Coral Reefs
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RESEARCH

Acroporids in northwestern Philippines with varied thermotolerance host similar photosymbionts

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Abstract Coral reefs worldwide are threatened by rapid warming of the oceans, yet many corals persist despite thermal stress. Reefs in northwestern Philippines are frequently exposed to elevated temperatures (maximum monthly mean sea surface temperature of 29–30 °C, based on long-term records), presenting an opportunity to examine intercolony variation in thermotolerance among coral populations exposed to thermal stress. Whether this variation correlates with the identity of Symbiodiniaceae, the coral's microalgal symbiotic partner, remains an important question for understanding the mechanisms underlying coral thermal resilience. In this study, we assessed the thermotolerance of individual colonies of three *Acropora* species, *A. digitifera*, *A. millepora*, and *A.* cf. *tenuis*, from a reef in Anda, Pangasinan, Philippines, using controlled heat-stress assays to evaluate survival and bleaching response. Thermotolerance varied within and among species, yet ITS2 metabarcoding of Symbiodiniaceae communities revealed that the corals host four closely related strains of *Cladocopium patulum* (formerly referred to as "type C3u"). Inter- and intraspecific differences in thermotolerance did not show strong correlation with symbiont composition. These findings suggest that while Symbiodiniaceae communities may contribute to heat resilience in corals, they do not solely explain the marked difference in thermotolerance among individuals.

Keywords *Acropora digitifera* · *Acropora millepora* · *Acropora* cf. *tenuis* · Heat tolerance · ITS2 metabarcoding · Bolinao-Anda Reef Complex (BARC)

Introduction

Coral reefs are among the most productive ecosystems on earth and are hotspots of biodiversity supporting an estimated one million multicellular species that inhabit coral reefs (Fisher et al. 2015). Healthy reefs are vital providers of ecosystem goods and services to human populations in tropical and subtropical regions (Cinner et al. 2012; Hoegh-Guldberg et al. 2018). Despite their great importance, coral reefs are rapidly declining due to extreme and abrupt changes in the environment, including, but not limited to, global warming, ocean acidification, destructive fishing, pollution, and the introduction of exotic species (Hughes et al. 2017, 2018; Eddy et al. 2021). Among these, the rapid rise of seawater temperature due to global warming is the biggest threat to these valuable ecosystems (Oliver et al. 2019; Eddy et al. 2021).

Like other multicellular organisms, corals are holobionts, ecological units that integrate the host and its associated microorganisms (Baedke et al. 2020). The coral host forms close associations with microeukaryotes (e.g., fungi, dinoflagellates, apicomplexans), archaea, bacteria, and viruses

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that work together or against each other depending on the environment (van Oppen and Nitschke 2022). Among these microorganisms, dinoflagellate microalgae in the family Symbiodiniaceae (colloquially known as zooxanthellae) provide the majority of nutritional and energetic requirements of the host in return for a habitat with stable light conditions and vital (micro)nutrients (Falkowski et al. 1984; Trench 1993; Voolstra et al. 2021; Wiedenmann et al. 2023).

Different coral-Symbiodiniaceae pairings are linked to distinct holobiont phenotypes. Thermotolerant species are often dominated by *Durusdinium*, whereas thermosensitive taxa, such as Indo-West Pacific acroporids, are typically dominated by *Cladocopium* (Qin et al. 2019; Torres et al. 2021). Despite their general sensitivity, acroporids can alter their photosymbionts in response to stressors. For example, on the Great Barrier Reef, *Acropora millepora* symbionts were shown to shift from *Cladocopium* to *Durusdinium* following temperature-induced bleaching (Berkelmans and van Oppen 2006). Similarly, *Pocillopora* symbionts were reported to change from *C. latusorum* to *D. glynii* after a mass bleaching event (Palacio-Castro et al. 2023). However, while *Durusdinium* is often linked to enhanced thermal tolerance, corals that associate with it often exhibit reduced growth rates due to lower nutritional provision by the symbiont under normal temperature levels (Abrego et al. 2008; Cantin et al. 2009; Wall et al. 2020), although there are exceptions (Kemp et al. 2023; Turnham et al. 2023). Aside from *Durusdinium*, some members of *Cladocopium* have been correlated with increased coral thermotolerance. For example, corals in the Persian/Arabian Gulf, where temperatures can reach 36 °C, are usually associated with *Cladocopium thermophilum* (Hume et al. 2015). Thermotolerant *Acropora* in the South China Sea were also found to associate with *Cladocopium* spp. (Gong et al. 2019; Ip et al. 2022). Nonetheless, symbiont associations alone may not fully account for variation in coral thermal tolerance, which can also be shaped by acclimatization history, interactions with other holobiont partners, and host traits (van Woesik et al. 2022).

Host traits and photosymbiont type may explain why differences in thermal tolerance are often observed even within the same coral population, and sometimes among individuals found in the same reef area. For example, in an American Samoan reef (< 100 km^2) exposed to slightly higher temperatures, some individuals of *Acropora hyacinthus*, *A. gemmifera*, *Pocillopora damicornis*, and *Porites cylindrica* exhibited better thermal tolerance compared to others (Morikawa and Palumbi 2019). Similar patterns were observed in *A. hyacinthus* (Naugle et al. 2024) and *A. spathulata* (Denis et al. 2024) from the Great Barrier Reef where thermotolerance varied among conspecific colonies within and among reefs. Variation was also recorded in *Montipora capitata* individuals from a small reef patch in Hawaii (Stat et al. 2011; Drury et al. 2022), as well as in *A. digitifera* and *A. hyacinthus* from small reef patches in Palau where differences in survival under controlled heat-stress experiments were observed (Cornwell et al. 2021; Humanes et al. 2022). Such within-population differences in thermotolerance may arise from host genetic factors that shape colony phenotypes (e.g., colony size, tissue thickness, skeletal density) (Brown 1997; Enríquez et al. 2005; Voolstra et al. 2021; Shah et al. 2022) or from symbiont community composition (Kavousi et al. 2020; Drury et al. 2022).

Understanding coral and photosymbiont thermotolerance is especially important because reefs in the Coral Triangle are rapidly declining due to rising sea surface temperatures and recurring summer heatwaves that cause bleaching (Peñaflor et al. 2009; McLeod et al. 2010; Mellin et al. 2024; Handiani et al. 2025). The Bolinao-Anda Reef Complex (BARC) in the northern West Philippine Sea region of the South China Sea has experienced several widespread bleaching events over the past decades (Yap et al. 1992; Arceo et al. 2001; Kleypas et al. 2015; Quimpo et al. 2020), yet some colonies continue to persist (Harrison et al. 2021), suggesting variation in thermal resilience among individuals and species. Whether this variation in thermal tolerance among individuals and closely related species is primarily associated with photosymbiont composition, host factors, or an interplay of the two remains an open question.

To examine coral thermotolerance and its link to Symbiodiniaceae community composition, we conducted short-term heat-stress assays on three species of acroporids, *Acropora digitifera*, *A. millepora*, and *A.* cf. *tenuis,* and profiled their associated Symbiodiniaceae using ITS2 metabarcoding. By focusing on a reef repeatedly affected by thermal stress, this study contributes to ongoing efforts to understand coral-symbiont relationships and their role in thermotolerance across multiple species and regions within the Coral Triangle.

