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REPORT

Pocillopora host–symbiont interactions along an extreme environmental gradient

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Abstract Pocilloporid corals and their Symbiodiniaceae symbionts have co-evolved. Host–symbiont associations might be driven by adaptation to distinct ecological niches. Here, we used single nucleotide polymorphisms (SNPs) to examine host population structure, characterised Symbiodiniaceae associations in shaded and exposed areas of coral using Internal Transcribed Spacer (ITS2) metabarcoding, and identified photobiological phenotypes of *Pocillopora acuta* colonies from two acidic, deoxygenated and highly variable temperature mangrove environments versus two adjacent reef locations. We found two genetic clusters of *P. acuta* with evidence of potential hybrid individuals. Limited admixture suggests low levels of gene flow between the reef and mangrove sites. Each of the two lineages was predominantly associated with either reef or mangrove habitats, with distinct dominant symbionts (*Cladocopium* (reef) and *Durusdinium* (mangrove)), each with different photobiological strategies. Hybrid individuals exhibited greatest heterogeneity in ITS2 profiles compared to the two other populations. Our results provide evidence that the two lineages are part of a known species complex as suggested by population structure and morphological differences. The genetic distinctiveness of the sampled populations emphasises the unique diversity within the extreme environments. Consequently, conservation efforts should aim to minimise additional anthropogenic impacts at these sites.

Keywords Genetic diversity · Population structure · *Pocillopora* · Symbiodiniaceae · Photobiology

Introduction

There are global efforts to enhance coral resilience through novel active interventions (Anthony et al. 2017; van Oppen et al. 2017; Kleypas et al. 2021) due to ongoing habitat loss and degradation of essential ecosystem services (Stella et al. 2011; Hughes et al. 2017; IPCC 2023). Within this context, corals living in extreme and/or marginal coral habitats (Schoepf et al. 2023) have gained increasing attention (Camp et al. 2019; Burt et al. 2020) for their potential to provide naturally resilient coral populations (Caruso et al. 2021; Savary et al. 2021; Camp 2022) either through refuge or innate tolerance (Camp et al. 2018b) or to act as a natural laboratory to study the mechanisms corals use to survive hostile conditions (Camp et al. 2018a).

Mangrove lagoons are an example of an extreme and/or marginal coral habitat (Rogers 2017; Camp et al. 2019; Maggioni et al. 2021). Mangrove coral systems have been documented at numerous sites around the world including in the Caribbean (Rogers 2017; Stewart et al. 2021) and the Indo-Pacific (Camp et al. 2016, 2019, 2020), where taxonomically diverse coral communities are present despite suboptimal

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conditions (Camp et al. 2019, 2020; Stewart et al. 2021). However, the ability of corals to live in extreme environments often comes with fitness trade-offs (Camp et al. 2019; Scucchia et al. 2023). Additionally, mangrove corals have been found to associate with different Symbiodiniaceae species and different bacterial communities compared to neighbouring reefs (Camp et al. 2019; Haydon et al. 2021; Ros et al. 2021; Tanvet et al. 2023). These community differences may be due to the potential limited dispersal capacity of corals in extreme systems (Lord et al. 2023). However, how coral host population structure across reef to mangrove systems influences Symbiodiniaceae community composition has yet to be considered and is an objective of this study for the coral species *Pocillopora acuta*.

Pocillopora acuta is a dominant coral species found within the Woody Isles mangrove lagoon on the Great Barrier Reef (GBR). *Pocillopora acuta* within this system has been extensively studied in comparison with the neighbouring reef specimens that live in benign environmental reef conditions (Camp et al. 2019; Haydon et al. 2023). However, *Cladocopium-Durusdinium* dynamics at intermediate sites along the reef-to-mangrove gradient remain unknown. Pocilloporid corals and their Symbiodiniaceae symbionts exhibit co-phylogeny (Johnston et al. 2022; Thornhill et al. 2014), with niche diversification in the coral host as the primary driver of this symbiont speciation (Byler et al. 2013). Mixed-mode transmission of algal endosymbionts has been observed in brooding Pocilloporid corals where larvae obtain symbionts vertically but can also acquire symbionts from the environment (Byler et al. 2013; Quigley et al. 2018). Since offspring of *P. acuta* initially obtains symbionts from their parents, the diverging symbiont community structure across Woody Isles mangrove and the Low Isles reef habitats may reflect reproductively isolated coral populations. Alternatively, the species-specific associations between *P. acuta* and members of Symbiodiniaceae across mangrove and reef habitats (Camp et al. 2019, 2020; Haydon et al. 2021; Ros et al. 2021) could reflect proliferation of rarer specialised algal symbionts that are better adapted to extreme environments (Oliver and Palumbi 2011; Camp et al. 2019). On ecological timescales, host–symbiont partnerships can be flexible depending on abiotic conditions (Johnston et al. 2022). For example, corals are capable of symbiont shuffling across environmental gradients (Hennige et al. 2010). Self-shading in corals can lead to the creation of microhabitats with shaded and exposed environments (Lewis et al. 2022). Whether microhabitats result in different Symbiodiniaceae associations for *P. acuta* has not been considered, and specifically whether the Symbiodiniaceae found associating with the mangrove *P. acuta* are indeed present on the reef when distinct (shaded vs. exposed) parts of the colonies are sampled remains unknown.

