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RESEARCH

Symbiodiniaceae shifts over the last decade on the hottest coral reefs on Earth

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Abstract Corals in the Persian/Arabian Gulf (PAG) are resilient to various stressors, whose levels exceed those of coral reefs globally. These corals thereby offer insight into mechanisms underlying thermal resilience, e.g., regarding the role of endosymbiotic microalgae in the family Symbiodiniaceae. Previous studies have identified the thermotolerant species *Cladocopium thermophilum* as broadly associated with corals in the southern PAG. However, algal-host specificity at the within-species level and the temporal stability of these associations are not well understood. Here we sampled two dominant stony corals (*Porites harrisoni*, $n=119$ and *Platygyra daedalea*, $n=79$) at three sites in the southern PAG and the neighboring Gulf of Oman (GO) to explore algal symbiont assemblage and specificity, whereby a prior dataset provided the opportunity to assess symbiont community stability in *P. daedalea* across a decadal time frame. Using high-throughput ITS2 marker gene sequencing and the SymPortal framework, we identified distinct, largely non-overlapping ITS2 type profiles of *C. thermophilum* as the dominant symbiotic partners in *P. harrisoni* and *P. daedalea* in the southern PAG, highlighting high host fidelity at the subspecies level. Despite this, we observed notable changes in *C. thermophilum* genotype diversity and an overall decrease over the course of a decade. By comparison, algal symbiont diversity in the neighboring GO corals increased, with formerly prevalent ITS2 type profiles being replaced by novel genotypes. Decadal data on *P. daedalea* suggest a shift in algal symbiont assemblage signified by the decline of formerly dominant algal type profiles and the emergence of novel genotypes. It is currently unknown whether the respective coral colonies associated with novel algae or became rare or extinct themselves. Understanding long-term algal population dynamics is critical to forecast how algal lineage loss or, alternatively, an increase in algal diversity will impact coral resilience and survival.

Zusammenfassung Korallen im Persisch-Arabischen Golf (PAG) sind widerstandsfähig gegenüber verschiedenen Stressfaktoren, deren Ausmaß weit über dem von Korallenriffen weltweit liegt. Diese Korallen bieten daher Einblicke in die Mechanismen, die ihrer hohen Hitzetoleranz zu-

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grunde liegen, z. B. hinsichtlich der Rolle endosymbiotischer Mikroalgen aus der Familie der Symbiodiniaceae. Frühere Studien haben gezeigt, dass die hitzetolerante Algenart *Cladocopium thermophilum* im südlichen PAG weit verbreitet mit Korallen assoziiertist. Die innerartliche Spezifität der Algen und die zeitliche Stabilität dieser Verbindungen sind bislang nur unzureichend untersucht. In dieser Studie haben wir zwei dominante Steinkorallen (*Porites harrisoni*, n = 119 und *Platygyra daedalea*, n = 79) an drei Standorten im südlichen PAG und im benachbarten Golf von Oman (GO) untersucht, um die Symbiontenzusammensetzung und -spezifität zu erforschen. Hierbei bot ein früherer Datensatz die Möglichkeit, die Stabilität der Symbiontengemeinschaft in *P. daedalea* über einen Zeitraum von zehn Jahren zu bewerten. Mittels Hochdurchsatz ITS2-Markergensequenzierung und unter Verwendung des SymPortal-Frameworks identifizierten wir unterschiedliche, weitgehend nicht überlappende ITS2 type profiles von *C. thermophilum* als dominierende Symbiosepartner in *P. harrisoni* und *P. daedalea* im südlichen PAG. Dies weist auf eine hohe Wirtstreue auf Unterart-Ebene hin. Nichtsdestotrotz konnten wir im Laufe eines Jahrzehnts bemerkenswerte Veränderungen in der Genotypenvielfalt von *C. thermophilum* und einen allgemeinen Rückgang beobachten. Im Vergleich dazu nahm die Vielfalt der Algensymbionten in den benachbarten GO-Korallen zu, wobei die früher vorherrschenden ITS2 type profile durch neue Genotypen ersetzt wurden. Die Daten zu *P. daedalea* aus dem letzten Jahrzehnt deuten auf eine Verschiebung in der Zusammensetzung der Algensymbionten hin, die sich durch den Rückgang ehemals dominanter Algentypen und das Auftreten neuer Genotypen äußert. Hierbei ist unklar, ob die jeweiligen Korallenkolonien mit neuen Algen assoziiert waren oder selbst seltener geworden oder ausgestorben sind. Das Verständnis der langfristigen Dynamik der Algenpopulationen ist entscheidend, um vorherzusagen, wie sich der Verlust genetischer Linien oder alternativ eine Zunahme der Algenvielfalt auf die Widerstandsfähigkeit und das Überleben der Korallen auswirken wird.

Keywords Symbiodiniaceae · Persian/Arabian Gulf · Thermal resilience · Climate change · ITS2 marker gene · Temporal sampling

Introduction

Coral holobiont thermal resilience has been linked to several factors, including stress tolerant symbionts of the family Symbiodiniaceae (Coles and Brown 2003; Palumbi et al. 2014; LaJeunesse et al. 2018). Among and within coral-associated Symbiodiniaceae genera, heat tolerance varies widely (Swain et al. 2017; Tchernov et al. 2004). Symbiont associations in many coral species are stable over time (Goulet 2006; Lewis et al. 2024; Smith et al. 2017; Hume et al. 2015), and shifts in community composition following bleaching or extreme events are often transient, rather than persistent (LaJeunesse et al. 2009; Hume et al. 2020). Bleaching events have increased in frequency and severity, with two global coral bleaching events occurring in the past decade alone (Reimer et al. 2024). As a consequence, corals are severely threatened by climate change (Hughes et al. 2018). Studying ‘extreme environments’ (e.g., sites featuring variable and extreme water temperatures, high salinities, recurrent hypoxia) can inform our understanding of coral thermal resilience and offer valuable insights into potential adaptive mechanisms in a rapidly changing climate (Riegl and Purkis 2012; Burt et al. 2020; Camp et al. 2020). Coral communities in the Persian/Arabian Gulf (PAG) withstand exceptionally high summer temperatures and high levels of salinity, which are fatal to their conspecifics elsewhere (Riegl et al. 2018; Burt et al. 2019). Further, the southern PAG experiences large seasonal temperature variations (< 20 °C in winter months, > 35 °C in summer months), whereas the neighboring Gulf of Oman (GO) experiences lesser variation and temperature extremes, with temperatures of < 25 °C in winter and > 30 °C in summer (Yao and Johns 2010; Coles and Riegl 2013). Given the young geological formation of the PAG and its transition to a hot climate, the corals in these waters have had ~6,000 years to adapt to these extreme conditions (Hume et al. 2015). Consequently, they provide valuable insights into the response of coral reefs to rapid global warming. A crucial factor in the survival of corals in the world’s warmest reefs is the relationship with their symbiotic algae, notably *Cladocopium thermophilum* (Hume et al. 2015, 2016; D’Angelo et al. 2015).

At large, corals in the PAG and GO are mainly associated with symbionts from the three Symbiodiniaceae genera *Symbiodinium* (former clade A), *Cladocopium* (former clade C), and *Durusdinium* (former clade D) with varying symbiont diversity within each genus (Ziegler et al. 2017; LaJeunesse et al. 2018). Overall, symbiont diversity in the PAG and GO is low compared to other geographic regions (Howells et al. 2020). Although a comprehensive algal species description is lacking at large (Parkinson et al. 2025), corals of the same genus usually associate with one or two major ITS2 type sequences, suggesting high fidelity of host–symbiont pairings (Ziegler et al. 2017). However, Symbiodiniaceae communities in the Arabian Seas at large (encompassing the PAG and GO, as well as the Red Sea) are also strongly structured by geographic region (Ziegler et al. 2017; Oladi et al. 2019). Corals in the PAG prevalently form associations with symbionts of the genus *Cladocopium*. Main associations are with the ITS2 type C3 and further with the specific ITS2 subtype C3-C3gulf, designating the species *Cladocopium thermophilum* (Hume et al. 2015). By comparison, corals in the neighboring, cooler waters of the GO host a similar diversity as found in the PAG, but symbiont associations are mainly composed of the genus *Durusdinium* (Howells et al. 2020; Ziegler et al. 2017; Oladi et al. 2019). Notably, *Durusdinium* is commonly associated with increased thermal tolerance in corals from the the Caribbean and Great Barrier Reef (Berkelmans and van Oppen 2006; Stat and Gates 2011; Cunning et al. 2017). The Arabian Seas (i.e., the Red Sea, the PAG, but not the GO) seem to contrast this common notion of *Durusdinium* being the most thermally tolerant Symbiodiniaceae genus (LaJeunesse et al. 2010, 2016; Pettay et al. 2015) as corals here host mostly symbionts from the genus *Cladocopium* (Terraneo et al. 2019, 2023; Buitrago-López et al. 2023; Voolstra et al. 2021). Thus, inferring thermal tolerance ad hoc for a symbiont genus can be misleading.