Materials and methods

Coral collection

Thirty healthy colonies each of *Acropora* cf. *tenuis* and *A. millepora*, and 40 colonies of *A. digitifera* from a depth of 4–5 m in Anda, Pangasinan, northwestern Philippines (16.31487° N, 120.03128° E), were haphazardly selected and marked using small stainless steel tags. To increase the likelihood of obtaining different genotypes, colonies at least 5 m apart were chosen (Howlett et al. 2024). Colonies were considered healthy if they showed no visible signs of bleaching or tissue sloughing (i.e., detachment of coral tissue from skeleton, observed as exposed white skeleton without overlying tissue). Collections were conducted with permission

from the Philippines Department of Agriculture Bureau of Fisheries and Aquatic Resources (DA-BFAR Gratuitous Permit No. 0169-19 and 0324-24). A small piece containing at least 20 branches was collected from each colony using a hammer and chisel. Coral pieces were transported to the outdoor hatchery of the Bolinao Marine Laboratory where they were held in flow-through seawater tanks maintained at ~ 29 °C (Fig. S1 and Table S1) for a day until fragment preparation. The same tank was used for each species and was cleaned between each run. Sixteen fragments (~ 3 cm in length) were cut from the apical branch tips of each colony and attached to cement nubbin holders using cyanoacrylate glue (Dizon et al. 2008). Nubbins (1600 in total) were labeled with small plastic tags to enable tracking of parent colonies.

Heat-stress assays

Coral fragments attached to fragment holders ($n = 16$ per colony) were randomly placed into eight (8) 40-L plastic tanks (4 control and 4 heat-stress tank replicates) supported with artificial lighting (100 µmol m^{-2} s^{-1}) on a diel cycle (12:12 light–dark cycle), continuous seawater flow, and thermostat-regulated seawater temperature. All the coral fragments were initially acclimated at 29 °C (maximum monthly mean sea surface temperature, MMM, at the Bolinao-Anda Reef Complex) (Quimpo et al. 2020) for 3 days. The tanks were then heated slowly (ramping) by 1 °C a day, until 33 °C was reached. This temperature, which is 3–4 °C above the MMM, was used to induce bleaching. Fragments were maintained at this temperature until the end of the experiment. The duration of the short-term heat-stress assays (Grottoli et al. 2021) varied across species and was terminated when 15–30% of fragments displayed mortality (4 days for *A. millepora* and *A.* cf. *tenuis;* 7 days for *A. digitifera*). In this study, mortality was defined as loss of all coral tissue with no intact tissue remaining on the coral skeleton (Humanes et al. 2024). During the exposure period, the coral fragments were observed at least thrice daily (morning ~ 09:00, midday ~ 12:00, and late afternoon ~ 16:00) to monitor health status and mortality. Colonies that showed signs of bleaching or mortality in the control tanks were excluded from the final analysis to avoid confounding factors unrelated to heat stress. To verify that the laboratory conditions were stable throughout the course of the experiment, temperature and pH were checked using a handheld meter (LAQUAact-PC110, Horiba, UK) (Fig. S2 and Table S2) thrice daily in addition to the data collected by submersible HOBO loggers (Onset, USA) placed in each tank. Coral fragment color was documented at the start (pre-exposure) and end (post-exposure) of the experiment using a Tough TG-5 Waterproof Digital Camera (Olympus, USA) with black, white, and coral color reference cards (Siebeck et al. 2006) to capture subtle, quantitative changes in tissue coloration.

Survival analysis

Kaplan–Meier (KM) survival analysis (Kaplan and Meier 1958) was used to compare survivorship among *Acropora* species subjected to heat stress, as it allows analysis of time-to-event data and accommodates censored observations (i.e., fragments still alive at the end of the experiment). KM survival curves were made using the GGally package (Schloerke et al. 2018) to visualize the data and log-rank tests were done to compare survivorship among species. This nonparametric approach incorporates exact survival times (i.e., time until a fragment is recorded as dead) and has been used in studies that evaluated survival of coral fragments or individuals over time (Dizon and Yap 2006; Hazraty-Kari et al. 2022).

Thermotolerance classification of colonies

Classification of thermotolerance of conspecific *Acropora* colonies was based on (1) incidence of mortality (IOM), (2) fragment color change ($\%\Delta C$), and (3) colony stress index (CSI) which is the combination of both (1 & 2). IOM is based on direct counts of dead fragments observed at the end of the experiment, $\%\Delta C$ is a quantitative measure of bleaching based on photographs taken of each fragment before and after heat exposure, while CSI is the total value of normalized IOM and normalized average fragment color change ($\%\Delta C_{ave}$).

Incidence of mortality

Incidence of mortality (IOM) was computed by dividing the number of dead fragments (n) by the total number of fragments (N) subjected to high temperature per colony, multiplied by 100%. Dead fragments were defined as those that had completely sloughed off tissue from the skeleton.

$$\text{IOM} = \frac{n}{N} \times 100\%$$

Colonies with IOM greater than or equal to 50% were tagged as thermosensitive (S), while those with less than 50% were tagged as thermotolerant (T). Because of the gradual temperature ramping and short duration of exposure, colony mortality was generally low and many colonies had the same ranking.

Fragment color change

Color change in heat-stressed fragments was estimated using mean gray values (Mclachlan and Grottoli 2021). Images of

the coral fragments were converted to gray scale, and the mean gray value (MGV) of each heat-stressed fragment (M_F) was measured using ImageJ. To account for differences in image brightness, the MGV of a 1 cm^2 white standard (M_s) was measured for each photo. Normalized MGV (nMGV) was computed by dividing fragment MGV (M_F) by the standard MGV (M_S) multiplied by 100%.

$$\text{nMGV} = \frac{M_F}{M_S} \times 100\%$$

To get percent color change ($\%\Delta C$), initial nMGV (nMGV_i; from pre-exposure fragment images) was subtracted from final nMGV (nMGV_f; from post-exposure fragment images) then divided by nMGV_i.

$$\%\Delta C = \frac{\text{nMGV}_f - \text{nMGV}_i}{\text{nMGV}_i} \times 100\%$$

Percent color change per fragment ($n = 8$) was averaged per colony ($\%\Delta C_{\text{ave}}$). Higher values reflect increased bleaching severity, indicated by fragments becoming visibly whiter. Colonies were ranked based on their $\%\Delta C_{\text{ave}}$ with the top 20% of the sampled population classified as thermosensitive and the bottom 20% as thermotolerant, ensuring that the worst and best performing colonies were identified for subsequent analyses.

Colony stress index

To obtain a representative measure of the coral heat-stress response, IOM and $\%\Delta C_{\text{ave}}$ were combined per colony per species. Spearman correlation was first used to assess association between IOM and $\%\Delta C_{\text{ave}}$ across species, as bleaching (color loss) does not always equate to mortality. IOM and $\%\Delta C_{\text{ave}}$ were then merged into a single metric by getting the sum of each measure normalized to their respective minimum and maximum values per species.

$$\text{Normalized IOM or } \%\Delta C_{ave} = \frac{x - x_{\min}}{x_{\max} - x_{\min}}$$

The sum of normalized IOM and $\%\Delta C_{\text{ave}}$, colony stress index (CSI), was then used to classify colony thermotolerance based on their ranks per species. The bottom 20% of colonies with least change relative to original phenotypes were classified as thermotolerant and the top 20%, with the most change, as thermosensitive.

$$\text{CSI} = \text{normalized IOM} + \text{normalized } \%\Delta C_{\text{ave}}$$

To compare thermotolerance characteristics of all acroporid colonies regardless of species, incidence of mortality of all colonies (IOM_{all}) was derived by min–max normalization of IOM values of all colonies at day 10 of the experiment (four days at 33 °C). Similarly, the percent color change of all colonies ($\%\Delta C_{\text{all}}$) was obtained by min–max normalization of $\%\Delta C_{\text{ave}}$ values. The colony stress index of all colonies (CSI_{all}) was computed as the sum of IOM_{all} and $\%\Delta C_{\text{all}}$.