This study combines population analysis of the coral host and Symbiodiniaceae community analysis at two mangrove lagoon sites and two adjacent reef sites on the Great Barrier Reef (GBR) to: i) determine the degree of isolation between *P. acuta* coral communities along the mangrove-reef gradient; ii) assess if sampling shaded and exposed areas of the coral reveals intra-colony Symbiodiniaceae communities; and iii) evaluate whether intra-habitat sites have the same host and Symbiodiniaceae structures. Additionally, for a subset of specimens, we identified their photobiological phenotypes to assess potential trade-offs related to photosynthetic light harvesting across the environmental gradient. The outcomes of this research provide important information on the genetic structure of *P. acuta* in extreme mangrove systems that have implications for their considered use in future active interventions.

Materials and methods

Sample collection

Corals were sampled across four sites along a natural environmental gradient from the reef site (Low Isles) to the adjacent Woody Isles mangrove lagoon on the northern GBR, Australia (Fig. 1a–c; Fig. S1). Sampling was conducted in October 2022. At each site, six coral colonies were sampled between 0.5 and 2.0 m depth while snorkelling. Collected colonies were at least 1 m distance from each other to limit sampling of clones. From each colony, five fragments (< 5 cm in length) were removed using bone cutters. Different light regions of a coral branch were sampled to examine whether intra-colony differences in Symbiodiniaceae communities were present (Fig. S2). Twenty fragments used in photobiological measurements were temporarily stored in native seawater (see section Coral photobiological-based phenotype). Samples used for host and symbiont analysis ($n = 96$) were preserved in 100% ethanol and stored at 4 °C at the University of Technology Sydney, Australia, until further processing.

Abiotic factors: temperature and pH

Temperature and pH were measured every hour from February 2022 to February 2023 in the inner mangrove lagoon and on the outer reef with HOBO MX2501 loggers (calibration temperature: 25 °C). Data points for pH and temperature outside 25 ± 10 °C were removed from the analysis due to manufacturer's accuracy guidelines (Methods S1; Fig. S3; Fig. S4). Temperature for both sites was measured with a second logger (HOBO Pendant) as a back-up (Fig. S5). The pH probes were calibrated with NBS buffers and corrected for a Tris buffer (Dickson lab)