Cladocopium thermophilum (Hume et al. 2015, 2016) harbors distinct lineages (putative subspecies) that associate with different coral taxa/species, as revealed by SymPortal analyses (Hume et al. 2019). The *C. thermophilum* group comprises a distinct evolutionary lineage within *Cladocopium* that is approximately 5 MYA old (Hume et al. 2016). Thus, despite its pervasive presence in the PAG, it originated elsewhere, likely harboring genetic adaptations that contribute to the increased thermal tolerance of corals in the PAG (Hume et al. 2016). A specific lineage of the *C. thermophilum* group experienced rapid evolutionary expansion in the PAG during the Holocene period, coinciding with the formation of the PAG and its transition to a hot climate (Hume et al. 2016). This expansion occurred within the last 6,000 years, approximately at the same time that the genome of *Platygyra daedalea*, a common coral host of *C. thermophilum* in the southern PAG, was rapidly evolving (Smith et al. 2022). Howells et al. (2020) showed that corals (i.e., *Acropora downingi*, *Cyphastrea microphthalma*, *Platygyra daedalea)* sampled across seasons and through a period of heat stress between 2012 and 2014 in the PAG exhibited a high degree of symbiont fidelity to *C. thermophilum*. The association with a narrow range of symbionts and their temporal stability suggests that these symbionts are crucial for the survival of corals in the harsh conditions of the PAG, specifically in the southern PAG. In turn, this implies a putative vulnerability if these symbionts are affected by environmental change.

The PAG is warming at more than twice the rate of the world's seas, prompting increasingly frequent, longer, and more severe marine heat waves (Riegl et al. 2018; Lachkar et al. 2021). Thus, corals in the PAG live exceptionally close to their upper thermal tolerance thresholds (Howells et al. 2016) and are being challenged by repeated episodes of heat stress (Riegl et al. 2018; Burt et al. 2019). This has pushed coral populations beyond their physiological limits and resulted in the loss of major branching reef builders (Burt 2024). For these reasons, conditions for corals are expected to become even more stressful in the PAG. Following this, here we sought to investigate contemporary Symbiodiniaceae associations in the PAG and GO of *P. harrisoni* and *P. daedalea*, two of the most common extant coral species in the PAG. This also provided an opportunity to assess long-term stability of previously identified associations (Howells et al. 2020; Hume et al. 2016; Ziegler et al. 2017), an approach that remains rare (Thornhill et al. 2006; Lewis et al. 2024; Goulet and Coffroth 2003). We sampled 119 and 79 colonies of *Porites harrisoni* and *Platygyra daedalea,* respectively, at three sites along the PAG and GO coasts of the United Arab Emirates to provide a contemporary inventory of within-species/lineage level Symbiodiniaceae diversity. Further, we conduct a decadal comparison of endosymbiont association in *P. daedalea* between 2012 (Howells et al. 2020) and 2022 (this study) to assess to what extent Symbiodiniaceae community composition has changed in the PAG and GO and whether Symbiodiniaceae diversity was lost, has increased, or stayed the same.

Material and methods

Sample collection

Samples of the two coral species *Porites harrisoni* ($n = 119$) and *Platygyra daedalea* ($n = 79$) were collected from two locations in the Persian/Arabian Gulf (Saadiyat Reef, SY: 24.599528, 54.422667; Al Saada Reef, SA: 24.085250, 52.243333) and one location from the Gulf of Oman (Al Aqah, AA: 25.491694, 56.363861) in May/June 2022 (Supplementary Table S1). Al Aqah is also known as Snoopy Island, so the abbreviations AA and SI are equivalent in supplementary datasets. At Al Saada Reef, no samples of *P. daedalea* were taken due to an insufficient number of healthy appearing colonies. At each location, samples were collected using SCUBA at depths of 2–11 m. Coral colonies were sampled approximately 5 m apart from each other to minimize sampling clonal genotypes (Baums et al. 2006). Coral plugs (~2 cm diameter) from each colony were drilled with a Nemo underwater drill (Nemo Power Tools LLC, Nevada, USA) fitted with a diamond tip corer. Samples were stored in sealable plastic bags upon underwater collection and transported to shore in a cooler filled with seawater from the respective site. Coral fragments were incubated in DESS buffer (Yoder et al. 2006) overnight, and subsequently, the tissue was blasted off the skeleton using an airbrush (Voolstra et al. 2023). The tissue slurry was transferred to 2 mL cryotubes and stored in DESS buffer at 4 °C until transport to the laboratory facilities at the University of Konstanz, Germany, where samples were stored at −20 °C prior to DNA extraction.

DNA extraction and sequencing

DNA was extracted using the Qiagen DNeasy Blood & Tissue kit (Qiagen, Hilden, Germany) using a modified protocol for coral tissue (Voolstra et al. 2023). Briefly, coral tissue slurry in DESS buffer was centrifuged at 10,000 × *g* for 3 min at room temperature to pellet the tissue slurry, and the supernatant DESS buffer was decanted. The tissue slurry was homogenized using a Polytron PT 1200 E (Kinematica, Switzerland); then, 90 µL was pipetted into a new 2 mL tube and topped with 90 µL of ATL buffer as well as 20 µL Proteinase K for a total volume of 200 µL. The mixture was vortexed and incubated at 56 °C for at least two and up to six hours (in the case of *P. daedalea*) to lyse the tissue. After adding 4 µL of RNase A and incubating the sample for 2 min at room temperature, the manufacturer's protocol was followed. The elution volume was 30 µL AE buffer for all samples. DNA quantity and quality were assessed with a NanoDrop 2000 spectrophotometer. Extracted DNA was sent to the NGS Competence Center Tübingen (NCCT), Germany, for library preparation and sequencing of the internal transcribed spacer 2 region (ITS2). Amplicon libraries were prepared using the primers SYM_VAR_5.8S2 (5'-GAATTGCAGAACTCCGTGAACC-3') and SYM_VAR_REV (5'-CGGGTTCWCTTGTYTGACTTCATGC-3') (Hume et al. 2018a, b), and samples were subsequently sequenced on an Illumina MiSeq platform (MiSeq v3; 600 cycles, PE300). Raw sequencing data are accessible at NCBI under BioProject PRJNA1188806 (https://www.ncbi.nlm.nih.gov/bioproject/PRJNA1188806).

SymPortal analysis

Demultiplexed paired-end sequencing files were uploaded to SymPortal (Hume et al. 2019) at https://symportal.org/ to determine ITS2 type profiles. In brief, the SymPortal analytical framework conducts a standardized quality control on submitted paired-end FASTQ files, including the removal of artifact and non-Symbiodiniaceae sequences, and Symbiodiniaceae genera are identified through BLAST (Camacho 2009). Genus-separated ITS2 sequences are then processed to determine ITS2 type profiles. Hereby, recurring ITS2 sequences are denoted as 'defining intragenomic variants' (DIVs). Sets of DIVs comprise ITS2 type profiles. The nomenclature of these ITS2 type profiles reflects the presence of their DIVs in order of abundance, with ITS2 type profiles being representative of Symbiodiniaceae taxa, i.e., provisional genotypes. For instance, an ITS2 type profile starting with 'C3/C3gulf' denotes a symbiont genotype containing the ITS2 sequences C3 and C3gulf with both sequences being codominant. Similarly, an ITS2 type profile denoting 'C3-C3gulf' indicates higher abundance of C3 over C3gulf. Both type profiles are indicative of the species *Cladocopium thermophilum* (Hume et al. 2015, 2016). For this study, post-MED ITS2 sequences (Supplementary Table S2) and ITS2 type profile abundances (Supplementary Table S3) were used for all analyses. We implemented permutational analysis of variance (PERMANOVA) testing (Anderson 2005) with 9,999 permutations in the vegan v2.6–4 package in R (Oksanen et al. 2023) on ITS2 type profile abundances to assess the difference in Symbiodiniaceae community between sites (SA, SY, AA) and species (*P. daedalea*, *P. harrisoni*) on the dataset collected in 2022. We further visualized the dissimilarity between ITS2 type profiles by plotting PCoA coordinates based on Bray–Curtis square-root between-profile distances of ITS2 type profiles, as output by SymPortal (Supplementary Files 1–3) in R using the ggplot2 v3.4.1 package (Wickham 2011). The SymPortal run for this dataset can be accessed at https://symportal.org/data_explorer/?Study=202307_afiesinger_UAE_GS.