DNA extraction and PCR

Prior to thermal stress experiments, two fragments (~ 3 cm) were sampled from each colony and fixed in 5 mL of 100% ethanol. Tissue was collected from these fragments using an airbrush with 0.2 µm-filtered artificial seawater. Tissue slurries were stored on ice until DNA extraction. The coral slurry was centrifuged for 5 min at 10,000 g at 4 °C. The seawater was removed, and the pellet was resuspended in 400 µL of complete 2% CTAB buffer (Murray and Thompson 1980). Cells were lysed by incubation for an hour at 60 °C; then, 400 µL of chloroform:isoamyl alcohol (24:1) solution was added. The solution was vigorously mixed by hand for 2 min then centrifuged at 10,000 g at 4 °C for phase separation. The aqueous phase was transferred into a fresh tube, and 600 µL of isopropanol was added. DNA was precipitated for 2–3 h on ice then pelleted by centrifugation at 12,000 g at 4 °C for 30 min. The pellet was washed twice with 1 mL cold 70% ethanol and centrifuged at 10,000 g at 4 °C for 10 min. The pellet was resuspended in 25–50 µL ultrapure, nuclease-free water. DNA quality was checked by agarose gel electrophoresis and quantity was measured using a Qubit 3.0 fluorometer (Thermo Fisher Scientific, USA). Genomic DNA samples were stored at − 20 °C.

Identification of symbiont communities

ITS2 libraries were constructed using the Herculase II Fusion DNA Polymerase Nextera XT Index Kit V2 (Agilent Technologies, Santa Clara, CA, USA) and the primer pair ITSintfor2 (GAATTGCAGAACTCCGTG) (Coleman et al. 1994) and ITS-reverse (GGGATCCATATGCTTAAG TTCAGCGGGT) (LaJeunesse 2002). Libraries were subjected to paired-end, multiplexed sequencing at Macrogen, South Korea, using the MiSeq platform to generate 300 base pair reads (Illumina, USA). Raw sequence data were deposited in the NCBI Sequence Read Archive under BioProject accession number PRJNA1295142. The SymPortal pipeline (Hume et al. 2019) was used to analyze the resulting ITS2 sequences and to identify the Symbiodiniaceae community present in the acroporid samples. SymPortal is a bioinformatic pipeline that identifies the putative taxa within a Symbiodiniaceae community from ITS2 amplicon data. By considering the intragenomic diversity in every Symbiodiniaceae genome, SymPortal constructs ITS2 type profiles based on combinations of defining intragenomic

variants (DIVs) (Hume et al. 2019). ITS2 type profiles are often used as proxies for putative genotypes and may, in some cases, reflect clonal symbiont strains, although their identities remain unresolved. Here, we refer to them as "strains" for simplicity, to describe possibly ecologically distinct ITS2 type profiles. The pipeline includes quality-checking steps to increase the reliability of ITS2 sequence annotation and profile prediction (Schloss et al. 2009; Eren et al. 2015; Sayers et al. 2022).

Statistical analyses

All statistical analyses were conducted in R (R Core Team 2023) using RStudio (Posit team 2025). Data handling and plotting were done using the tidyverse suite of packages (Wickham et al. 2019).

Heatmaps and bar plots were generated to visualize the distribution of Symbiodiniaceae-related ITS2 sequences and predicted ITS2 type profiles among the samples. Principal coordinates analysis (PCoA) plots (Gower 2015), weighted UniFrac (Lozupone et al. 2007), and Bray–Curtis dissimilarity (Bray and Curtis 1957) computed from square root-transformed abundance of ITS2 sequences derived from SymPortal were used to visualize compositional similarities or groupings of samples. Weighted UniFrac incorporates both phylogenetic relationships and relative abundances, whereas Bray–Curtis dissimilarity quantifies differences in taxon abundance between samples. Distance-based redundancy analysis (dbRDA) (Legendre and Anderson 1999) was done using the capscale function to explore how ITS2 sequence composition varied with explanatory variables (i.e., IOM_{all}, $\%\Delta C_{all}$, and CSI_{all}). Clustering of coral colonies based on Symbiodiniaceae-related ITS2 sequence composition was checked by permutational multivariate analysis of variance (PERMANOVA) (Anderson 2017) using the adonis2 and the pairwiseAdonis functions (Martinez Arbizu 2020). Dispersion among groups was compared by permutational analysis of dispersion (PERMDISP) (Anderson 2006) using the betadisper function. Bootstrapping was applied to both PERMANOVA and PERMDISP analyses to account for unequal sampling sizes and assess the robustness of group differences and dispersion estimates. To test for differences in thermotolerance metrics among groups, we used the Kruskal–Wallis test (Kruskal and Wallis 1952), followed by Dunn's post hoc pairwise comparisons (Dunn 1964). Rarefaction curves were generated using the rarecurve function to evaluate whether sampling depth was sufficient to capture the diversity of ITS2 sequences across samples. The functions capscale, adonis2, betadisper, diversity, specnumber, and rarecurve are part of the vegan package (Oksanen et al. 2020).

Results

Thermotolerance of *Acropora* species

All colonies of *A. digitifera* ($n = 40$), *A. millepora* ($n = 30$), and *A.* cf. *tenuis* ($n = 30$) survived the pre-exposure stage prior to heat-stress application. All fragments in the control tanks remained healthy, except for five fragments from five different colonies of *A.* cf. *tenuis* that showed bleaching during the experiment (Fig. S3 and Table S3). The colonies from which these fragments originated were excluded from thermotolerance and symbiont community analyses (Table S4).

Thermotolerance among *Acropora* species differed based on incidence of mortality (IOM) (log-rank test P-value < 0.001; Fig. 1a). *Acropora digitifera* showed the highest survival under elevated temperature, followed by *A. millepora*, and *A.* cf. *tenuis* (Fig. 1a, Table 1). Comparison of IOM at day 10 revealed lower IOM_{all} in *A. digitifera* (median = 0, IQR = 0–0) compared to *A. millepora* (0.063, 0–0.34) and *A.* cf. *tenuis* (0.13, 0–0.38) (Fig. 1b, Table S5). Percent color change ($\%\Delta C_{all}$) also differed among species, with *A. digitifera* (0.09, 0.05–0.18) showing lower $\%\Delta C$ compared to *A. millepora* (0.31, 0.25–0.48) and *A.* cf. *tenuis* (0.28, 0.21–0.28) (Fig. 1B, Table S5). Colony stress index (CSI_{all}) was lower in *A. digitifera* (0, 0–0) compared to *A. millepora* (0.38, 0.28–0.78) and *A.* cf. *tenuis* (0.36, 0.21–0.72) (Fig. 1b, Table S5). Considering the outcomes of time-to-event analysis (log-rank test) and common time point metrics (IOM_{all}, $\%\Delta C_{all}$, and CSI_{all}) together, we ranked thermotolerance of the three coral species as follows: *A. digitifera* > *A. millepora* ≥ *A. cf. tenuis*.

Thermotolerance classification of colonies

Although IOM and $\%\Delta C$ showed high correlation (Fig. S4), use of these metrics individually resulted in identification of differing numbers of heat tolerant and heat sensitive colonies. While IOM values showed limited variation due to the short duration of the experiment (Fig. S5 and Table S6), $\%\Delta C$ reflected finer differences among colonies but tended to underestimate bleaching intensity (Fig. S6 and Table S7). Thus, we combined these metrics to address imbalanced grouping and the similarity of IOM rankings among colonies for each species. This merging resulted in a colony stress index (CSI), which was used to make an operational thermotolerance classification scheme. Using this classification scheme, the bottom 20% were categorized as thermosensitive and the top 20% as thermotolerant. This metric yielded the same number of thermotolerant and thermosensitive colonies per species (Fig. 1c and Table S8).