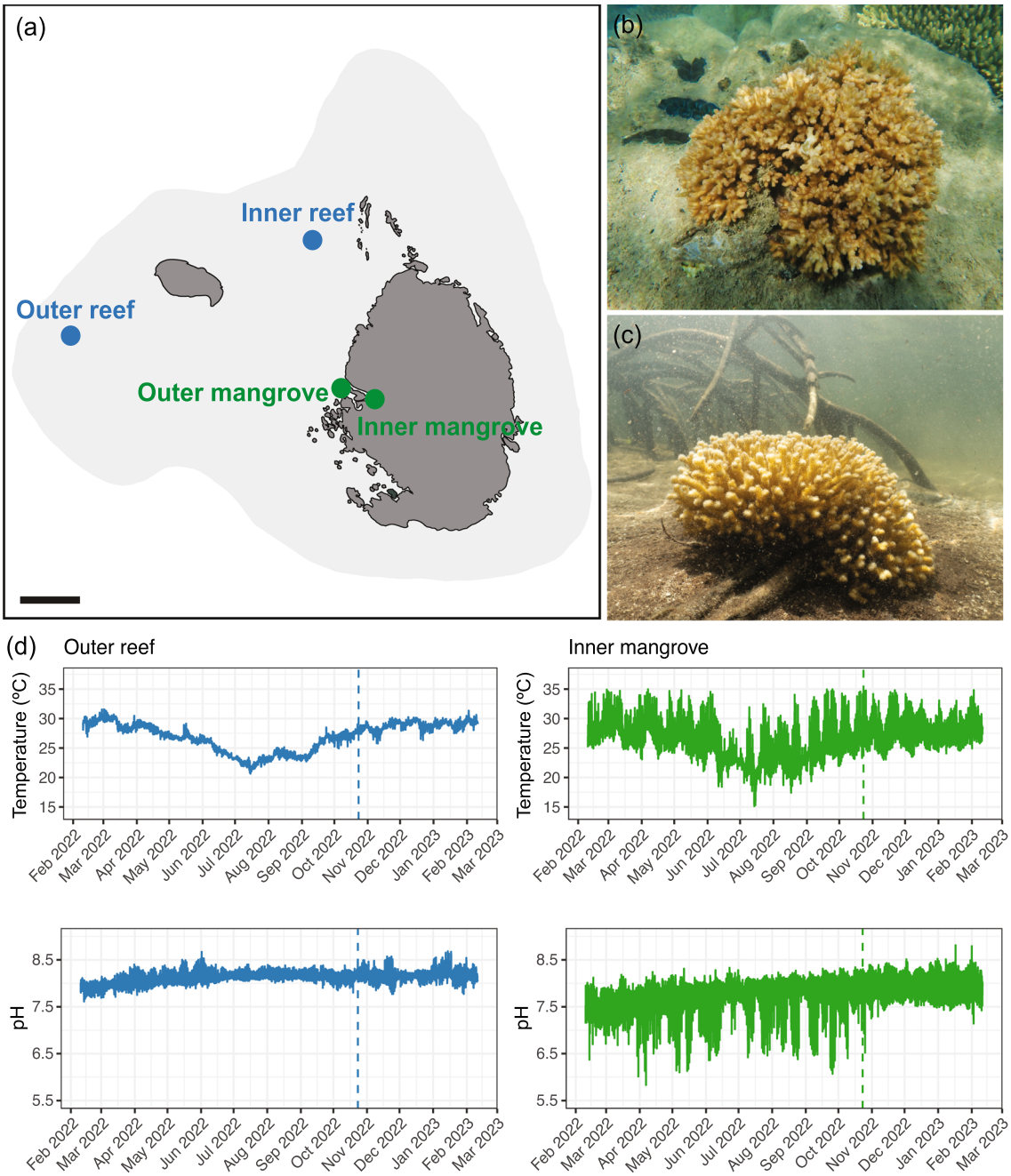

Fig. 1 Study site and environmental conditions. **a** Coral sampling occurred across a gradient from the Low Isles reef (blue dots) towards the nearby Woody Isles mangrove lagoon (green dots) on the northern Great Barrier Reef. Black line represents a 100 m distance. **b** Colony of *Pocillopora acuta* sampled on the outer reef site. Photo: Chiara M. Duijser. **c** *P. acuta* colony sampled in the inner mangrove lagoon. Photo: Jake Crosby. **d** Temperature and pH measurements for the outer reef and inner mangrove habitats collected every hour from February 2022–2023. Data points outside calibration range (25 ± 10 °C) were removed. Blue and green dotted lines represent the coral sampling time

for total scale as per Hu et al. (2022). Temperature and pH were compared between habitats using a Wilcoxon rank sum test when assumptions for a two sample t test were violated. Shapiro–Wilk test was used to check normality of the data, and Levene's test was used to assess homogeneity of variance. All statistical analyses were performed using R v.4.2.3 (R Core Team 2021).

SNP genotyping

Coral host samples were sent to Diversity Arrays Technology (DArT, Australia) for sequencing. Raw reads were processed using DArT PL's proprietary algorithm DArTsoft14 (Methods S2). The DArTseq analytical pipeline resulted in 36,706 SNPs which were filtered and analysed using packages *dartR* v.2.7.2 (Gruber et al. 2018) and *adegenet* v.2.1.10 (Jombart 2008). Before filtering, data were checked for algal symbiont contamination by running a BLAST alignment against 12 Symbiodiniaceae reference genomes (http://sampgr.org.cn/index.php/download) using the function gl.blast. One inner reef sample failed the DArTseq protocol. SNPs were filtered using removal of secondaries, reproducibility > 0.995, locus call rate > 0.95, individual call rate > 0.80, read depth ≤ 5 and ≥ 50, minimum allele frequency > 0.05, removal of monomorphic loci and imputation of missing data using nearest neighbour function. We tested an alternate filtering process to ensure the data were not impacted by any filtering step (or overfiltering; Method S6). We tested for the presence of clones based on a calculated genomic relationship matrix using the function gl.grm (Speed and Balding 2015; Goudet et al. 2018; Gruber et al. 2018). Clones with the greatest proportion of missing data were removed.

