effects, with "tank" included as a random effect, and "individual" nested within the parent "colony". Model validation included checking for outliers, overdispersion, normality and homoscedasticity of variances using the DHARMa package in R (Hartig 2022), and assessing the importance of random effects. To account for high model complexity, we built generalized linear models (GLMs). Colony was initially added as a fixed effect to GLMs but was not significant and removed from the final models. Each species was run as a separate model.

2.3 | Experiment 2: Does Cumulative Nightly Low Oxygen Increase Coral Stress?

In the second experiment we determined how long low O_2 could persist before bleaching and/or mortality occurred. We performed experiments on each species individually to assess their bleaching and mortality every day for 5 days (four nights), under both nightly fluctuating and chronic low O_2 exposure at ambient temperature, 28.5°C. Each species was collected and tried separately between February and April 2023 (Figure S2).

With each species, we collected 10 colonies, each from two different reefs with different O_2 and temperature histories (Figure 1a). *Acropora cervicornis* colonies were collected from the outer bay site and the intermediate site. The other two species were both collected from the intermediate and inner bay sites. Each colony was fragmented to produce 20 growing ramets. These were evenly distributed between 9 aquarium tanks with 2 ramets per tank, for a total of 20 fragments per tank, and 180 fragments per species. As in the first experiment, each fragment was approximately 6 cm long and included a growing tip or edge. *Porites furcata* and *A. cervicornis* fragments were glued to ceramic stands and allowed to recover for 1 week prior to starting experiments. In each trial, i.e., species, there were three tanks per treatment: chronic low O_2 (1 mg L^{-1}), fluctuating with nightly low O_2 (~1 mg L^{-1} for 6 h in the dark), and a fully oxygenated control (6 mg L^{-1}). Within each tank, air tubing supplied either regular air or N_2 gas to the seawater. O_2 in tanks was measured every minute with a galvanized O_2 probe that was connected to an automated dissolved O_2 controller regulating the amount of nitrogen flowing to the tanks (BarrelEye Designs, Atlas Scientific, accuracy $\pm$0.05 mg L^{-1}). This automatically adjusted O_2 in each tank so that conditions remained between 0.5 and 1.0 mg L^{-1} during all low O_2 exposures.

In the nightly low O_2 treatment, water was deoxygenated at the start of the dark cycle, and low O_2 was maintained for 6 h, then N_2 gas was fully stopped allowing seawater to slowly reoxygenate. Aquarium lighting provided 12 h of simulated day-light conditions, with the intensity evenly ramping up to a maximum PAR of 712 μmol photons m^{-2} s matching average PAR measured hourly from 12:00 to 14:00 over 5 days on the inner bay reef site (LI-250A Light Meter). After reaching full intensity during the first 6 h, lights were ramped down to attain full darkness in the following 6 h, mimicking the daily light cycle (Aqua Illumination Hydra 64 HD LED Reef Lights). Aquarium circulation pumps provided a flow rate of 30 L m^{-1} within tanks and submersible aquarium heaters kept temperature stable (28°C–29°C) (AQUANEAT 480 GPH Power-head submersible pumps; EHEIM water heaters). Each tank was filled with 68.4 L of seawater and at the start of each light cycle, 12 L of seawater was slowly siphoned from tanks and replaced with the same amount of fresh seawater, i.e., daily tank volume turnover of 12 L. Constant N_2 bubbling during water changes avoided increasing O_2 levels in the chronic treatment tanks. The effect of pH was measured with one pH logger in each of the three different treatment tanks (chronic, nightly, control), and measurements were recorded every 30 min for the full 5 day duration of each experiment (Hobo Onset pH logger MX2501). During the *A. tenuifolia* and *P. furcata* trails, the pH in the chronic and nightly low O_2 treatments remained at or above the pH measured in the control tanks (ranging from 7.7 to 8.4). In the chronic *A. tenuifolia* trial, mean pH was 8.12 $\pm$ 0.06 (mean $\pm$ SD), and never dropped below 7.88, compared to the nightly treatment which averaged 8.03 $\pm$ 0.10 with a minimum = 7.72. During the *P. furcata* trial, pH in the chronic treatment tank was on average 8.22 $\pm$ 0.04 with a minimum of 8.16, while the nightly trial averaged 8.30 $\pm$ 0.035 with a minimum of 8.24. pH loggers used in the *A. cervicornis* trial failed. However because the same methodology and seawater system was used for all three species, it is unlikely pH differed across treatments.

At the beginning of the experiment, and after each daily water change, all corals were photographed from their tanks. Both bleaching and mortality were recorded based on visual observation and photographs. Bleaching intensity was initially assessed through MIG analysis, but due to low photographic quality (corals had to remain in experimental tanks), we relied on between-treatment visual comparisons. Bleaching responses were therefore recorded as binary responses (yes/no), and positive bleaching was obvious (Figure S3). As in Experiment 1, mortality was documented when a fragment incurred tissue loss over more than 50% of its surface area.