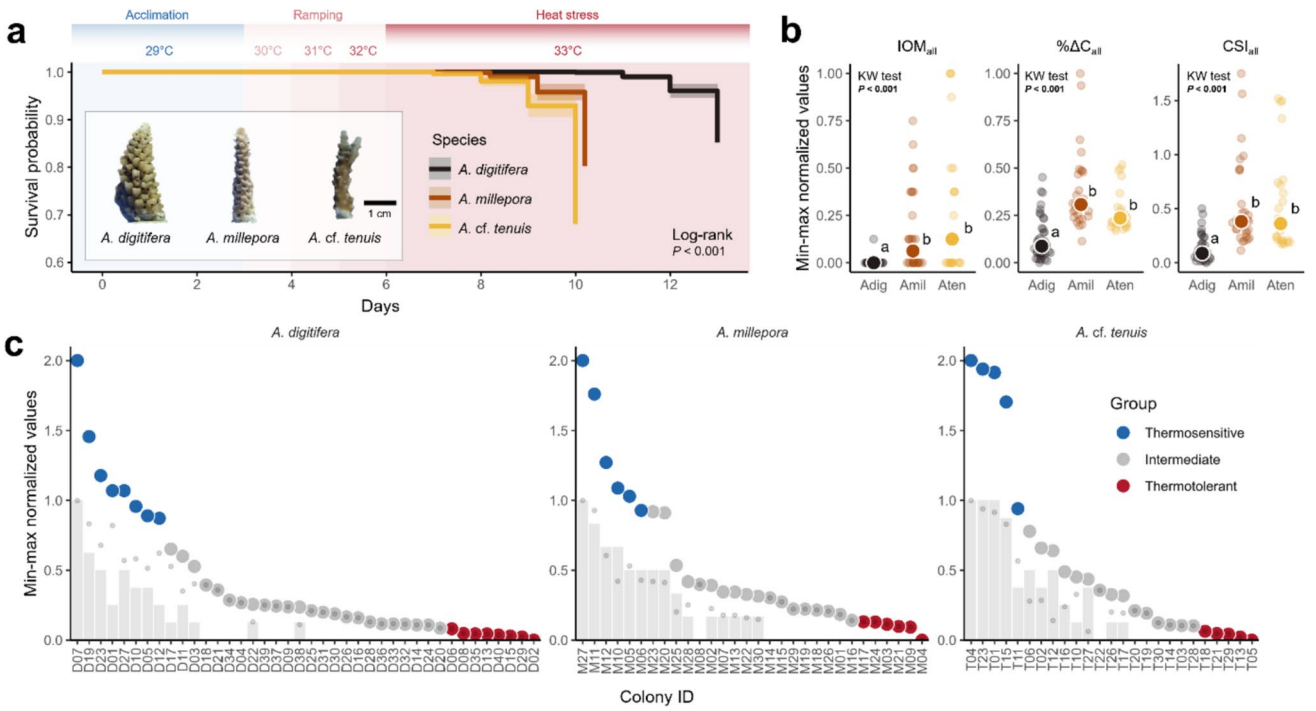

Fig. 1 Interspecific and intraspecific variation of thermotolerance in *Acropora*. **a** Survival probabilities of corals subjected to 33 °C over time. Line colors represent the different species (*A. digitifera*, black; *A. millepora*, brown; *A. cf. tenuis*, yellow). The background color gradient indicates the temperature at each stage of the experiment. The experiment was terminated at day 10 for *A. millepora* and *A.* cf. *tenuis*, and at day 13 for *A. digitifera*. Statistical differences in survival among species were assessed using the log-rank test. The inset shows representative images of coral fragments from each species (scale bar, 1 cm). **b** Min–max normalized incidence of mortality (IOM_{all}), min–max normalized percent color change ($\%\Delta C_{all}$), and colony stress index (CSI_{all}) at day 10 for all species. Big circles represent median values. Statistical differences in thermotolerance metrics among species were determined using Kruskal–Wallis test. Letters to the right of median values indicate significant differences among groups (P-value ≤ 0.05) based on Dunn's test with Benjamini–Hochberg correction. **c** Ranking of colonies based on CSI_{all} (big circles). Colors represent thermotolerance classifications (red, thermotolerant; gray, intermediate; blue, thermosensitive). Bars represent IOM_{all} and small circles represent $\%\Delta C_{all}$

Table 1 Pairwise log-rank test among *Acropora* species with BH-corrected P-values (Q-values). Q-values ≤ 0.05 are highlighted in bold

Group 1	Group 2	Q-value
A. millepora	*A. digitifera*	**< 0.001**
A. cf. *tenuis*	*A. digitifera*	**< 0.001**
A. cf. *tenuis*	*A. millepora*	**< 0.001**

Symbiodiniaceae communities of *Acropora* species and individuals

Out of 8,620,518 raw paired ITS2 sequences, 7,889,145 sequences (mean count of 83,044 ± 12,643) passed quality checking and were classified as Symbiodiniaceae (Fig. S7a). Rarefaction curves plateaued for all samples, confirming that sequencing effort was adequate to capture ITS2 sequence diversity and that comparisons among samples and groups were not biased by differences in sequencing depth (Fig. S7b). Eight defining intragenomic variants (DIVs) were observed, all affiliated with the genus *Cladocopium*. From these DIVs, four ITS2 type profiles dominated by ITS2 type C3u (*Cladocopium patulum*) were constructed: C3u-C3xu-C3-C115, C3u-C3xu-C3-C115-C3xv, C3u-C3-C115-C3xt, and C3/C3u-C115-C21ab-C3ge. *Durusdinium* sequences were also detected but at counts too low to be considered as DIVs (< 200 sequences) (Fig. S8, Table S9).

Overall Symbiodiniaceae composition showed a weak correlation with *Acropora* thermotolerance. Distance-based redundancy analysis (dbRDA) showed a significant but weak relationship between photosymbiont community structure and thermotolerance parameters ($F = 2.834$, $P = 0.0324$), explaining only 5.80% of the variation (Fig. 2a). Among the parameters, only IOM_{all} correlated, albeit weakly, with photosymbiont composition (Table S10). CSI_{all} was collinear with the other parameters and was removed from the analysis. Thermotolerance metrics showed no consistent differences when compared across ITS2 profiles in the combined dataset of all three acroporids, although IOM_{all}, $\%\Delta C_{all}$, and CSI_{all} distributions were marginally skewed to the right for C3u-C3xu-C3-C115 and C3u-C3xu-C3-C115-C3xv

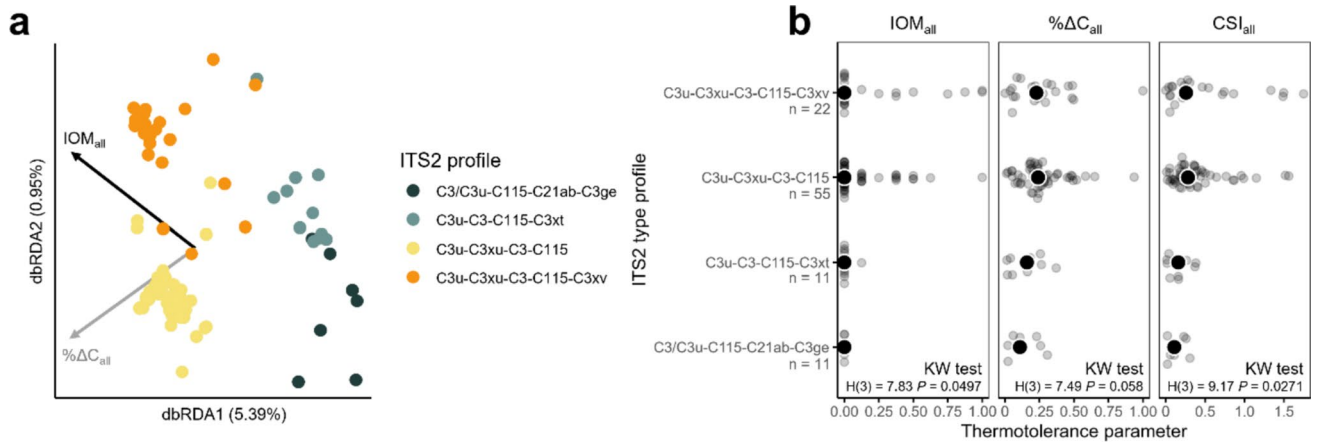

Fig. 2 Symbiodiniaceae composition and *Acropora* thermotolerance. **a** Distance-based redundancy analysis (dbRDA) shows correlation between ITS2 sequence composition (colored by ITS2 profile) and thermotolerance parameters. Black arrow indicates significant correlation with ITS2 sequence composition. **b** Distribution of thermotolerance parameter values across ITS2 profiles. Big circles indicate median values. Statistical differences in thermotolerance metrics among ITS2 type profiles were determined using Kruskal–Wallis test