Decadal comparison of Symbiodiniaceae diversity

To compare Symbiodiniaceae population diversity over the course of a decade, we used a publicly available dataset (Howells et al. 2020) (NCBI BioProject PRJNA532516 https://www.ncbi.nlm.nih.gov/bioproject/PRJNA532516), which comprised 395 coral samples from three coral species collected in the PAG (Delma: 24.520800, 52.278100; Saadiyat: 24.598600, 54.420100; Ras Ghanada: 24.848200, 54.690300) and the GO (Dibba: 25.603100, 56.348500; Al Aqah: 25.492900, 56.363500) between 2012 and 2014. We collected specimens at two of the same locations (Saadiyat Reef, SY, and Al Aqah, AA) sampling the same coral populations of *Platygyra daedalea* as Howells et al. (2020) did a decade ago (SY and AA) from similar depths (6 m at SY and 2–5 m at AA, Supplementary Table S1, while Howells et al. (2020) sampled at 4–7 m at each site). It remains undetermined to what extent identical colonies were sampled. For detailed methodologies on the sampling scheme, DNA extraction, and sequencing protocols, refer to Howells et al. (2020). Samples from both datasets (2012 and 2022) were combined and processed together in SymPortal. Of note, Howells et al. (2020) used a different primer set. A possible amplification bias arising from this, while being a concern in complex bacterial microbiome analyses, is not expected to confound the analysis here. This is because Symbiodiniaceae assemblages are in general far less complex (i.e., typically one dominant algal symbiont) and comparative analyses were conducted on robust ITS2 type profiles, i.e., sets of diagnostic sequences, instead of single ITS2 sequences. A comparison between the two primer pairs used in Howells et al. (2020) and this study found little taxonomic bias in resolving Symbiodiniaceae taxa (Hume et al. 2018a, b). The revised primer pair used in this study exhibits higher target specificity, but retains ITS2 target diversity (Hume et al. 2018a, b). In other words, fewer non-target sequences are produced, but Symbiodiniaceae ITS2 sequence diversity is not affected. Post-MED ITS2 sequences (Supplementary Table S4) and ITS2 type profile abundances (Supplementary Table S5) from selected samples (i.e., *Platygyra daedalea* from SY and AA) were used for the analysis. The SymPortal run can be accessed at https://symportal.org/data_explorer/?Study=202402_afiesinger_UAE_GS_10yearcomp.

Rarefaction curves were plotted based on ITS2 post-MED sequences from the combined dataset (*P. daedalea*, 47 colonies from SY in 2012, 39 in 2022; 32 colonies from AA in 2012, 40 in 2022; Supplementary Table S4) to assess whether sequencing effort was similar and comparable for both sampling campaigns to infer biodiversity patterns. We implemented PERMANOVA testing on ITS2 type profile abundances with 9999 permutations to assess the contribution of site and year in explaining Symbiodiniaceae community difference in the combined dataset. Further, to test for significant differences in Symbiodiniaceae population diversity between the two time points at each site separately (SY and AA), we used the nonparametric statistical test Analysis of Similarities (ANOSIM) (Somerfield et al. 2021) with 999 permutations and pairwise PERMANOVAs with 9999 permutations on the absolute abundances of the post-MED ITS2 sequences (Supplementary Table S4) and the predicted ITS2 type profiles (Supplementary Table S5) from the combined dataset. We further visualized the dissimilarity between ITS2 type profiles of *P. daedalea* in 2012 and 2022 by plotting PCoA coordinates as output by SymPortal based on Bray–Curtis square-root between-profile distances of ITS2 type profiles (Supplementary Files 4–6) in R using the ggplot2 package. We used SIMPER tests (in the vegan R package) to determine which symbionts contribute to the statistical difference between years at each site.

Symbiodiniaceae community assessment

Relative abundances of ITS2 type profiles were plotted as barplots using the ITS2 type profile abundance table output by SymPortal for both the 2022 dataset and the combined dataset of *P. daedalea* at the sites SY and AA of both sampling years (2012 and 2022). To examine the specificity between ITS2 type profiles and the study factors (i.e., site and year), we created a schematic to visually depict profiles with the categorical levels of the samples in which they were detected (sensu Hume et al. 2020). We combined a dendrogram based on hierarchical clustering of the square-root transformed UniFrac distance matrix of each Symbiodiniaceae genus (Supplementary Files 7–9) with the number of samples each ITS2 type profile was found in for each year (2012 vs. 2022) and the categorical information of the site at which each profile was found. Dendrograms were drawn on hierarchical clustering of UniFrac square-root transformed distance matrices output by SymPortal of each Symbiodiniaceae genus using hclust() in the stats v4.1.3 package (R Core Team 2022) and the dendextend v1.17.1 package in R (Galili 2015). The dotplot depicting the number of samples each ITS2 type profile was found in was drawn with ggplot2 (Wickham 2011), and the categorical information for each profile was added using a custom script in R available at https://github.com/afiesinger/UAE_PAG_Symbiodiniaceae.

Results

Study overview

To assess coral-associated Symbiodiniaceae diversity in an extreme environment, we sampled two common stony coral species, *Platygyra daedalea* and *Porites harrisoni*, from the southeastern PAG (site SY) and the more thermally extreme southwestern PAG (site SA) in May/June 2022 (Fig. 1). Further, we compared the Symbiodiniaceae community of the same coral species from the nearby, more environmentally benign GO (site AA). A total of 198 colonies were sampled at the three locations, ranging from 39 to 40 sampled colonies for each species at each site.

Looking at ITS2-based Symbiodiniaceae genus-level diversity, after applying an abundance threshold of 1% for each post-MED ITS2 sequence detected in all samples, 175 of 198 samples harbored a single genus (*Symbiodinium*, *Cladocopium*, or *Durusdinium*), 22 samples harbored two Symbiodiniaceae genera, and only 1 sample contained ITS2 sequences from all three algal genera (Supplementary Figure S1, Supplementary Table S2). The 22 samples comprised sequences from *Symbiodinium* and *Cladocopium* ($n = 16$) and to a lesser extent from *Symbiodinium* and *Durusdinium* ($n = 2$) as well as *Cladocopium* and *Durusdinium* ($n = 4$). Most of these samples had sequences majoritively from one genus (> 81% of either *Symbiodinium*, *Cladocopium*, or *Durusdinium*). The one sample that contained sequences from all three genera originated from a *Porites harrisoni* colony of the GO site (AA) and was dominated by sequences of *Cladocopium* (88%), whereas *Symbiodinium* and *Durusdinium* sequences comprised about 5% each.

Looking at ITS2 type profiles (no ITS2 sequence abundance cutoff), we identified a total of 42 ITS2 type profiles across all colonies, and 149 of 198 samples were associated with single algal ITS2 type profiles from one of the three genera (*Symbiodinium*: $n = 5$, *Cladocopium*: $n = 97$, *Durusdinium*: $n = 47$), attesting to a high level of specificity. The remaining 42 samples harbored ITS2 type profiles from two genera in varying relative abundances, while 7 samples had ITS2 type profiles from all three genera, i.e., *Symbiodinium*, *Cladocopium*, or *Durusdinium*. There were

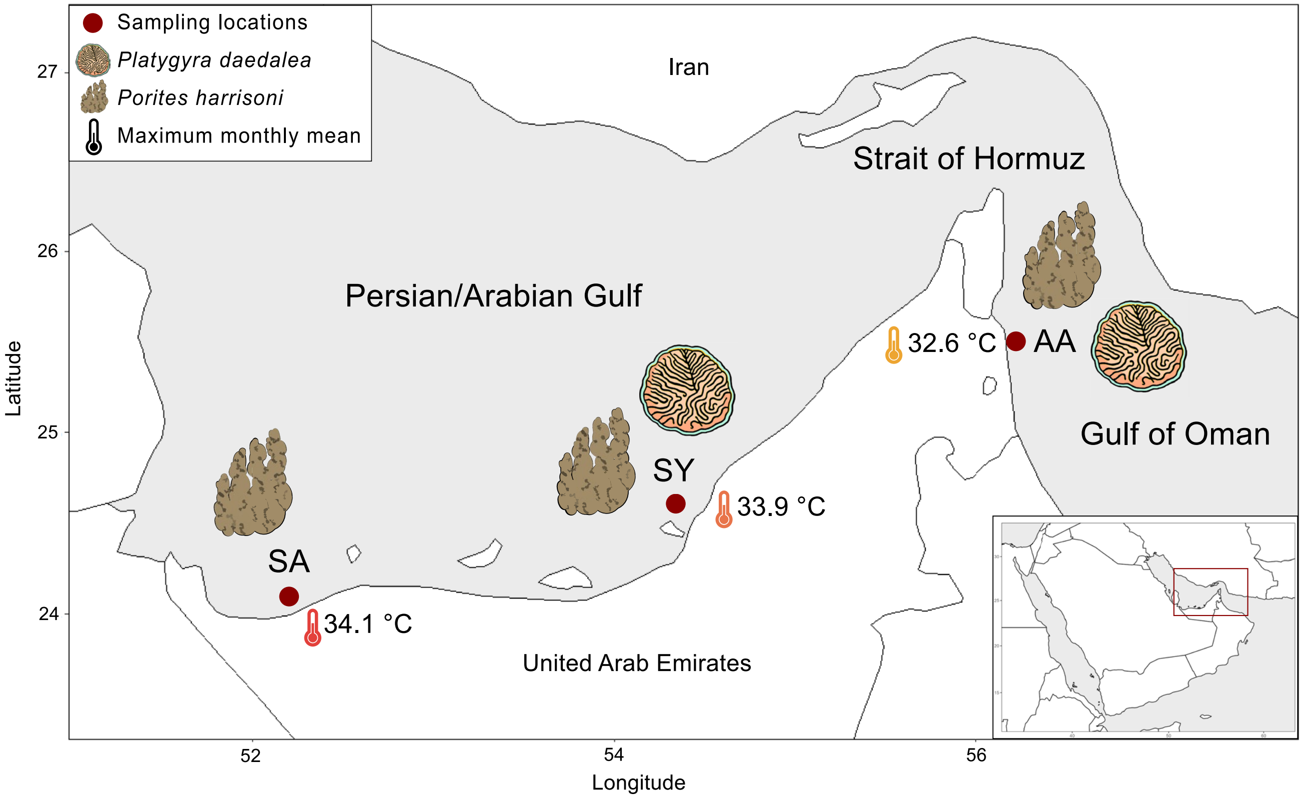


Fig. 1 Map of sampling sites and sampled coral species in the Persian/Arabian Gulf and Gulf of Oman. Site codes are SA: Al Saada Reef; SY: Saadiyat Reef; AA: Al Aqah. The maximum monthly mean (MMM) temperature for each site is depicted, derived from the NOAA Coastwatch Data Analysis Tool available at https://eastcoast.coastwatch.noaa.gov/cw_software.php