We determined if (1) bleaching intensity or (2) mortality differed between oxygen treatment through time (days). We built generalized linear mixed models, where O_2 *treatment*, *duration*, their interaction, and *colony* were included as fixed effects. "Tank" and "individual" were added as random effects, but "individual" had a small effect, and was removed to improve model fit. Each species was run as a separate model. Outliers, overdispersion, normality and homoscedasticity of variances, and random effects were assessed with the DHARMa package.

In both experiments, the target O_2 used in treatments was based on minimum O_2 recorded across reef sites, i.e. experimental low O_2 conditions fell between the red dotted lines in Figure 2b.

2.4 | Does In Situ Hypoxic Pressure Predict Species Distribution?

We estimated the amount of *hypoxic pressure* experienced by each species on each reef site during the past 2 years. This estimation was made by combining the field observations of low

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O_2 events at each site with the laboratory observations of each species' bleaching response from low O_2. We first identified the number (n) of distinct time periods in which nighttime O_2 fell below the O_2 threshold used in experiments (i.e., $<1.0\,mg\,L^{-1}$) and recorded the duration (d) of the event as the number of successive nights of low O_2 on each reef over the last 2 years (Equation 1).

The sites differ in both the number and duration of low O_2 events, with the inner bay experiencing both more frequent and longer events than the outer bay (Figure 5b). No *in situ* events longer than four nights were recorded, so the bleaching response of every species falls within the range of experimental conditions measured, allowing a species-specific expected bleaching severity (B_{spp}) to be estimated for each event based on its duration. To characterize the hypoxic pressure (P) for each species at each site, we simply sum these expected bleaching responses across all n hypoxic events observed on the reefs:

$$P_{spp} = \sum_{i=1}^{n} B_{spp}(d_i) \quad (1)$$

where the bleaching intensity depends on the species (indexed by spp) and the duration of each event (indexed by i). We used bleaching intensity as the choice exposure variable, because these responses could be measured within 24 h of environmental exposure. However, mortality was closely linked to bleaching. Over 70% of the bleached fragments experienced severe tissue loss, resulting in mortality, in the days following experimental O_2 exposure (see below). We then compared coral abundance to hypoxic pressure across all six reefs.

3 | Results

3.1 | The Abundance of *A. cervicornis* Is Decreased on Hotter, Oxygen-Depleted Reefs

To establish the differences in coral reef composition between the three primary study sites, we counted the living coral species on each reef site. Live stony coral reef cover was similar across sites (i.e., 23.1% Outer bay, 19.2% Intermediate, 19.7% Inner Bay) and *Porites furcata, Agaricia tenuifolia*, and *Acropora cervicornis* were the most common species, both within and across sites (Figure 1, S4 and S5; Table S1). However, the abundance of *P. furcata* progressively increased towards the inner bay, while the abundance of *A. cervicornis* dropped to virtually zero, resulting in *Porites* dominated reefs in the inner bay and *A. cervicornis* and *A. tenuifolia* dominated reefs in the outer bay. This shift in dominance suggests species distribution is ecologically and/or environmentally mediated.

We found evidence of environmental differences in the 2 years of hourly logger data from each reef. Both environmental O_2 and temperature differed across sites, forming a persistent oxy-thermal gradient across the three shallow reefs. Nightly low O_2 varied inversely with warming severity across reefs, such that hotter reefs experienced more severe low O_2 at night. In contrast, O_2 during the day showed the opposite pattern of supersaturation, such that hotter reefs experienced higher O_2 (Figure 2a–c). The inner bay reef was the hottest and had the lowest nightly O_2 while conditions on the outer bay reef were markedly less extreme (Figure 2). Conditions on the intermediate reef fell between those measured on the inner and outer bay reefs.

The temperatures across the reefs ranged from 27.04°C to 33.02°C, with average daily maxima highest in the inner bay (29.8°C ± 1.0°C SD), followed by the intermediate reef (29.4°C ± 0.9°C), with the outer bay coolest (29.1° ± 0.9°C) (site effect: $p<0.001$). O_2 ranged from 0.32 to ~12.5 $mg\,L^{-1}$ and average daily minimum values were lowest in the inner bay (4.89 ± 1.6 SD) compared to the other sites: intermediate: 5.35 ± 1.12; outer bay: 5.39 ± 1.45 (site effect: $p<0.001$). Across these reefs, the lowest O_2 minima occurred in the inner bay (0.32 for ~2 h), while the outer bay only reached a low of 0.97 $mg\,L^{-1}$ (Figure 2b–d). Cumulatively, this suggests warming, low O_2, or both, could be important mediators of coral distribution on these reefs.