compared to C3u-C3-C115-C3xt and C3/C3u-C115-C21ab-C3ge (Fig. 2b, Table S11). This suggests that within the Bolinao-Anda Reef Complex, the ability to evaluate direct links between symbiont identity and thermotolerance in acroporids is constrained by the predominance of distinct strains of the same symbiont species, *Cladocopium patulum*.

The composition and diversity of photosymbionts based on ITS2 type profiles did not differ across colonies of the three species. Each coral colony harbored only one *Cladocopium* ITS2 type profile. Four ITS2 type profiles in total were observed across *A. digitifera* and *A. millepora* colonies, while only two were observed in *A.* cf. *tenuis* colonies (Fig. 3a-c). Based on the UniFrac dendrogram (Fig. 3), C3u-C3xu-C3-C115 and C3u-C3xu-C3-C115-C3xv are closely related ITS2 type profiles found in all acroporid species examined. C3u-C3xu-C3-C115 was the most common, present in 16 *A. digitifera*, 21 *A. millepora*, and 18 *A.* cf. *tenuis* individuals, while C3u-C3xu-C3-C115-C3xv was found in eight *A. digitifera*, seven *A. millepora*, and seven *A.* cf. *tenuis*. ITS2 type profiles C3u-C3-C115-C3xt and C115-C21ab-C3ge were detected only in *A. digitifera* and *A. millepora* colonies but were more prevalent in the former species. C3u-C3-C115-C3xt was present in ten *A. digitifera* and one *A. millepora* individual, while C115-C21ab-C3ge was in six *A. digitifera* and one *A. millepora* individual.

The composition of Symbiodiniaceae communities based on all ITS2 sequences differed among the three *Acropora* species (Tables 2 & TabS12, Figs. 3a–c & S9a). *Acropora digitifera* exhibited more within-species variation and distinct ITS2 sequence distribution among colonies (Table 2 and Fig. 3d). This pattern remained robust after controlling for unequal sample sizes (100 bootstrapped PERMANOVA and PERMDISP replicates; Tables S13, TabS14 and Fig. S10). Pairwise comparisons using a single representative iteration, defined as the resample with a pseudo-F statistic closest to the median, confirmed overall interspecific differences (Table S15; Fig. S10). There was no significant difference between *A. digitifera* and *A. millepora*, whereas both species differed significantly from *A.* cf. *tenuis*, which exhibited the most homogeneous symbiont communities.

No clear patterns in Symbiodiniaceae community composition could be discerned between thermotolerant and thermosensitive individuals of each species. Based on ITS2 type profiles, only *A. cf. tenuis* showed segregation of symbionts with thermotolerance. Strain C3u-C3xu-C3-C115 was present in all thermotolerant colonies (5 out of 5) and C3u-C3xu-C3-C115-C3xv was present in 80% of thermosensitive individuals (4 out of 5) (Fig. 4a), which was supported by differences in ITS2 sequence abundances (Fig. 4b, FigS9b-d, and Table 2). However, these two closely related strains were also distributed across colonies of *A. digitifera* and *A. millepora* with varying thermotolerance characteristics. Moreover, *Durusdinium* ITS2 sequences did not correlate with a thermotolerant phenotype in the acroporids, as these were detected mostly in colonies with intermediate tolerance (Fig. S11).

Discussion

Thermotolerance varies among and within species

Short-term thermal stress assays revealed differences in thermotolerance among *Acropora* species and among individuals within each species. Our results were consistent with previous observations on corals from the same site (Da-Anoy et al. 2019), with *A. digitifera* as most

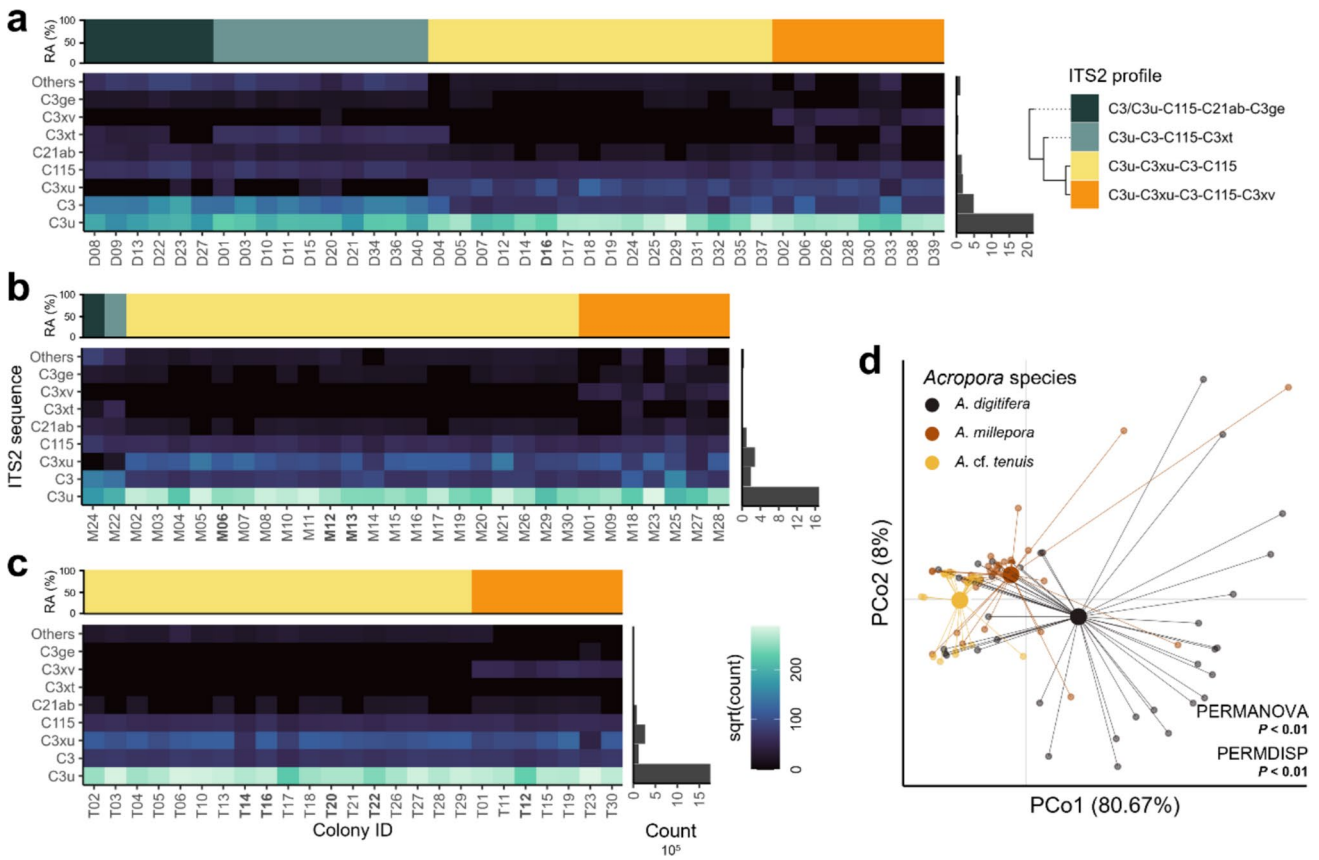

Fig. 3 Symbiodiniaceae composition of **a** *Acropora digitifera*, **b** *A. millepora*, and **c** *A.* cf. *tenuis* colonies. Heatmap colors represent square root-transformed counts of ITS2 sequences in coral colonies. Bar graphs to the right of each heatmap represent total ITS2 sequence counts. The color bar on top of each heatmap denotes relative abundance (RA) of ITS2 type profiles. The dendrogram beside the ITS2 profile legend depicts similarity among ITS2 profiles based on weighted UniFrac. Colony IDs in bold indicate presence of *Durusdinium*-related ITS2 sequences. **d** PCoA plot based on weighted UniFrac of *Cladocopium* ITS2 sequences among *Acropora* species. Colors denote *Acropora* species. Lines depict the distance of each sample (small circles) to the group centroid (large circles)