no colonies that were associated with ITS2 type profiles from more than three genera (Supplementary Figure S1, Supplementary Table S3). *Cladocopium thermophilum* (ITS2 majority sequence C3-C3gulf or C3/C3gulf) (Hume et al. 2015) was the most dominant species in samples harboring *Cladocopium* ITS2 type profiles in the PAG and GO of both coral species. Similarly, *Durusdinium glynnii* (D1) (Wham and LaJeunesse 2016) and *Durusdinium trenchii* (D1-D4) (LaJeunesse et al. 2014) were the major algal species in samples harboring *Durusdinium* type profiles in *P. harrisoni*, while ITS2 type profiles with the D5 ITS2 majority sequence were dominant in *P. daedalea* in the PAG and GO. *Symbiodinium microadriaticum* (A1) (LaJeunesse 2017) was the dominant species of all samples harboring *Symbiodinium* type profiles in both coral species at all sites. Principal coordinates analysis (PCoA) of ITS2 type profiles revealed distinct Symbiodiniaceae community composition across host species and sampling sites (Supplementary Figure S2). *Cladocopium* exhibited clear host-specific clustering and site-level separation. Overall, ITS2 type profile associations were significantly structured by host species, sampling location, or both (PERMANOVA: Site $R^2 = 0.163$, Species $R^2 = 0.100$, Species:Site $R^2 = 0.089$; $p = 0.0001$; Supplementary Data S1), although a large proportion of the difference remained unexplained (Residuals $R^2 = 0.649$). To further disentangle the observed differences, we conducted pairwise PERMANOVAs on site and host species. In pairwise site comparisons, the highest differentiation was between the two PAG sites SY and SA (pairwise PERMANOVA, $R^2 = 0.148$, $p = 0.0001$; Supplementary Data S1), followed by the variation between SA and AA (pairwise PERMANOVA, $R^2 = 0.138$, $p = 0.0001$), and SY and AA (pairwise PERMANOVA, $R^2 = 0.116$, $p = 0.0001$). However, the strength of differentiation was low overall. Pairwise comparison between *P. daedalea* and *P. harrisoni* showed significant differentiation in symbiont community composition across all sites (pairwise PERMANOVA, $R^2 = 0.100$, $p = 0.0001$; Supplementary Data S1).

Symbiodiniaceae diversity in *Porites harrisoni*

At the hottest site in the southwestern PAG, i.e., Al Saada Reef (SA), all *Porites harrisoni* colonies harbored *C. thermophilum* ITS2 type profiles ($n = 40$, 100%), as indicated by the characteristic C3-C3gulf and C3/C3gulf ITS2 majority sequences (Fig. 2; Supplementary Table S3). This confirms

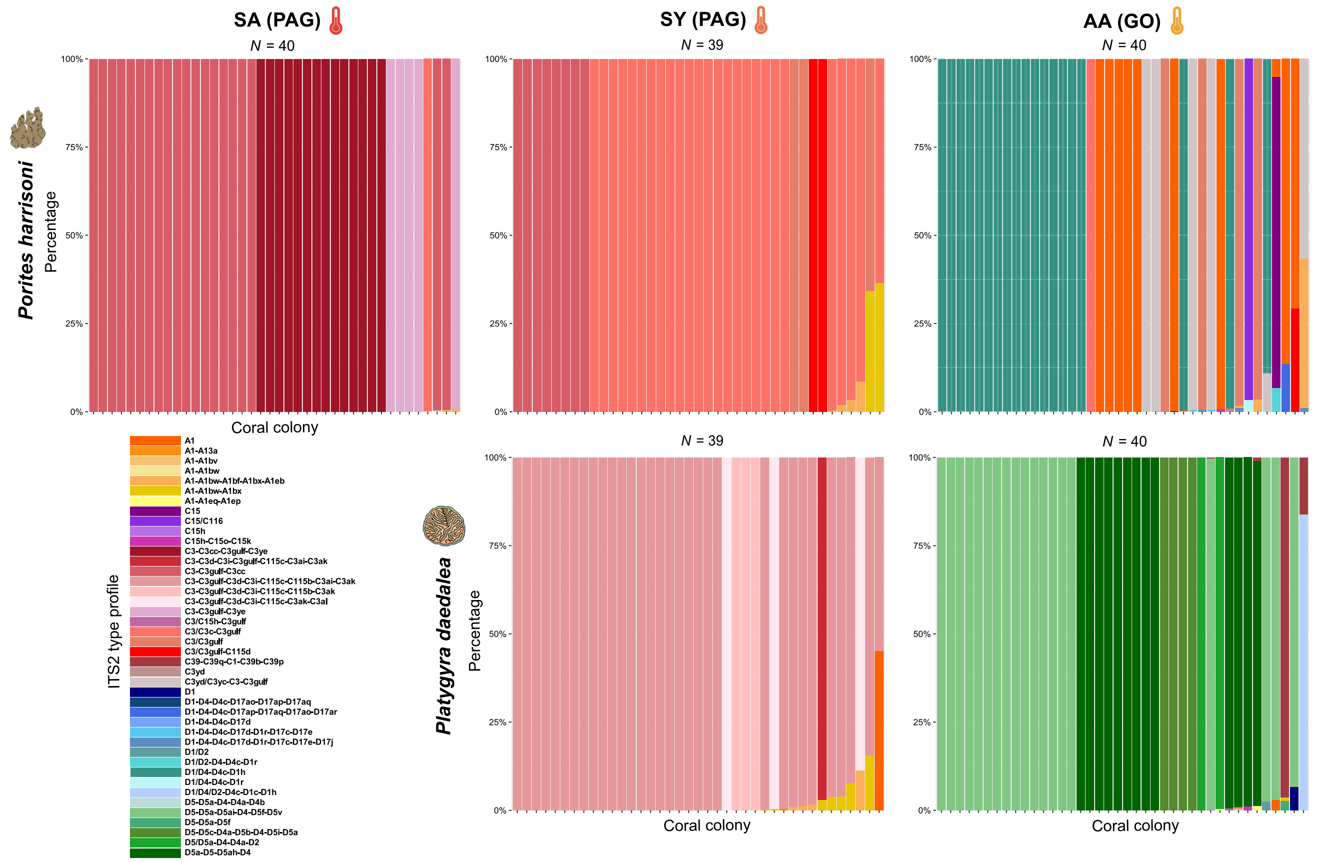
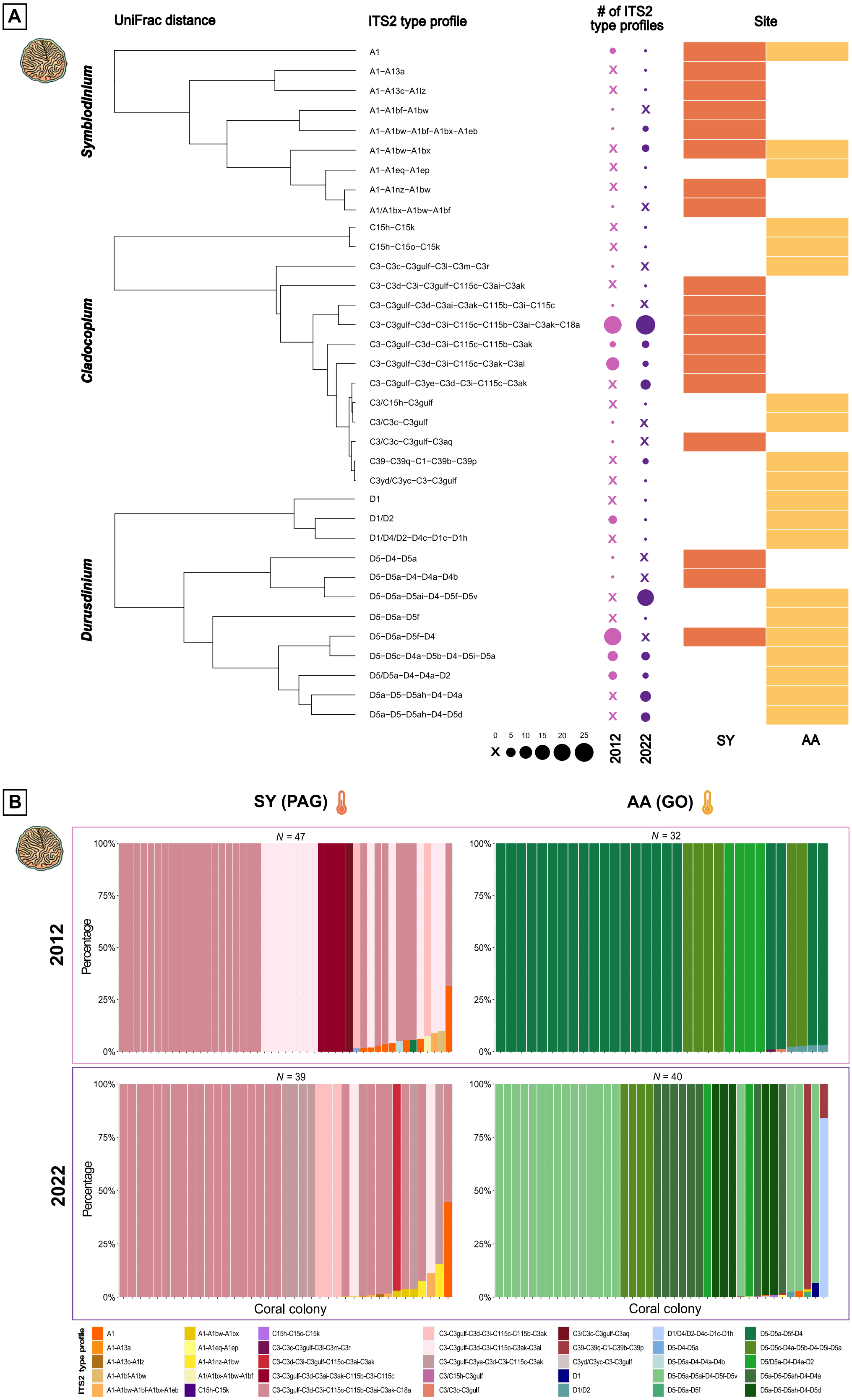