3.2 | Experiment 1: Low O_2 as Primary Driver of Stress, Amplified by Warming

To determine the physiological importance of warming and low O_2 for each species, we exposed corals to 25°C, 28°C, 31°C, 34°C under both low O_2 and well-oxygenated control conditions for 6 h in the dark (Figure 3, Table S2). At ambient temperatures of 28°C, *A. cervicornis* responded to low O_2 with a 30% increase in visible bleaching, 50% reduction in photosynthetic capacity, and with 72% of fragments losing at least half of their live tissue, i.e. mortality (O_2*28°C interaction, $p<0.001$ for all three traits). These low O_2-driven responses were amplified at 31°C, the temperature at which all *A. cervicornis* fragments died in the low O_2 treatment (O_2*31°C interaction, $p<0.001$). In comparison, temperatures of 31°C with no oxygen stress did *not* cause any bleaching, loss of photosynthetic capacity or mortality. At the highest temperature, 34°C, which has not yet been measured on these reefs, ~40% of the *A. cervicornis* fragments bleached regardless of O_2 treatments. However, at this temperature, mortality differences across O_2 treatments did occur, and 75% of the *A. cervicornis* fragments in the control O_2 treatment died compared to 100% in the low O_2 treatment (Table S2).

In *A. tenuifolia*, the extreme temperatures of 34°C caused ~10% of its fragments to bleach without added low O_2 stress. With additional low O_2 stress, bleaching significantly increased to 26% (Figure 3, $p<0.001$). Similarly, loss of photosynthetic capacity and tissue were significantly more severe under the combination of low O_2 and 34°C, i.e., 100% mortality from low O_2 compared to 15% under temperature alone (treatment differences at 34°C: $p<0.001$). *Porites furcata* was the most tolerant species, showing little to no signs of stress across all treatments. While extreme temperatures can cause coral stress alone, these results identify night-time low O_2 as the primary driver of the observed bleaching and mortality at temperatures common across this reef system, i.e., 28°C–31°C (Figure 2d).

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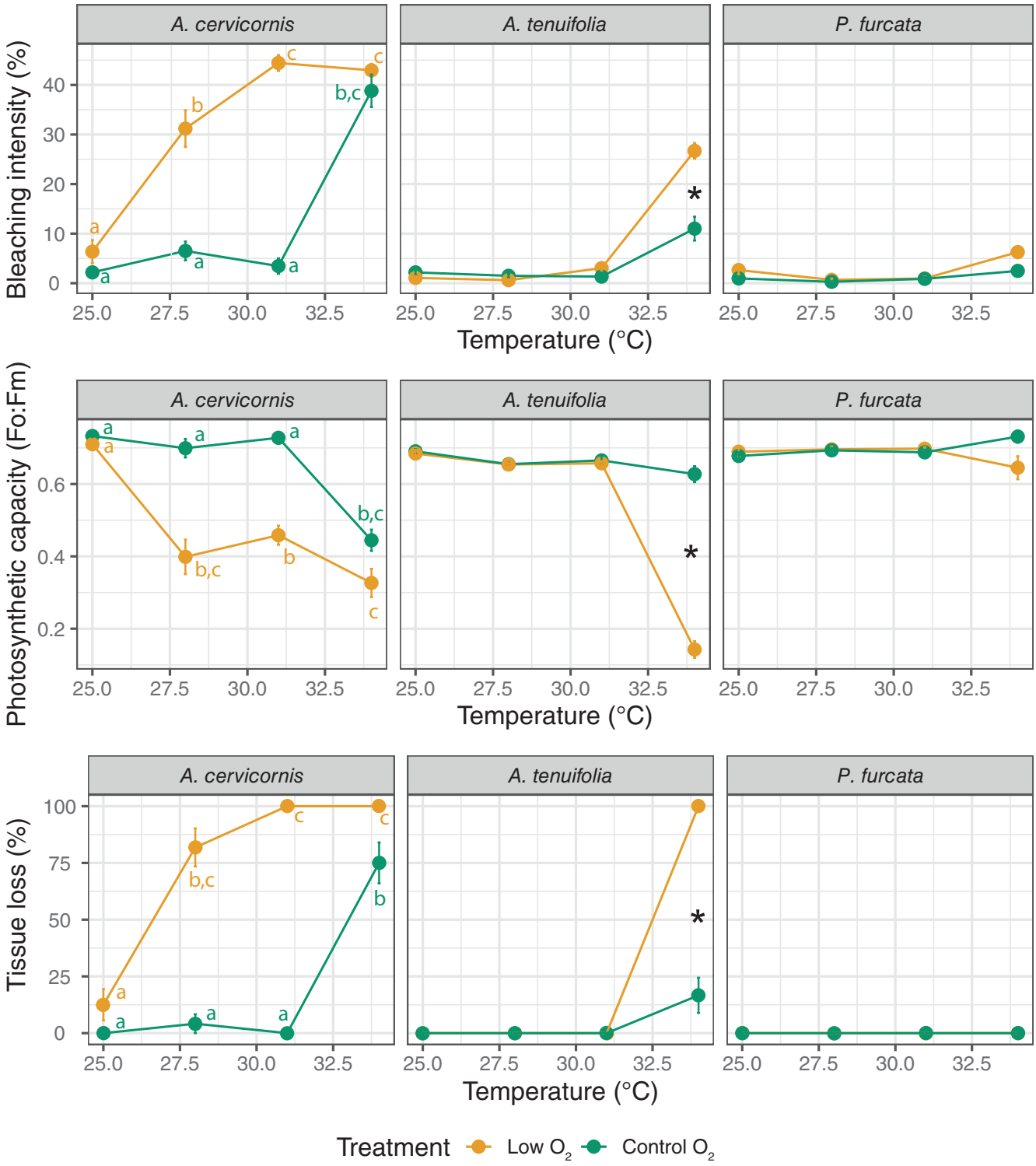