Table 2 PERMANOVA and PERMDISP results of weighted UniFrac of ITS2 sequences between high and low heat tolerance colonies and among *Acropora* species (9,999 permutations). *P*- or *Q*-values ≤ 0.05 are highlighted in bold

PERMANOVA				PERMDISP	
	R^2	*F*	*P*-value/*Q*-value	F	*P*-value/*Q*-value
High vs. low heat tolerance					
A. digitifera	0.0374	0.545	0.581	0.179	0.664
A. millepora	0.0398	0.414	0.871	0.562	0.613
A. cf. *tenuis*	0.551	9.83	**0.0152**	2.06	0.175
Interspecific					
All	0.222	13.1	**< 0.001**	14.1	**< 0.001**
A. digitifera—*A. millepora*	0.0999	7.55	**0.004**	3.30	**0.001**
A. digitifera—*A.* cf. *tenuis*	0.260	22.1	**< 0.001**	5.36	**< 0.001**
A. millepora—*A.* cf. *tenuis*	0.142	8.74	**< 0.001**	1.50	0.143

thermotolerant, followed by *A. millepora* and *A.* cf. *tenuis* as most thermosensitive. Our findings differ from surveys on the Great Barrier Reef from 2015–2016, which showed *A. tenuis* (currently recognized as *A. kenti*) (Bridge et al. 2024) as most thermotolerant, followed by *A. millepora* and *A. digitifera* as thermosensitive (Hoogenboom et al. 2017). Thermotolerance also varied among individual colonies within each species, mirroring observations in *A. digitifera* from Palau (Humanes et al. 2022, 2024; Lachs et al. 2023) and *A.* cf. *tenuis* from the Philippines (Baquiran et al. 2025). Reports of high intercolony phenotypic variation among *A. millepora* from the Great Barrier Reef and *A. cervicornis*

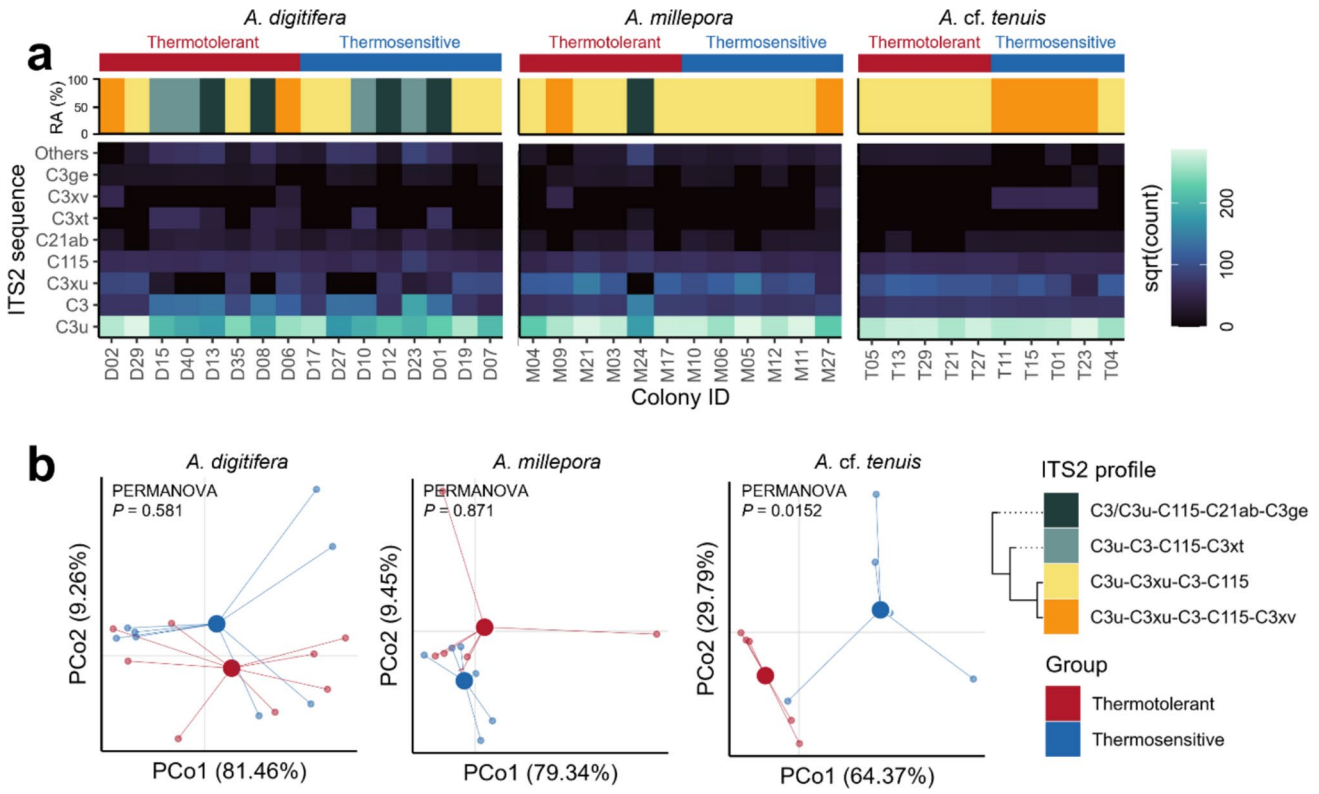

Fig. 4 Symbiodiniaceae composition between thermotolerant and thermosensitive colonies of *Acropora digitifera*, *A. millepora*, and *A.* cf. *tenuis*. **a** Heatmaps represent square root-transformed counts of ITS2 sequences in thermotolerant and thermosensitive colonies. The topmost color bar denotes thermotolerance group (red, thermotolerant; blue, thermosensitive). The second color bar depicts relative abundance (RA) of ITS2 profiles. **b** PCoA plots based on weighted UniFrac of *Cladocopium* ITS2 sequences in thermotolerant and thermosensitive colonies. Colors denote thermotolerance group with lines illustrating the distance of each sample (small circle) to the group centroid (big circle). The dendrogram beside the ITS2 profile legend depicts similarity among ITS2 profiles based on weighted UniFrac

from Florida Keys also support this observation (Granados-Cifuentes et al. 2013; Million et al. 2022). However, recent taxonomic revisions within the genus *Acropora* highlight the presence of cryptic diversity and inconsistencies between morphological and molecular classifications (Bridge et al. 2024). As such, comparisons must be interpreted with caution, as some populations may indeed represent different species. In our study, species identification was based on in situ observations of colony morphology without genetic confirmation.