Fig. 2 Symbiodiniaceae diversity of *Porites harrisoni* and *Platygyra daedalea* in the Persian/Arabian Gulf (PAG) and Gulf of Oman (GO) from 2022. Depicted are barplots of ITS2 type profile abundances of *Porites harrisoni* and *Platygyra daedalea* from the three sampled reef sites Al Saada Reef (SA), Saadiyat Reef (SY), and Al Aqah (AA). Each bar depicts ITS2 type profiles for one coral sample. For each location and coral species, the number of colonies sampled (*N*) is depicted above each panel. The order of colonies is sorted by ITS2 type profile, starting (from left to right) with all colonies harboring only one profile and increasing in 'background' profile abundance. *Symbiodinium* ITS2 type profiles are generally depicted in shades of yellow/orange, *Cladocopium* ITS2 type profiles are depicted in red/violet, while *Durusdinium* ITS2 type profiles are in blue/green colors

previous findings that *C. thermophilum* is dominant in the southern PAG (Hume et al. 2016). The majority of these colonies ($n = 36$, 90%) also harbored exactly one *C. thermophilum* ITS2 type profile. In the case of the 4 colonies harboring additional type profiles, these were < 0.75% relative abundance, further attesting to the notion that corals are dominated by single symbiont genotypes (Baums et al. 2014; Lewis et al. 2024; Goulet 2006). Notably, we found distinct *C. thermophilum* type profiles across different colonies, suggesting that *C. thermophilum* diversity and fidelity exist at the genotype level (Parkinson et al. 2015; Hume et al. 2020, 2019). Of note, some of the algal type profiles were shared between coral colonies. However, genotypes of the respective coral host colonies are undetermined at present, preventing to assess whether host clonal genotype structure aligns with shared algal ITS2 type profiles. Of the 36 colonies, 18 were dominated by C3-C3gulf-C3cc, 16 by C3-C3cc-C3gulf-C3ye, and 4 by C3-C3gulf-C3ye. The 4 colonies with mixed assemblages harbored the profiles C3-C3gulf-C3cc (2 colonies), C3-C3gulf-C3ye (1 colony), and C3/C3c-C3gulf (1 colony) at a relative abundance of > 92%. By comparison, background ITS2 type profiles could be mapped to genotypes of *S. microadriaticum* (A1-A1bw-A1bf-A1bx-A1eb, A1-A1bw, and A1-A1bv) or *Durusdinium* (D5-D5a-D4-D4a-D4b) at very low abundances (< 1%) (Fig. 2; Supplementary Table S3).

At the second PAG site, i.e., Saadiyat Reef (SY), a largely similar pattern could be observed in that all *P. harrisoni* colonies harbored *C. thermophilum* ITS2 type profiles ($n = 39$, 100%) (Fig. 2; Supplementary Table S3), of which 33 (85%) exclusively harbored one *C. thermophilum* and no other ITS2 type profiles. As in the SA site, we found a diversity of *C. thermophilum* type profiles: 8 colonies harbored C3-C3gulf-C3cc, 21 colonies C3/C3c-C3gulf, 2 colonies C3/C3gulf, and a further 2 colonies C3/C3gulf-C115d. For the 6 colonies that harbored Symbiodiniaceae besides *C. thermophilum*, *Symbiodinium microadriaticum* ITS2 type profiles were present at moderate to low abundances.


A
UniFrac distance
ITS2 type profile
# of ITS2 type profiles
Site
Symbiodinium
Cladocopium
Durusdinium
A1
A1–A13a
A1–A13c–A1lz
A1–A1bf–A1bw
A1–A1bw–A1bf–A1bx–A1eb
A1–A1bw–A1bx
A1–A1eq–A1ep
A1–A1nz–A1bw
A1/A1bx–A1bw–A1bf
C15h–C15k
C15h–C15o–C15k
C3–C3c–C3gulf–C3l–C3m–C3r
C3–C3d–C3i–C3gulf–C115c–C3ai–C3ak
C3–C3gulf–C3d–C3ai–C3ak–C115b–C3i–C115c
C3–C3gulf–C3d–C3i–C115c–C115b–C3ai–C3ak–C18a
C3–C3gulf–C3d–C3i–C115c–C115b–C3ak
C3–C3gulf–C3d–C3i–C115c–C3ak–C3al
C3–C3gulf–C3ye–C3d–C3i–C115c–C3ak
C3/C15h–C3gulf
C3/C3c–C3gulf
C3/C3c–C3gulf–C3aq
C39–C39q–C1–C39b–C39p
C3yd/C3yc–C3–C3gulf
D1
D1/D2
D1/D4/D2–D4c–D1c–D1h
D5–D4–D5a
D5–D5a–D4–D4a–D4b
D5–D5a–D5ai–D4–D5f–D5v
D5–D5a–D5f
D5–D5a–D5f–D4
D5–D5c–D4a–D5b–D4–D5i–D5a
D5/D5a–D4–D4a–D2
D5a–D5–D5ah–D4–D4a
D5a–D5–D5ah–D4–D5d
0 5 10 15 20 25
X
2012
2022
SY
AA
B
SY (PAG)
AA (GO)
2012
2022
N = 47
N = 32
N = 39
N = 40
100%
75%
50%
25%
0%
Percentage
Coral colony
Coral colony
ITS2 type profile
A1
A1-A13a
A1-A13c-A1lz
A1-A1bf-A1bw
A1-A1bw-A1bf-A1bx-A1eb
A1-A1bw-A1bx
A1-A1eq-A1ep
A1-A1nz-A1bw
A1/A1bx-A1bw-A1bf
C15h-C15k
C15h-C15o-C15k
C3-C3c-C3gulf-C3l-C3m-C3r
C3-C3d-C3i-C3gulf-C115c-C3ai-C3ak
C3-C3gulf-C3d-C3ai-C3ak-C115b-C3i-C115c
C3-C3gulf-C3d-C3i-C115c-C115b-C3ai-C3ak-C18a
C3-C3gulf-C3d-C3i-C115c-C115b-C3ak
C3-C3gulf-C3d-C3i-C115c-C3ak-C3al
C3-C3gulf-C3ye-C3d-C3i-C115c-C3ak
C3/C15h-C3gulf
C3/C3c-C3gulf
C3/C3c-C3gulf-C3aq
C39-C39q-C1-C39b-C39p
C3yd/C3yc-C3-C3gulf
D1
D1/D2
D1/D4/D2-D4c-D1c-D1h
D5-D4-D5a
D5-D5a-D4-D4a-D4b
D5-D5a-D5ai-D4-D5f-D5v
D5-D5a-D5f
D5-D5a-D5f-D4
D5-D5c-D4a-D5b-D4-D5i-D5a
D5/D5a-D4-D4a-D2
D5a-D5-D5ah-D4-D4a
D5a-D5-D5ah-D4-D5d