FIGURE 3 | Low O_2 is the primary driver of coral bleaching and mortality, with species-specific amplification from warming. Dark 6-h experiments exposing corals to a single night of low O_2 at temperatures ranging from 25°C to 34°C show *A. cervicornis* is the least tolerant species. In *A. cervicornis*, low O_2 at ambient temperatures ~28°C, resulted in a 50% reduced photosynthetic capacity, which then led to 72% mortality. Low O_2 combined with moderate warming to 31°C, resulted in 100% mortality (Column 1). *Agaricia tenuifolia* was also sensitive to low O_2, but only at the highest temperature tested: 34°C (Column 2). In contrast, *P. furcata* was the most physiologically tolerant of every combined O_2 and temperature combination, with no evidence of stress in any treatment (Column 3). Points and error bars show mean ± SE. Different letters within the *A. cervicornis* plots indicate statistically significant differences between O_2 treatments and temperatures ($p < 0.05$). Asterisks within the *A. tenuifolia* plots indicate statistically significant differences between the control and low O_2 treatment at 34°C (no other temperatures tested due to the lack of responses).

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3.3 | Experiment 2: Cumulative Nightly Low O_2 Increases the Coral Stress

To identify the duration of low O_2 that causes physiological stress in each species, i.e., hypoxia, we exposed corals to chronic and repeating nightly low O_2 for 5 days (1 mg L^{-1} at 28.5°C). Overall, chronic low O_2 resulted in the most bleaching and mortality, compared to repeated nightly low O_2 for both *A. tenuifolia* and *A. cervicornis* (Figure 4, Table S3, $p < 0.001$ across traits and species).

In comparison to chronic low O_2, the onset of bleaching was faster in the nightly low O_2 treatment. Approximately 25% of *A. cervicornis* fragments bleached after the first low O_2 night (Figure 4, Table S3, $p = 0.016$). All affected fragments died the following day (complete tissue loss). *Agaricia tenuifolia* exposed to nightly low O_2 had a similar response, but initial bleaching started after the second night and affected fewer fragments (~13%, Table S4). After four nights of low O_2, ~35% of *A. tenuifolia* fragments died ($p < 0.001$), and ~50% of *A. cervicornis* fragments died ($p = 0.041$).

In contrast, all *P. furcata* fragments remained healthy without any bleaching or mortality, regardless of treatment, throughout the full experiment. Based on these findings, we conclude the three species have different time-dependent hypoxic thresholds, with *A. cervicornis* sensitive to one night, *A. tenuifolia* to 3–5 nights, and *P. furcata* tolerant to more than five nights of low O_2.

Two additional findings from this experiment provide further insight into species' responses to low O_2. First, site of origin was significant for *A. tenuifolia*, but not the other two species. Bleaching and mortality responses in *A. tenuifolia* colonies collected from the inner bay reef were 15%–25% less severe than in colonies from the more well-oxygenated, intermediate site, in either chronic or nightly low O_2 treatments (Figure S6, Table S4). This suggests the *A. tenuifolia* inner bay population may be locally adapted to O_2 depleted environments. Secondly, low O_2-driven bleaching in both *A. tenuifolia* and *A. cervicornis* fragments was coupled with tissue sloughing and next-day mortality in 71% of the fragments. In these two species, the