Differences in thermotolerance among and within *Acropora* species on a single reef highlight the presence of substantial trait diversity among these corals. Such trait diversity likely reflects multiple underlying mechanisms that vary across taxa or individuals, including antioxidants and stress enzymes (Fitt et al. 2009; Diaz et al. 2016; Seveso et al. 2020), host morphology (Loya et al. 2001; Jimenez et al. 2011; Smith et al. 2017), and heterotrophy (Grottoli et al. 2018; Conti-Jerpe et al. 2020). For example, relatively thermotolerant species such as *Favites colemani* and *Montipora digitata* possess expanded antioxidant protein families and chaperones compared to more sensitive taxa (Da-Anoy et al. 2019, 2024). Similarly, interspecific differences in the expression of heat-shock proteins were observed in *Goniopora lobata*, *Porites lobata*, *Seriatopora hystrix,* and *Stylophora pistillata* (Seveso et al. 2020). Morphology and trophic traits also play a role, with finely branched corals tending to bleach more readily than encrusting corals (Loya et al. 2001), and species with greater heterotrophic flexibility generally exhibiting greater resilience (Conti-Jerpe et al. 2020).

Taken together, our findings emphasize substantial variation in thermotolerance both among and within *Acropora* species. Similar patterns of high intraspecific variability have been reported in *Acropora digitifera* in Palau (Humanes et al. 2022, 2024; Lachs et al. 2023) and in *A.* cf. *tenuis* in the Philippines (Baquiran et al. 2025), indicating that such variation is a common feature of acroporids, or potentially other coral groups. Natural variation in thermotolerance is not unexpected, as this is a complex trait that may be influenced by various genetic and environmental drivers (Fuller et al. 2020). Significant variation among and within species provides a reservoir of resilient individuals that offer multiple avenues for adaptation. This suggests that conservation

and restoration strategies could benefit from harnessing both species- and colony-level variation to buffer reefs against the looming changes in climate (van Oppen et al. 2015).

Photosymbiont community in acroporids

Symbiodiniaceae communities in acroporids from the BARC were dominated by genus *Cladocopium,* with four putative strains of *C. patulum* (formerly referred to as ITS2 type C3u) (Butler et al. 2023), C3/C3u-C115-C21ab-C3g3, C3u-C3-C115-C3xt, C3u-C3xu-C3-C115, and C3u-C3xu-C3-C115-C3xv. *Cladocopium patulum* has been reported in corals of the Western Indian Ocean (LaJeunesse et al. 2010; Chauka 2012; Chauka et al. 2016), Palau (Butler et al. 2023; Lewis et al. 2024), and in the South China Sea (SCS) (Ravelo and Conaco 2018; Da-Anoy et al. 2019; Chen et al. 2020; Torres et al. 2021). *C. patulum* is present in corals from the warmer southern SCS, including the Gulf of Thailand (Chankong et al. 2020), Singapore (Smith et al. 2020), Vietnam (Amid et al. 2018; Sikorskaya et al. 2022), and Malaysia (Lee et al. 2022; Rabbani et al. 2025), but is rarely found in corals of the cooler northern SCS (Chen et al. 2019; Qin et al. 2019). The prevalence of *Cladocopium patulum* in warmer waters and its rarity in the cooler northern SCS indicates a potential role in coral thermotolerance. *C. patulum* was detected in *A. hyacinthus* colonies from a reef in Hainan Island with relatively high seawater temperatures and nitrate concentrations (Li et al. 2024). This symbiont was also dominant in corals in the Huangyan Reef (Bajo de Masinloc), an atoll in the central SCS characterized by elevated sea surface temperatures (Chen et al. 2024). The high prevalence of *C. patulum* in SCS reefs may partly explain the observed thermotolerance of *Acropora* in the region. This species expresses a lipidome profile similar to *Durusdinium trenchii* (Sikorskaya et al. 2022), suggesting that it may exhibit comparable thermotolerance traits. In contrast, at Passu Keah, another atoll in the central SCS, *A. formosa* from the warmer inner lagoon harbored fewer *C. patulum* compared to those from the cooler outer reef (Qin et al. 2021). This suggests that presence or an increase in abundance of *C. patulum* may also be influenced by other environmental factors.

Cladocopium patulum is a host-generalist (LaJeunesse et al. 2010; Butler et al. 2023) abundant in environmental samples from the South China Sea (Lin et al. 2024). *C. patulum* likely accumulates in corals that acquire their symbionts from the environment. This symbiont has been detected in *Acropora*, but not in *Pocillopora*, *Seriatopora*, *Stylophora*, and *Porites* corals, which are known to vertically transmit photosymbionts (Ravelo and Conaco 2018; Da-Anoy et al. 2019; Torres et al. 2021). This pattern parallels the dominance of *C. madreporum*, another host generalist, in Palauan corals that also acquire photosymbionts through horizontal transmission (Butler et al. 2023; Lewis et al. 2024).

In the BARC, *Acropora* are dominated by *C. patulum*, suggesting that horizontal acquisition may facilitate establishment of this symbiont. The BARC has experienced several mass bleaching events. While acroporids suffered high mortality during the 1983 and 1998 events (Yap et al. 1992; Arceo et al. 2001), they showed comparatively lower bleaching prevalence than other coral taxa in 2016 (Quimpo et al. 2020). Although historical symbiont data are unavailable, the current dominance of *C. patulum* raises the possibility that its presence contributed to coral resilience in recent thermal stress events. This underscores the potential role of host-generalist *Cladocopium* species in enhancing heat tolerance across reefs.

Comparison of ITS2 profiles of corals from other regions near the Coral Triangle, such as Palau (*C. madreporum*) and the Great Barrier Reef (*C. proliferum*), indicates that host-generalist *Cladocopium* species are widespread and may play similar functional roles across geographically distinct reefs (Butler et al. 2023; Lewis et al. 2024). Although largely observational, these patterns suggest that regional variation in Symbiodiniaceae composition could influence bleaching susceptibility and resilience. Further comparative studies will be necessary to test whether differences in ITS2 type profiles correspond with differences in bleaching outcomes across the Coral Triangle.

Thermotolerance among *Acropora* shows weak correlation with photosymbiont composition

Corals in the genus *Acropora* occupy a more autotrophic niche relative to other scleractinian species with greater heterotrophic capacity (Conti-Jerpe et al. 2020). Prolonged exposure to stressors, such as abnormal temperature conditions, triggers expulsion of photosymbionts, making *Acropora* especially vulnerable to warming ocean conditions. Although we observed clear interspecific differences in thermotolerance, this was only weakly correlated with photosymbiont type. For instance, ITS2 type profiles C3/C3u-C115-C21ab-C3g3 and C3u-C3-C115-C3xt were more frequently detected in *A. digitifera*, which has relatively higher thermotolerance, though these same profiles also occurred in *A. millepora*. This suggests that symbiont identity alone cannot account for the observed interspecific variation in heat resilience and that host biology likely plays a stronger role. Evidence from hybridization and selective breeding studies support this view. Hybrids of *A. tenuis* (thermosensitive) and *A. loripes* (thermotolerant) showed enhanced resilience compared to their sensitive parent (Chan et al. 2018), and offspring from thermotolerant *A. digitifera* parents exhibited greater thermotolerance than those from thermosensitive broodstock (Humanes et al. 2022, 2024). These findings, together with other studies demonstrating heritable variation in bleaching responses (Howells et al. 2025; Kler Lago et al.

2025), imply that thermotolerance traits have some level of heritability. In the context of our results, the presence of closely related symbiont strains across colonies with differing thermal responses further supports a role for host-driven variation. Nonetheless, host–symbiont interactions likely remain important, with thermotolerance emerging from their combined effects rather than either component alone. Future studies integrating detailed holobiont phenotyping (e.g., photosynthetic efficiency, calcification, and nutrition) with genomic approaches will be crucial to disentangle the relative contributions of hosts and their symbionts to coral thermotolerance (Conti-Jerpe et al. 2020; Ros et al. 2020; Voolstra et al. 2020; Marzonie et al. 2024).