◂**Fig. 3** Decadal comparison of Symbiodiniaceae diversity of *Platygyra daedalea* between 2012 and 2022. **(A)** Prevalence of ITS2 type profiles, as proxies for Symbiodiniaceae genotypes, compared between the datasets of Howells et al. (2020) and the present study, corresponding to the sampling years 2012 and 2022, respectively. The data are illustrated in a genus-separated format, with each row representing an individual ITS2 type profile. Each profile is identified by its name and the number of samples in which it was detected, visualized through a dotplot distinguishing between the two collection years 2012 and 2022. Adjacent to each ITS2 type profile, categorical information related to the sampling site is provided as a binary matrix plot, i.e., whether the respective profile occurred in *P. daedalea* at site SY, AA, or both. The relatedness among the ITS2 type profiles is depicted to the left of the profile names, using a dendrogram constructed from hierarchical clustering based on UniFrac-derived distances, calculated from the average abundance of defining intragenomic variants (DIVs) for each profile, illustrating the change in Symbiodiniaceae populations over time as revealed by the disappearance of prominent symbiont genotypes and the appearance of novel genotypes. **(B)** Barplot of ITS2 type profiles per site (SY and AA) and year (2012 and 2022) of *P. daedalea* for the combined dataset from Howells et al. (2020) and this study. Each bar denotes a colony; the upper row depicts the 2012 dataset, the lower row depicts the 2022 dataset; the first column is Saadiyat Reef (SY) in the PAG and the second column is Al Aqah (AA) in the GO. For each site and year, the number of colonies sampled (*N*) is depicted above each panel. Colors indicate genus-/species-level assignment of ITS2 type profiles, denoting the change in genotype prevalence over time

(A1-A1bw-A1bx was present in two colonies at > 32% relative abundance; A1-A1bw-A1bf-A1bx-A1eb was present in four samples at < 8%.)

In the neighboring waters of the GO at site Al Aqah (AA), a remarkably different pattern could be observed. Out of 40 colonies, more than half ($n = 23$, 57.5%) were exclusively associated with one symbiont species of either *Durusdinium trenchii* (profile D1/D4-D4c-D1h, $n = 16$ colonies), *Symbiodinium microadriaticum* (profile A1, $n = 5$ colonies), or *Cladocopium thermophilum* (profiles C3/C3gulf and C3/C3c-C3gulf, $n = 2$ colonies) (Fig. 2; Supplementary Table S3). For the remaining 17 colonies (42.5%), ITS2 type profiles of *D. trenchii*, *S. microadriaticum*, *C. thermophilum,* C15, and C3 were present in varying abundances. Of these, 3 colonies were dominated by *D. trenchii* (profile D1/D4-D4c-D1h; relative abundance > 88%), 4 colonies were dominated by *S. microadriaticum* (profile A1; relative abundance > 64%), and 1 colony harbored a mix of A1-A1bw-A1bf-A1bx-A1eb and C3yd/C3yc-C3-C3gulf at comparable relative abundances (40% and 53%, respectively). Additionally, three colonies were dominated by *C. thermophilum* (profile C3/C3gulf; relative abundance > 76%) and another three were dominated by the variant C3yd/C3yc-C3-C3gulf (> 84% relative abundance). C15, reported to be commonly associated with *Porites* sp. in the GO (D'Angelo et al. 2015; Ziegler et al. 2017; Hume et al. 2018a, b), was only found in a few *P. harrisoni* colonies at site AA: One colony was dominated by C15 (83.9%), while another codominantly harbored C15/C116 (85.8%). Lastly, *D. trenchii* genotypes were often present as background symbionts: D1-D4-D4c-D17d-D1r-D17c-D17e-D17j (< 1% relative abundance, $n = 3$), D1-D4-D4c-D17d-D1r-D17c-D17e (< 0.5%, n = 3), and D1-D4-D4c-D17ao-D17ap-D17aq, D1-D4-D4c-D17d, and D1-D4-D4c-D17ap-D17aq-D17ao-D17ar (< 14%, $n = 1$ each). Low-abundance symbionts included profiles of *S. microadriaticum* (A1-A1bw-A1bf-A1bx-A1eb), *C. thermophilum* (C3/C3gulf-C115d, C3/C3gulf, C3yd/C3yc-C3-C3gulf), as well as C3yd and C15 (C15h-C15o-C15k).

Symbiodiniaceae diversity in *Platygyra daedalea*

At SY in the PAG (insufficient number of *P. daedalea* colonies at SA, see Methods), a total of 26 out of 39 colonies (66.7%) harbored a single ITS2 type profile, all of which were *C. thermophilum* genotypes (22 associated with C3-C3gulf-C3d-C3i-C115c-C115b-C3ai-C3ak, 3 with C3-C3gulf-C3d-C3i-C115c-C115b-C3ak, and 1 colony with C3-C3gulf-C3d-C3i-C115c-C3ak-C3al) (Fig. 2; Supplementary Table S3). The remaining 13 colonies were all dominated by *C. thermophilum* genotypes (C3-C3gulf-C3d-C3i-C115c-C115b-C3ai-C3ak, C3-C3gulf-C3d-C3i-C115c-C3ak-C3al, C3-C3gulf-C3d-C3i-C115c-C115b-C3ak, and C3-C3d-C3i-C3gulf-C115c-C3ai-C3ak) with varying degrees of *S. microadriaticum* genotypes (A1-A1bw-A1bf-A1bx-A1eb, A1-A1bw-A1bx, and A1-A13a) at low abundances (< 13%). Of all the *C. thermophilum* genotypes present, C3-C3gulf-C3d-C3i-C115c-C115b-C3ai-C3ak was most prevalent (present in 30 out of 39 colonies). Profiles belonging to the genus *Durusdinium* were not detected in *P. daedalea* at this site.

In the less thermally extreme GO at site AA, 29 out of 40 *P. daedalea* colonies (72.5%) harbored a single ITS2 type profile with D5 and/or D5a majority sequences (15 samples associated with D5-D5a-D5ai-D4-D5f-D5v, 9 with D5a-D5-D5ah-D4, 4 with D5-D5c-D4a-D5b-D4-D5i-D5a, and 1 colony with D5/D5a-D4-D4a-D2) (Fig. 2; Supplementary Table S3). The remaining 11 colonies (27.5%) had more than one ITS2 type profile with the following dominant profiles: D5a-D5-D5ah-D4 (in 4 colonies at a relative abundance of > 80%), D5-D5a-D5ai-D4-D5f-D5v (in 4 colonies at a relative abundance of > 76%), D5/D5a-D4-D4a-D2 (in 1 colony at 90.3%), D1/D4/D2-D4c-D1c-D1h (in one colony at 79.3%), and C39-C39q-C1-C39b-C39p (in 1 colony at 93.7%). The latter profile was also present in 3 of the colonies at low abundance (< 15%). Lastly, profiles that were present at low abundances of < 5% included *S. microadriaticum* variants (A1, A1-A1bw-A1bx, and A1-A1eq-A1ep), C3 and C15 genotypes (C3yd/C3yc-C3-C3gulf, C15h-C15o-C15k, C15h, C3/C15h-C3gulf), *D. glynnii* variants (D1/D2 and D1) as well as D5-D5a-D5f (Fig. 2; Supplementary Table S3).

Decadal comparison of Symbiodiniaceae population diversity in *Platygyra daedalea* between 2012 and 2022