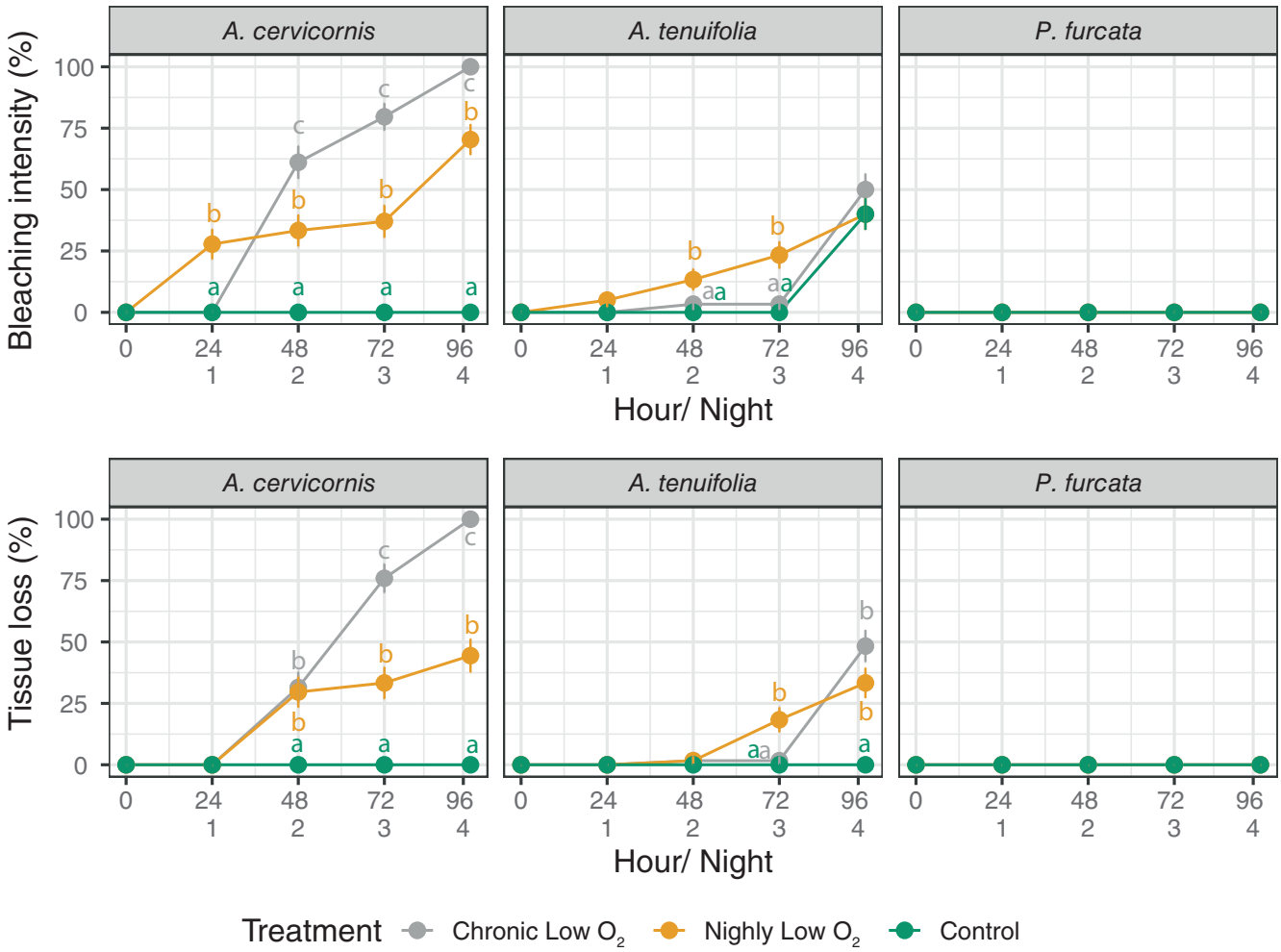

FIGURE 4 | Repeated nightly low O_2 increases stress responses in *A. cervicornis* and *A. tenuifolia*. A single night of low O_2 caused ~25% of *A. cervicornis* fragments to bleach, and bleaching progressively increased with repeated nightly low O_2 (orange lines; left column). *Agaricia tenuifolia* fragments withstood the same stress for three nights before a similar ~25% bleaching response was observed (orange lines, middle column). Chronic low O_2 resulted in the most severe bleaching and mortality for both affected species, with twice as many fragments dying after 96 h (gray lines). *Porites furcata* showed no signs of stress at any point during the experiment (last column). Points and error bars show mean ± SE when traits were assessed. Different letters next to points indicate statistically significant differences between treatments (colored, or white showing paired treatment effects), within a given day ($p < 0.05$).

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physiological endpoints for corals exposed to low O_2 appear to be rapidly precipitating bleaching with patchy tissue loss and next day mortality (Figure S3).

3.4 | Hypoxic Bleaching Pressure on Reefs Predict Species' Distributions

To relate these laboratory responses across species to the community composition across reefs, we first counted all *in situ* hypoxic events on each reef during the 2-year monitoring period. Hypoxic events are defined as nights with $O_2 < 1\,mg\,L^{-1}$, which we know can cause coral stress from Experiment 2 results (Figure 5a). We found hypoxic events were most common on the inner bay reef, where a total of eight events ranging in durations of 1–2 nights occurred (Figure 5b). The longest event was four nights and occurred on the intermediate reef, however it was the only event measured during this period at that site. Only two events occurred on the outer bay reef, each for only one night (Table S5).