While host traits are important, symbiont diversity and physiology may nevertheless play a role in thermotolerance. In our dataset, the two ITS2 type profiles noted in *A. digitifera* and *A. millepora* were absent in *A.* cf. *tenuis*, which could have influenced the response of the latter species to elevated temperatures. Thermally stressed Symbiodiniaceae produce excessive reactive oxygen species (ROS), one of the major drivers of coral bleaching (Warner et al. 1999; Tchernov et al. 2004; Wooldridge 2009; Wiedenmann et al. 2013, 2023; Marangon et al. 2025). However, this view has been challenged by recent evidence suggesting that ROS may be a consequence rather than a cause of bleaching, with the breakdown of host–symbiont nutrient cycling as a more direct driver of symbiont expulsion (Rädecker et al. 2021; Schlotheuber et al. 2024). Regardless of the order of events, certain symbiont genotypes can effectively mitigate oxidative stress to maintain symbiosis under heat stress. For example, two genotypes from *Cladocopium proliferum* displayed divergent responses to elevated temperatures (Levin et al. 2016). The thermosensitive genotype suffered reduced photosynthetic efficiency and increased ROS, while the thermotolerant genotype upregulated ROS-scavenging and heat-shock protein genes. Subsequent studies have confirmed similar physiological divergence among these *C. proliferum* genotypes from the Great Barrier Reef (Howells et al. 2012; Beltrán et al. 2021; Butler et al. 2023), and among C15 genotypes of *Porites* spp. in Palau (Hoadley et al. 2021), indicating that even within a single Symbiodiniaceae species, functional responses to heat stress can vary. Thus, the absence of certain ITS2 type profiles in *A.* cf. *tenuis* could indicate the loss of potentially thermotolerant symbiont types, which may have contributed to its poorer thermal performance. The limited symbiont diversity observed in *A.* cf. *tenuis* may further constrain the range of viable host–symbiont combinations available under thermal stress. Alternatively, this pattern may reflect reduced host buffering capacity, where a more thermosensitive host is less able to maintain associations with a broader range of symbiont types. Together, these underscore the complex interplay between host traits and symbiont physiology in shaping thermotolerance.

Thermotolerance of conspecifics does not correlate with photosymbionts

The variation of thermotolerance among colonies of the same species did not show correlation with Symbiodiniaceae composition. Lack of clear correlation between interindividual thermotolerance and algal symbiont communities has also been reported in *A. digitifera* from Palau (Humanes et al. 2022, 2024; Lachs et al. 2023). These results imply that intraspecific thermotolerance variation in *Acropora* is not solely influenced by its photosymbionts.

The disconnect between intraspecific thermotolerance and photosymbiont composition may be attributed to other colony-specific traits and environmental factors. Other sources of intraspecific variation in thermotolerance include morphology (Brown 1997; Enríquez et al. 2005; McWilliam et al. 2022), gene expression and epigenetics (Granados-Cifuentes et al. 2013; Devlin-Durante et al. 2016; Drury et al. 2022), age (Devlin-Durante et al. 2016), microhabitat (Nakamura and van Woesik 2001; Morikawa and Palumbi 2019), and microbiome (Glasl et al. 2016; Ziegler et al. 2017; Baquiran et al. 2025). Nevertheless, though photosymbiont profile was not the primary determinant of individual holobiont thermotolerance in our study, a specific photosymbiont strain may complement host traits, contributing to overall fitness under thermal stress. This pattern was observed in Okinawa, where unique combinations of *Montipora capitata* genotypes and *Cladocopium* strains explained intraspecific variation in thermotolerance (Kavousi et al. 2020). Background photosymbionts may also influence holobiont performance during and after heat stress. This was observed in *Orbicella faveolata* and *Siderastrea siderea* in the Caribbean, where background *Durusdinium* contributed to bleaching recovery (Buzzoni et al. 2023). Together, these findings highlight the need for deeper investigations into the functional roles of host-photosymbiont pairings.

Overall, the observed ITS2 type profiles indicate that adaptive potential may not only arise from differences among host species or broad symbiont groups, but could also extend to genotypic variation within the same symbiont lineage. In the Bolinao-Anda Reef Complex, *Acropora* harbored four distinct *C. patulum* ITS2 type profiles, suggesting a relatively limited set of symbiont types within the local photosymbiont pool. In contrast to a study reporting high diversity of symbiont strains across individual colonies (Lewis et al. 2024), our results may reflect environmental filtering or host selection that favors specific host–symbiont pairings under local conditions. Such constraints may narrow the range of viable associations, potentially favoring partnerships that are better suited to prevailing environmental conditions. Nevertheless, future studies employing methods like SNPs or microsatellite markers that provide a higher degree of genotypic resolution relative to ITS2 type

profiling (Davies et al. 2023) may reveal a wider diversity of symbiont genotypes and a broader repertoire of host–symbiont partnerships. Recognizing and harnessing both host and symbiont variation will be important for strategies aimed at enhancing coral persistence under climate change.

There remain many gaps in our understanding of how host and symbiont traits interact to influence holobiont thermotolerance. Despite weak correlations between symbiont composition and thermotolerance, the consistent dominance of a *Cladocopium patulum* ITS2 type profile per colony likely limited our ability to detect or resolve finer symbiont-driven differences. This suggests that host traits and other microbial associates may play a more prominent role in shaping thermal resilience in *Acropora*. To address these, we recommend standardizing taxonomic markers and integrating multiomics approaches to improve species identification, functional characterization, and culturing methods. Culturing Symbiodiniaceae will also allow co-culture experiments with corals to verify the effects of Symbiodiniaceae on coral holobiont thermotolerance and help explain the processes underlying this intimate partnership. We recommend long-term co-culture experiments that assess the physiology of the holobiont, including both the host coral and its symbionts, the genetic makeup of its members, and their responses to the environmental conditions. These studies will provide a deeper understanding of coral holobiont thermotolerance and inform strategies for reef conservation.

Conclusions

Here, we show that acroporid corals from the same reef area in northwestern Philippines are dominated by *Cladocopium* symbionts. Several putative strains of *C. patulum* were detected among the corals, with individual colonies each harboring a single ITS2 type profile. Interspecific and intraspecific differences in thermotolerance did not clearly correlate with symbiont composition. Collectively, our findings suggest that, while the diversity of symbionts associated with these acroporids represents functional diversity that may contribute to adaptation to warmer temperatures, variation in thermotolerance cannot be attributed solely to association with specific types of Symbiodiniaceae. Thus, further studies on taxonomic and functional diversity of Symbiodiniaceae and coral hosts, extending to other members of the holobiont (i.e., bacteria, archaea, fungi, other microeukaryotes, viruses), will greatly enhance our understanding of coral holobiont thermotolerance and could be harnessed to improve the tolerance of corals in the face of progressively warming oceans.

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Author contributions John Bennedick Quijano was responsible for data curation, formal analysis, methodology, software, visualization, writing—original draft preparation, and writing—review and editing. Jake Ivan P. Baquiran took part in conceptualization, data curation, investigation, methodology, and writing—review and editing. Madeleine J.H. van Oppen participated in conceptualization, writing—original draft preparation, and writing—review and editing. Patrick C. Cabaitan and Peter L. Harrison were responsible for funding acquisition, writing—original draft preparation, and writing—review and editing. Cecilia Conaco performed conceptualization, methodology, supervision, writing—original draft preparation, and writing—review and editing.

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Data availability The data files that support the findings of this study are available on Figshare: https://doi.org/10.6084/m9.figshare.28380719.v3. The R codes and documentation that support the analyses and findings of this study are available at GitHub: https://github.com/jbquijano/000_aten and Zenodo: https://doi.org/10.5281/zenodo.16410969.

Declarations

Competing interests The authors declare that they have no competing interests.

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