The circumstance that we sampled the same reefs as those by a previous study a decade ago (Howells et al. 2020) provided a unique opportunity to compare symbiont community composition of *Platygyra daedalea* in the PAG (site SY) and GO (site AA) over a long temporal scale. Sequencing effort was similar and comparable between the two studies to infer biodiversity patterns (Supplementary Figure S3). We found striking differences between the two time points in that prevalent ITS2 type profiles in 2012 were absent in 2022 and vice versa for all three Symbiodiniaceae genera (i.e., *Symbiodinium*, *Cladocopium*, *Durusdinium*) (Fig. 3A, Supplementary Figure S4). More specifically, (i) dominant ITS2 type profiles in 2012 were not present in 2022 or diminished in abundance, (ii) several ITS2 type profiles appeared at AA in 2022 that were not observed in 2012 at either location, (iii) only very few type profiles were present in both years or at both sites (Fig. 3A, Supplementary Table S5). Of the 35 ITS2 type profiles found across both sites and years, 17 were identified in 2012 and 26 in 2022, of which only 8 were identified in both years and 3 were shared between sites (Fig. 3A). Of a total of 9 *Symbiodinium* type profiles, 4 were present in 2012 and 7 were present in 2022, only 2 of which were present at both time points (A1, A1-A1bw-A1bf-A1bx-A1eb), and only 2 of which were shared between sites (A1, A1-A1bw-A1bx). Similarly, for *Cladocopium* of a total of 14 genotypes, 7 were present in 2012 and 10 were present in 2022, only 3 of which could be detected at both time points and none of which were shared between both sites. For *Durusdinium*, of 12 ITS2 type profiles found across both years, 6 were present in 2012 and 9 in 2022 with only 3 being present in both years, none of which were shared between sites SY and AA. Thus, Symbiodiniaceae assemblage was significantly different between sites, but more importantly, changed significantly at each site over the course of the decade (PERMANOVA; $p = 0.001$, Site $R^2 = 0.147$, Year $R^2 = 0.087$, Species:Site $R^2 = 0.088$, Residuals $R^2 = 0.678$; Supplementary Data S1). Focusing on temporal differences within sites, Symbiodiniaceae diversity slightly decreased overall from 2012 to 2022 (ANOSIM: $R = 0.2167$, $p = 0.001$, 2012: 12 ITS2 type profiles vs. 2022: 11 ITS2 type profiles) in the PAG (site SY), while conversely, it substantially increased in the GO (site AA) (ANOSIM: $R = 0.3543$, $p = 0.001$, 2012: 6 ITS2 type profiles vs. 2022: 17 ITS2 type profiles). Principal component analysis (PCoA) revealed strong genetic differentiation between ITS2 type profiles of *Durusdinium* compared to the other two genera and moderate differentiation by sampling year as well as collection site, particularly in *Cladocopium* and *Durusdinium* (Supplementary Figure S5).

In terms of within-species diversity for *C. thermophilum*, of the 7 genotypes present in 2012, only 3 were also present in 2022 (C3-C3gulf-C3d-C3i-C115c-C115b-C3ai-C3ak-C18a, C3-C3gulf-C3d-C3i-C115c-C115b-C3ak, C3-C3gulf-C3d-C3i-C115c-C3ak-C3al) (Fig. 3A). Of these, 2 were present at similar prevalence in both years, while 1 profile (C3-C3gulf-C3d-C3i-C115c-C3ak-C3al) was abundant and dominant (up to 100% relative abundance) in 13 colonies in 2012, but was found in only 2 colonies in 2022 (Fig. 3B). Furthermore, multiple genotypes (C3-C3c-C3gulf-C3I-C3m-C3r, C3-C3gulf-C3d-C3ai-C3ak-C115b-C3i-C115c, C3/C3c-C3gulf, C3/C3c-C3gulf-C3aq) disappeared in 2022, while 2 novel genotypes appeared in 2022 (C3/C15h-C3gulf, C3yd/C3yc-C3-C3gulf). Notably, all profiles harboring the *C. thermophilum*-specific sequence C3-C3gulf or C3/C3gulf contributed significantly (SIMPER test $p < 0.01$) to the dissimilarity between the two years, indicating that *C. thermophilum* genotype composition in the two coral populations changed. By comparison, *S. microadriaticum* ITS2 type profile diversity increased notably from 4 in 2012 to 7 in 2022 with the appearance of a novel profile at moderate prevalence (A1-A1bw-A1bx) (Fig. 3A). Likewise, *Durusdinium* diversity increased from 6 in 2012 to 9 in 2022 with a notable absence in 2022 of a very abundant genotype in 2012 (D5-D5a-D5f-D4), concomitant with the appearance of several novel ITS2 type profiles in 2022 that were undetected in 2012 (D1, D1/D4/D2-D4c-D1c-D1h, D5-D5a-D5f), some at high prevalence in 2022 (D5-D5a-D5ai-D4-D5f-D5v, D5a-D4-D5ah-D4-D4a, D5a-D5-D5ah-D4-D5d) (Fig. 3A). Similar to the *C. thermophilum* genotypes, ITS2 type profiles belonging to the genus *Durusdinium* contributed significantly (SIMPER test $p < 0.01$) to the dissimilarity between time points, suggesting that algal population diversity associated with *P. daedalea* changed within the 10 years between 2012 and 2022. We found a similar number of colonies that harbored > 1 symbiont type profile between both years in the PAG (14 out of 47 colonies (29.8%) in 2012 vs. 13 out of 39 colonies (33.3%) in 2022) (Fig. 3B). While a diversity of background symbionts from *Symbiodinium*, *Cladocopium*, and *Durusdinium* was found in colonies in 2012, the majority of colonies with background symbionts in 2022 harbored different type profiles of *S. microadriaticum* (12 out of 13 colonies, 92.3%). Conversely, in the GO, *P. daedalea* exhibited a very uniform algal symbiont association in 2012 with few colonies having > 1 ITS2 type profile (6 out of 32 colonies, 18.75%), while this number almost doubled in 2022 (11 out of 40 colonies, 27.5%) alongside an increased diversity of symbiont genotypes, including from the genus *Symbiodinium*, which were absent in 2012 (Fig. 3B).

Discussion

To assess extant algal species and population diversity, we sampled two common coral species, *Porites harrisoni* and *Platygyra daedalea*, at two sites in the southern PAG and one site in the neighboring, less extreme GO. These two coral species are representative of the remaining coral biodiversity in the southern PAG, as they are among the few taxa (estimates are typically around three to four major genera per site and a maximum of eleven genera across all of the southern PAG) that have persisted under the increasingly extreme environmental conditions, particularly bleaching-related mortality from recurrent marine heat waves (Burt 2024). Notably, although the PAG is already one of the most extreme environments where corals live, it is currently warming at twice the rate of the world's oceans (Al-Rashidi et al. 2009; Riegl et al. 2018). Thus, besides the assessment of the contemporary species and population diversity, it is of importance to understand stability of symbiont diversity and host association over time under increasing warming. To address this aspect, we assessed the change in Symbiodiniaceae community composition over a long time period by comparing symbiont diversity associated with *P. daedalea* populations at two reefs sampled in 2012 (Howells et al. 2020) and 2022 (this study). This was achieved by combining the two datasets, taking advantage of the circumstance that both studies employed sequencing of the ITS2 marker gene region and subsequent SymPortal analysis, a standardized framework for symbiont comparison based on ITS2 type profiles (Davies et al. 2023; Hume et al. 2019).

Extant Symbiodiniaceae diversity shaped by host specificity and environment

The broad differences between Symbiodiniaceae associations in the PAG and GO underscore the role of the environment, such as thermal stress, as a driving force in shaping symbiotic partnerships. Corals in the PAG, particularly at the thermally extreme southwestern site SA, were exclusively dominated by *Cladocopium thermophilum* ITS2 type profiles, consistent with the previously recognized thermal tolerance of this algal species (Hume et al. 2015; Ochsenkühn et al. 2017). In contrast, corals in the GO exhibited a more diverse symbiont community, including a notable presence of diverse type profiles of *Symbiodinium microadriaticum* and *Durusdinium* (D5 majority sequence). This pattern likely reflects the GO's relatively milder conditions, which may enable the persistence of a broader range of symbiont genera. These findings align with previous observations of coral-Symbiodiniaceae associations, where extreme environments favor the dominance of specialized, thermally resilient symbionts (Baker et al. 2013; LaJeunesse et al. 2018). Despite such environmentally driven constraints, host specificity was a factor influencing Symbiodiniaceae composition (PERMANOVA results: Site $R^2 = 0.163$, Species $R^2 = 0.099$, Species:Site $R^2 = 0.089$; $p = 0.0001$) with distinct ITS2 type profiles observed in *P. daedalea* and *P. harrisoni* at each site. In other words, distinct genotypes within discrete Symbiodiniaceae species associated with distinct coral host species. Similar findings were observed in the Caribbean for strains of *Symbiodinium 'fitti'* that associate specifically with *Acropora palmata* or *A. cervicornis* (Reich et al. 2021). It is also worthwhile to note that *Porites harrisoni* assumingly transmits its algal symbionts vertically, whereas *Platygyra daedalea* acquires its symbionts horizontally (Howells et al. 2016). Horizontal transmission is commonly associated with increased ecological and adaptive flexibility, while vertical transmission favors stability and fidelity, although this difference was not a discernable factor in our study. Moreover, despite restricted gene flow between the PAG and GO, the occasional presence of overlapping host and symbiont genetic clusters suggests that some exchange does occur (Howells et al. 2020; Smith et al. 2022), which may underlie the presence of shared, albeit rare algal symbiont associations.

At large, diversity of associated Symbiodiniaceae in both coral species was rather low in the PAG ($n = 18$ out of 42 algal ITS2 type profiles) and associations were more diverse in the GO ($n = 31$ out of 42 algal ITS2 type profiles). Despite the low diversity in the PAG, the number of ITS2 type profiles of *C. thermophilum* within PAG corals is notable ($n = 7$). In line with previous analyses (Hume et al. 2019; Howells et al. 2020), *C. thermophilum* comprised multiple genotypes that were associated in a host species-specific manner. Such host fidelity likely reflects evolutionary adaptations that optimize host-algal symbiosis under localized conditions. However, it remains to be determined to what level such specificity extends. It may extend to a coral–algal genotype-genotype or allele-matching level (Baums et al. 2014; Parkinson et al. 2015), both of which are supported by the observation that certain ITS2 type profiles are shared between colonies, while others are not. Incorporation of colony and algal symbiont high-resolution genotyping in future studies should provide further insight.