We then coupled these hypoxic event counts and their durations with species' experimental bleaching responses, i.e., Figure 5a, and calculated the expected hypoxic pressure each species sustained on each reef (Equation 1, Figure 5c, Table S5). *Porites furcata* experienced no pressure, as it did not demonstrate any bleaching or mortality during the experiments. Pressure for *A. cervicornis* was highest on the inner bay, followed by the intermediate reef, and lowest on the outer bay reef where it is still living. *Agaricia tenuifolia* pressure was highest on the intermediate reef where the longest event occurred, i.e., four consecutive nights of hypoxia, and lowest on the outer bay reef. We found these hypoxic pressure values closely mirrored both *A. tenuifolia* and *A. cervicornis* distribution across the three primary reefs (Figure 1b). Furthermore, species abundance across all six sites was negatively correlated with hypoxic pressure for both affected species ($p = 0.026$, $n = 6$), implying species distribution is related to hypoxia pressure on these reefs (Figure 5d). This provides a physiological hypothesis for why these reefs have differing community compositions.

With this physiological hypothesis, *P. furcata* should be able to thrive on every reef because it has the highest hypoxia tolerance. But we found 7% fewer *P. furcata* colonies on the outer bay reef where environmental conditions are least stressful compared to the inner bay (Figure 1). Survey data offer the possibility this is from interspecific ecological relationships that mediate *P. furcata* distribution. This is demonstrated in the weak negative correlation whereby the percentage of *P. furcata* declines marginally with increasing *A. tenuifolia* and *A. cervicornis* abundance across the four reefs (Figure 5e, $p = 0.087$, $n = 4$). This suggests *P. furcata* may be a poor competitor on increasingly cool oxygenated reefs where the fight for light, food and ultimately space on the reef involves more successful benthic competitors.

4 | Discussion

This study identifies low O_2 as an important factor shaping the composition of coral reefs. The framework-building species *Acropora cervicornis* was unable to physiologically endure a single night of low O_2. This explains its absence on the inner bay reef, where similar nocturnal O_2 conditions occurred eight times during the last 2 years. The low-profile species *Agaricia tenuifolia* was more tolerant and persisted under low O_2 conditions for more than three nights. *Porites furcata,* another low profile species, was the most tolerant of the three species. It was also the dominant species on the inner bay reef. By integrating these laboratory responses with field measurements, we found exposures to nightly low $O_2 < 1\,mg\,L^{-1}$ offer an explanation for why shallow reefs in Bahía Almirante are dominated by homogeneous low-relief coral communities instead of highly structured communities comprised of *A. cervicornis*.

Low O_2 appears to be the main driver of coral bleaching and mortality, not temperature. Laboratory experiments demonstrate this primarily in *A. cervicornis*. After 6 h of low O_2 at ambient temperatures, *A. cervicornis* colonies started dying in our experiments. A similar response was found for colonies in Florida at a slightly lower temperature 26.6°C (Johnson, Swaminathan, et al. 2021). Even at higher O_2 concentrations, one day of low O_2 exposure without additional warming caused stress in three different acroporid species from the Indo-Pacific and Great Barrier Reef (Alderdice et al. 2021; Deleja et al. 2022; Haas et al. 2014). While warming was not nessesary to see *A. cervicornis* stress responses to low O_2, it is important to note that warming does amplify species' hypoxic sensitivity. Studies on different marine invertebrates attribute temperature-dependent hypoxia sensitivity to increasing metabolic rates and concurrent decreasing O_2 supply, which typically decreases organismal hypoxia tolerance (Deutsch et al. 2015). This temperature-dependent hypoxia response is expected to be an added challenge for coral reefs under future warming (Lucey et al. 2023) and requires further investigation. However, in the warmest parts of the acroporid species' distributions, like Bahia Almirante, O_2 concentrations coupled with typical current temperatures (i.e., 27°C–31°C), are already problematic.

This small but growing body of research widely agrees that acroporids are highly sensitive to low O_2, but studies on other coral species are less common. Sensitivities to low O_2 in our study's weedy species agree with previous results for their congeners. Responses of *A. tenuifolia* colonies were roughly comparable to those of *Agaricia lamarcki*, which was able to survive low O_2 conditions for 5–7 days (Altieri et al. 2017). *Porites* spp. from the Red Sea showed no signs of sublethal bleaching after 10 days at $1.25\,mg\,L^{-1}$ (Alva García et al. 2022). This provides further consensus that acroporids are highly sensitive, followed by *Agaricia* and then *Porites*, and that this sensitivity is primarily dependent on the duration of hypoxia exposure each species can withstand.