STRUCTURE and Discriminant Analysis of Principal Components (DAPC) were run to identify population structure in the coral host. Structure was analysed using the StrAuto software (Chhatre and Emerson 2017) with a burn-in period of 25,000 followed by 100,000 Markov Chain Monte Carlo (MCMC) steps for K clusters ranging between 1 and 5 with five runs per K without setting prior populations. The optimal number of populations (K) was chosen based on the ΔK method and mean LnP(K) (Evanno et al. 2005). DAPC was run in R using find.clusters function from the *adegenet* package (Jombart 2008; Jombart et al. 2010).

Based on STRUCTURE and DAPC results, further analyses were performed on the estimated populations with potential hybrid individuals included. Individuals were classified as "hybrid" when they showed < 0.9 assignment to one genetic cluster based on STRUCTURE analysis. Tested population models can be found in Methods S3. Variation between populations was visualised using principal component analysis (PCA) (Jombart 2008; Gruber et al. 2018). Pairwise F_{ST} (fixation index) values were calculated to investigate genetic differentiation among sites as a measure of population structure using the gl.fst.pop function with 999 bootstraps. Additionally, analysis of molecular variance (AMOVA) was used to test for genetic variation at different hierarchical levels, i.e. between populations, between individuals within populations, and within individuals using 1000 permutations (Excoffier et al. 1992).

Coral photobiological-based phenotype

Light-Induced Fluorescence Transient-Fast Repetition Rate fluorometry (LIFT-FRRf; Soliense Inc., USA) was used for a subset of specimens (inner mangrove ($n = 10$) and outer reef ($n = 10$)) as a non-invasive technique to determine the photochemical efficiency of photosystem II (PSII) and identify photobiological phenotypes across sites (Kolber 1998; Suggett et al. 2022). On the research vessel, a small fragment (~ 3 mm in diameter) was taken from each collected sample, put in a numbered zip lock bag and kept open in an aerated aquarium filled with native seawater. Measurements were carried out within 1–2 h after collection. Each fragment was placed into the optical chamber filled with 1.5 mL filtered native seawater, which was exchanged after every measurement. Coral fragments were exposed to light pulses (470 nm) after a brief (5 min) period in darkness. The LIFT-FRRf delivered a series of sub-saturating flashlets (single turnover fluorescence), i.e. 100 flashlets with a length of 1.6 µs at 2.5 µs intervals and 127 flashlets of 1.6 µs at exponentially increasing intervals over ~ 30 ms, to examine PSII saturation and relaxation kinetics, respectively (Suggett et al. 2022). Measurement points were corrected with a baseline fluorescence signal for filtered native seawater. Model fits were performed in the LIFT-FRRf Soliense software. A detailed explanation of all parameters can be found in Table S1, Suggett et al. (2022) and at www.soliense.com.

Outlier samples were detected based on Mahalanobis distance within the *rstatix* v.0.7.1 package (Kassambara 2022); one observation from the inner mangrove was omitted after outlier detection. Photobiological-based parameters were normalised using the bestNormalize function. After normalisation, parameters were analysed using PCA, and a permutational multivariate analysis of variance (PERMANOVA) was performed on the PCA results to test for significant differences in overall photobiological phenotype. The effect of site and colony position and population and colony position on photobiological phenotypes was investigated using a PERMANOVA with the adonis2 function from the package *vegan* (Oksanen et al. 2022) with colony included as a random factor. The PERMANOVA assumption of homogeneity of dispersion around group centroids was checked using the function betadisper from the package *vegan* v.2.6.4 (Oksanen et al. 2022).

Symbiodiniaceae diversity

DNA was extracted from Symbiodiniaceae pellets using the Qiagen DNeasy Blood & Tissue Kit (Qiagen, Germany) according to the manufacturer's instructions (Methods S4). Different members of the Symbiodiniaceae family were characterised based on the Internal Transcribed Spacer 2 (ITS2) rDNA region using the ITSintfor2 (LaJeunesse et al.