Symbiodiniaceae community shifts in *P. daedalea* over the last decade in the PAG and GO

Coral–algal associations of *P. daedalea* in the PAG and GO exhibited notable changes over the course of 10 years, with implications for coral resilience in these harsh environments. By sampling the same species in the same locations over a decade apart, we captured considerable changes in the Symbiodiniaceae community structure within these coral populations, with a substantial shift in ITS2 type profiles. The changes in prevalence of *C. thermophilum* ITS2 type profiles are especially noteworthy, given its assumed importance in conferring thermal tolerance to PAG corals (Hume et al. 2015). In a previous study, bleaching resistance correlated with higher abundance of *C. thermophilum* at a coral population level (Howells et al. 2020). The decline of a formerly abundant genotype (C3-C3gulf-C3d-C3i-C115c-C3ak-C3al) alongside other genotypes and the emergence of novel ones indicate putatively important changes for the *P. daedalea* populations in both the PAG and GO. Interestingly, the most drastic difference could be observed in *Durusdinium* type profiles, where a formerly abundant ITS2 type profile (D5-D5a-D5f-D4) completely disappeared, while a previously undocumented type profile (D5-D5a-D5ai-D4-D5f-D5v) became prevalent in the GO. Thus, formerly dominant algal genotypes became rare or extinct in the course of a decade, prompting the question whether the respective coral colonies were able to associate with different algae or if they became rare or extinct themselves (Sampayo et al. 2008). While the observed within-species shifts in dominant Symbiodiniaceae genotypes are striking, they reveal—at the same time—a pattern of species-level (in the case of *Cladocopium thermophilum*) and genus-level (in the case of *Durusdinium* D5) stability (Howells et al. 2020). Long-term stability of host-algal associations has been demonstrated for many different habitats and across a variety of temporal scales (Goulet and Coffroth 2003). Studies show that while corals may exhibit temporary shifts in symbiont communities in response to bleaching (Thornhill et al. 2006; Hume et al. 2020), reciprocal transplantation (Sampayo et al. 2008), or experimental establishment of heterologous symbiont associations (Elder et al. 2023), these changes are typically constrained to compatible symbiont types and are often followed by reversion to the original symbiont community (LaJeunesse et al. 2009; Turnham et al. 2025). Of note is the long-term monitoring effort of a recent study (Lewis et al. 2024), which demonstrated that coral colonies retained genetically homogeneous symbiont populations across multiple years. The cases where intracolonial variation in symbiont genotypes was found were attributed to the persistence of coexisting clonal strains rather than novel symbiont acquisitions or shifts in symbiont identity. This suggests a level of symbiont fidelity that extends to the clonal level (i.e., algal genotypes within a species) with major implications for the ability of corals to counter ongoing warming through symbiont switching. Namely, the finely tuned and evolutionarily stable nature of coral–algal partnerships suggests that symbiont switching is not a readily accessible pathway for coping with warming, as alternative associations are likely less attuned to the respective host genotype.

It should be noted that between the sampling of both studies, severe warming events occurred: A severe bleaching event with mass mortality was recorded in 2017, followed by an extreme temperature event in 2021, albeit with reduced mortality rates likely due to the already diminished coral populations at the PAG sites. At the time of sampling, we observed very low coral diversity, with *P. daedalea* being one of the last coral species on the disturbed reefs in the PAG, making it unfeasible to sample this species at the hottest site in the southwestern PAG. It is important to note that we cannot ascertain whether we sampled the same colonies as the previous study (Howells et al. 2020). Thus, we are unable to unequivocally determine the level of change in symbiont communities present within single colonies. In other words, one may argue that we simply sampled different colonies. Although this would explain the change-over of rare genotypes, it cannot explain the absence of formerly abundant genotypes and the presence of novel dominant ITS2 type profiles. Underlying this is the notion that sample sizes were sufficient to support population-level inferences about changes in community composition over the course of a decade. Despite the importance of long-term studies to capture consistency of host-algal association, thereby informing their stability under ongoing warming, dynamic interannual and seasonal changes in algal symbiont communities are not resolved, which further contribute to the understanding of host–symbiont dynamics.

Overall, we observed a modest decline in Symbiodiniaceae diversity (12 ITS2 type profiles in 2012 vs. 11 ITS2 type profiles in 2022; ANOSIM: $R = 0.2167$, $p = 0.001$) over the last decade in the PAG, consistent with the strong selective pressures of high temperatures and salinity that are thought to limit symbiont assemblages in this extreme environment (Howells et al. 2020). In contrast to the PAG, the GO exhibited a stark increase in Symbiodiniaceae diversity in *P. daedalea* (6 ITS2 type profiles in 2012 vs. 17 ITS2 type profiles in 2022; ANOSIM: $R = 0.3543$, $p = 0.001$). As a result, Symbiodiniaceae community composition became more dissimilar and diverse, with new profiles from all three genera (*Symbiodinium*, *Cladocopium*, and *Durusdinium*) appearing in 2022 that were not identified in 2012. Nevertheless, ITS2 type profiles with a D5 majority sequence were the most prominent in the GO in both years. We further observed some coral colonies in the GO exhibiting mixed symbiont associations, with varying relative abundances of symbionts from different genera. To date, the biological/ecological significance of such mixed associations remains unclear and warrants further investigation.

Decadal symbiont turnover highlights urgent need for conservation of coral population genetic diversity

Long-term studies are invaluable for tracking the impacts of prolonged environmental changes, such as those induced by climate change, emphasizing the benefit of standardized methodologies and analytical frameworks to allow for such comparisons (Davies et al. 2023; Hume et al. 2019; Voolstra et al. 2025). Although colony-level variability cannot be accounted for in the analysis here, the observed shifts in symbiont community composition at a population level likely reflect broader ecological processes, such as differential mortality, selective pressures, and the proliferation of thermally tolerant genotypes. While our study is limited to a single (seasonal) sampling, previous studies have demonstrated overall stability in Symbiodiniaceae community composition across seasons in the PAG and GO (Hume et al. 2015; Smith et al. 2017; D'Angelo et al. 2015; Howells et al. 2020). Our findings support that Symbiodiniaceae exhibit symbiont fidelity at the species level, i.e., all corals are associated with *C. thermophilum* in the southern PAG and the majority of corals associate with *Durusdinium* D5 ITS2 type profiles in the GO. However, and importantly, the turnover of prevalent genotypes is a warning sign of what we may experience in other places in the near future. Observed shifts in coral–microalgal associations, such as the emergence of novel genotypes or the decline of previously dominant ones, can arise from different processes. They may represent ecological dynamics, where local conditions favor particular symbionts, or adaptive responses, where selective pressures drive the retention of or novel association with thermally more tolerant genotypes (Hume et al. 2016, 2018a, b; Howells et al. 2016). Alternatively, some changes may be neutral, reflecting demographic stochasticity or drift within symbiont populations. However, it is important to note that host association itself is a selective step, and thus such drift would not necessarily be observed in microalgal assemblages found *in hospite*. Distinguishing among these processes is crucial, as the trajectory of symbiont turnover provides insight into whether shifts are transient fluctuations or reflect longer-term responses to environmental change. Without long-term, high-resolution data, the relative contribution of these processes remains unresolved. In *P. daedalea*, limited coral host genetic connectivity was observed between the PAG and its neighboring populations (Smith et al. 2022). This underscores the need for conservation strategies that preserve not only coral cover but also the genetic diversity of coral species and their symbiont communities, thereby supporting coral adaptability under ongoing climate change.

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Author contributions CRV conceived the study. CRV and AF conceptualized the study. CRV, RA, HM, GP, and AF collected the coral samples. JAB provided field support. CRV, LB, JV, NB, IB, and DJB provided funding. AF performed the laboratory work. AF and CRV conducted the data analysis, interpretation, visualization, and the writing of the manuscript with input from all authors. All authors approved the final manuscript .

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Data availability The SymPortal analysis of the dataset of *P. harrisoni* and *P. daedalea* collected in 2022 can be accessed at: https://symportal.org/data_explorer/?Study=202307_afiesinger_UAE_GS. The combined SymPortal analysis including *P. daedalea* from 2012 (Howells et al. 2020) and 2022 (this study) used for the decadal comparison can be accessed at https://symportal.org/data_explorer/?Study=202402_afiesinger_UAE_GS_10yearcomp. Source code for all analyses and figures is available at the following GitHub repository: https:/github.com/afiesinger/UAE_PAG_Symbiodiniaceae. Raw FASTQ sequencing files are accessible at NCBI under BioProject PRJNA1188806 (https://www.ncbi.nlm.nih.gov/bioproject/PRJNA1188806) as part of the Umbrella Project PRJNA749006 (https://www.ncbi.nlm.nih.gov/bioproject/PRJNA749006).

Declarations

Conflict of interest The authors declare no competing interests.

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