The time corals can persist under hypoxia seems to be related to the cumulative number of low O_2 nights they experience, regardless of daytime conditions. Diel cycling across tropical reefs consists of nocturnal respiration driving O_2 down at night and photosynthesis bringing it up during the day (Figure 2a; Pezner et al. 2023). Because corals mostly live in saturated or supersaturated waters during the day, and can produce their own internal O_2 supply, they may have a built-in buffer against nightly low O_2 (Giomi et al. 2019). While internal symbiont O_2 production does appear to provide some buffer against daytime low O_2 (Figure S7), it does not help stony corals cope at night (Haas et al. 2014;

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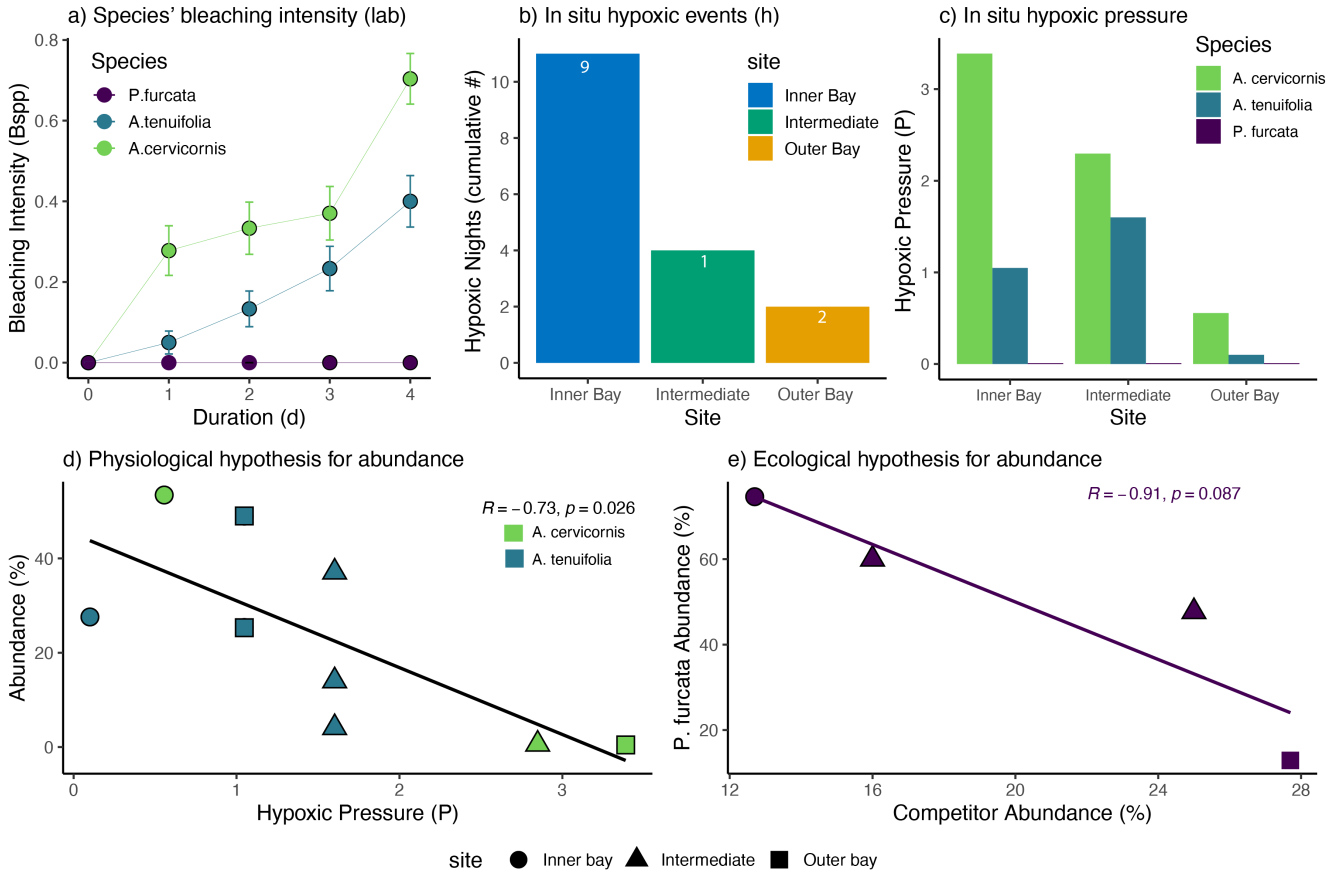

FIGURE 5 | Hypoxic events on reefs drive species abundance and community composition. (a) Bleaching intensity measured from fragments experimentally exposed to low O_2 for four consecutive nights (Exp. 2; Figure 4), with mean values representing B_{spp} in the hypoxic pressure metric. (b) The number of consecutive hypoxic events measured on each site. Events are defined as any night where $O_2 < 1.0\,mg\,L^{-1}$ (h) and the number of events per site are indicated in white text above bars. Event duration is the number of consecutive low O_2 nights per event (Table S5). (c) Hypoxic pressure sums the expected species' bleaching responses (a) from *in situ* hypoxic events during the 2-year monitoring period (b), given their duration and frequency. (d) Coral abundance, as a percentage of all living stony corals, tends to decrease with increasing pressure for the two impacted species, *A. cervicornis* (green shapes) and *A. tenuifolia* (blue shapes), providing a potential physiological hypothesis for species distribution. (e) In contrast, *Porites furcata* tends to progressively become less abundant on reefs compared to its two more hypoxia-sensitive coral competitors. This provides an ecological hypothesis for species' distribution differences. Reef sites in (d, e) are grouped into one of the three main reef zones (inner bay, intermediate, outer bay) based on proximity to the logger location.

Wijgerde et al. 2014). It also does not explain the detrimental effects we observed in *Agaricia* and *Acropora* when exposed to repeated nightly low O_2 and daily O_2 saturation (Figure 4). Accrued stress from repetitive nightly low O_2 (and daily O_2 saturation) has also been seen in coral host enzymes related to anaerobic metabolism, such as alanopine and strombine dehydrogenase activity, which both increased through a week-long exposure (Murphy and Richmond 2016). If the expression of cellular processes that clear these byproducts are only functional at night, i.e., hypoxia-inducible factor HIF-α (Alderdice et al. 2021; Levy et al. 2011), nighttime hypoxia will remain uncoupled from daytime hypoxia. More efforts to identify the physiological mechanisms behind these hypoxia-mediated responses are needed.

Ecological mechanisms appear to play a secondary role in shaping species distribution and abundance on these reefs. Prohibitive seafloor shading from large arborescent canopies of *A. cervicornis* colonies have made this species an effective competitor in many types of reef environments, including those with high light and low water flow (Baird and Hughes 2000), like the inner bay reef sites in this study (Adelson et al. 2022; Clark et al. 2022). But, with the physiological exclusion of *A. cervicornis* colonies from reefs with increasingly frequent hypoxic events, there appears to be a competitive release where the weedier, hypoxia tolerant coral species can thrive (Aronson et al. 2014; Ladd, Shantz, and Burkepile 2019). This change is highly visible in the inner bay reef, and throughout nearby shallow reefs in Bahia Almirante, where short statured, competitively subordinate weedy species form extensive table-like mats. Attributes of these weedy coral communities include reduced stony coral richness and increased soft corals, sponges and zoanthids (Figure S4, Table S1), and are associated with lowered reef architectural complexity, reduced carbonate production, and a measured loss of reef habitat, as well as lower fish and invertebrate diversity (Graham and Nash 2013; Perry et al. 2015). Hypoxia-mediated assemblages are also associated with higher temperatures, nutrient loads, lower flow rates, and increased pH variability (D'Croz, Del Rosario, and Gondola 2005; Lucey, Haskett, and Collin 2020). This will likely make it even more difficult for *A. cervicornis* to return to these reef communities.

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The implications for future low O_2 reef communities are apparent in looking at the trajectory of past community changes. A century ago, a reduction of coral biodiversity and increased dominance of the weedy species *P. furcata* was attributed to nutrient-driven low O_2 close to our inner bay site (Figure 1a, gray circle labeled 'TO' denoting Tierra Obscura) (Figuerola et al. 2021). These changes were followed by 100 years of slowed reef accretion rates, irreversible regime shifts, and ultimately complete reef shutdown, with all coral species ceasing to grow. More recently all three reefs in our current study had living *A. cervicornis*. But in September 2017, every colony died from low O_2 on the inner bay reef (Johnson, Scott, et al. 2021). Today we find *A. cervicornis* has been almost entirely extirpated from Bahía Almirante (Figures 1 and S4), with nightly low O_2 regularly surpassing its hypoxic threshold. This evidence not only emphasizes the likelihood that low O_2 has already caused coral community changes, but it also highlights the urgency of addressing future low O_2 to halt further changes.

Our findings indicate low oxygen is an important driver of coral reef simplification and community transitions to dominant low-relief coral taxa. Drawing on lessons from oxygen-deplete temperate coastalsystems can help guide efforts to reduce these impacts in tropical systems. This includes enacting strategies that reduce the amount of coastal nutrients from land-based activities, such as agriculture and waste-water management, as well as protecting mangroves against deforestation (Diez et al. 2019; Sanger et al. 2010). Efforts to mitigate low O_2 at local and regional scales can be successful (Kemp et al. 2009). These strategies should be considered high priorities for reducing the extirpation risk of hypoxia-sensitive species, such as acroporids, from tropical coral reefs.

Author Contributions

Noelle M. Lucey: conceptualization, data curation, formal analysis, investigation, methodology, project administration, resources, supervision, validation, visualization, writing – original draft, writing – review and editing. **Carolina César-Ávila:** data curation, investigation, methodology, writing – review and editing. **Alaina Eckert:** data curation, investigation, writing – review and editing. **Anushka Rajagopalan:** data curation, investigation, writing – review and editing. **William C. Brister:** data curation, investigation, writing – review and editing. **Esme Kline:** investigation, methodology, writing – review and editing. **Andrew H. Altieri:** funding acquisition, resources, writing – review and editing. **Curtis A. Deutsch:** conceptualization, data curation, resources, writing – review and editing. **Rachel Collin:** funding acquisition, project administration, resources, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All environmental, ecological, and experimental data associated can be found at https://doi.org/10.6084/m9.figshare.27188436.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.

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