2000) and ITS2-reverse (Coleman et al. 1994) primers. Amplified samples (Methods S5) were sent to the Australian Genome Research Facility for Next Generation Sequencing (Illumina MiSeq platform). ITS2 sequences were uploaded to the SymPortal framework to identify 'defining intragenomic variants' (DIVs). Based on these DIVs, distinct Symbiodiniaceae taxa were identified (Hume et al. 2019). The effect of habitat on ITS2 Symbiodiniaceae sequence diversity (based on generalised UniFrac distance with alpha = 0.5) (Chen et al. 2012; Marzonie et al. 2024) was investigated using a PERMANOVA with the adonis2 function from the package *vegan* (Oksanen et al. 2022). We also tested for an effect of colony position (shaded vs. exposed) nested within each habitat. Pairwise differences were analysed using the function pairwise.adonis in the *pairwiseAdonis* v.0.4.1 package (Martinez Arbizu 2020) based on 999 permutations. Additionally, relationship and correlation between the coral DArTseq distance matrix and symbiont ITS2 pairwise UniFrac distances were explored using Procrustes analysis and PROTEST function in the *vegan* package based on 999 permutations (Peres-Neto and Jackson 2001; Oksanen et al. 2022).

Results

Abiotic factors: temperature and pH

Temperature and pH from February 2022–2023 were highly variable in the inner mangrove, compared to the outer reef site that was comparatively more stable (Fig. 1d). The daily mean pH was lower and the range greater in the mangrove lagoon 7.81 (5.83–8.81) relative to the reef 8.11 (7.61–8.68; Wilcoxon rank sum test, $W = 5871.5$, $p < 0.001$). The low pH of 5.83 was documented at a temperature of 34.98 °C, and thus, caution is noted on the accuracy of this value (Methods S1). Average diel temperature was higher for the reef (27.0 ± 0.03 °C) compared to the mangrove (26.7 ± 0.03 °C) habitat (Wilcoxon rank sum test, $W = 60560$, $p = 0.025$). However, peak temperature (around 15:00 h), was significantly higher in the mangroves (28.7 ± 0.15 °C) by ~ 1.4 °C, compared to the reef (27.3 ± 0.13 °C) (Wilcoxon rank sum test, $W = 82{,}808$, $p < 0.001$). Additionally, minimum and maximum temperatures were more extreme for the mangrove habitat with a range of 15.1–35.0 °C (noting higher temperatures were excluded as they were outside of the calibration range; see methods) compared to 20.7–31.6 °C. Sampling conditions during the week of collection (20–26 October 2022) are reported in Fig. S6.

SNP genotyping

The DArTseq analytical pipeline was used to genotype 24 individuals of the coral *P. acuta* with 36,706 bi-allelic SNPs. One sample failed the DArTseq protocol. Before imputation based on nearest neighbour function, 1.31% of the loci were classified as missing data. Of note, two inner mangrove individuals were identified as clones. After sequencing processing, filtering and clone removal, 2,075 high-quality SNPs were retained for the analysis ($n = 22$).

Identification of genetic clusters and genetic structure between lineages

A Bayesian STRUCTURE analysis and DAPC were used to identify clusters present in the dataset. Both analyses detected two genetic clusters ($K = 2$), indicating the presence of two populations in the dataset with some evidence of hybrids. Individuals from the reef sites showed majority ancestry to population 1, whereas individuals from the mangrove sites showed majority ancestry to population 2 in STRUCTURE analysis (Fig. 2ab). Six individuals showed admixture and were assigned to a third population of potential hybrids, predominantly individuals sampled from the outer reef. These results are consistent with the PCA on the genotypes (SNPs) which show the same partitioning into distinct groups, where admixed individuals show less genetic similarity towards the two main clusters (Fig. 2b). The first two principal components explained 76.1% of the variation with the first principal component accounting for 61.4% of the variance.

Genetic structure was mainly present between populations (61.8%) and within individuals (i.e. genetic variation within an individual's genome; 42.2%; AMOVA, $p < 0.05$) (Table S2a). There is very strong genetic differentiation between individuals belonging to population 1 and population 2 ($F_{ST} = 0.810$). On the other hand, the potential hybrid individuals showed the lowest pairwise genetic structure compared to population 1 ($F_{ST} = 0.405$) and population 2 ($F_{ST} = 0.499$) (Table S2b). Comparison of the data with the hybrids included in the two main populations and the hybrids removed (model 2 and model 4, respectively; Methods S3) showed that the hybrid individuals skew the data by showing less genetic differences (Table S3). Interestingly, a genomic relationship matrix analysis suggests that many of the reef specimens (mostly sampled from the inner reef) are closely related (Fig. S7).

Along with distinct F_{ST} values, there are slight morphological differences observed between coral colonies across environments (Fig. S8). Morphological differences combined with strong population structuring suggest that the sampled individuals belong to two distinct lineages with some hybridisation potential (hereafter referred to as

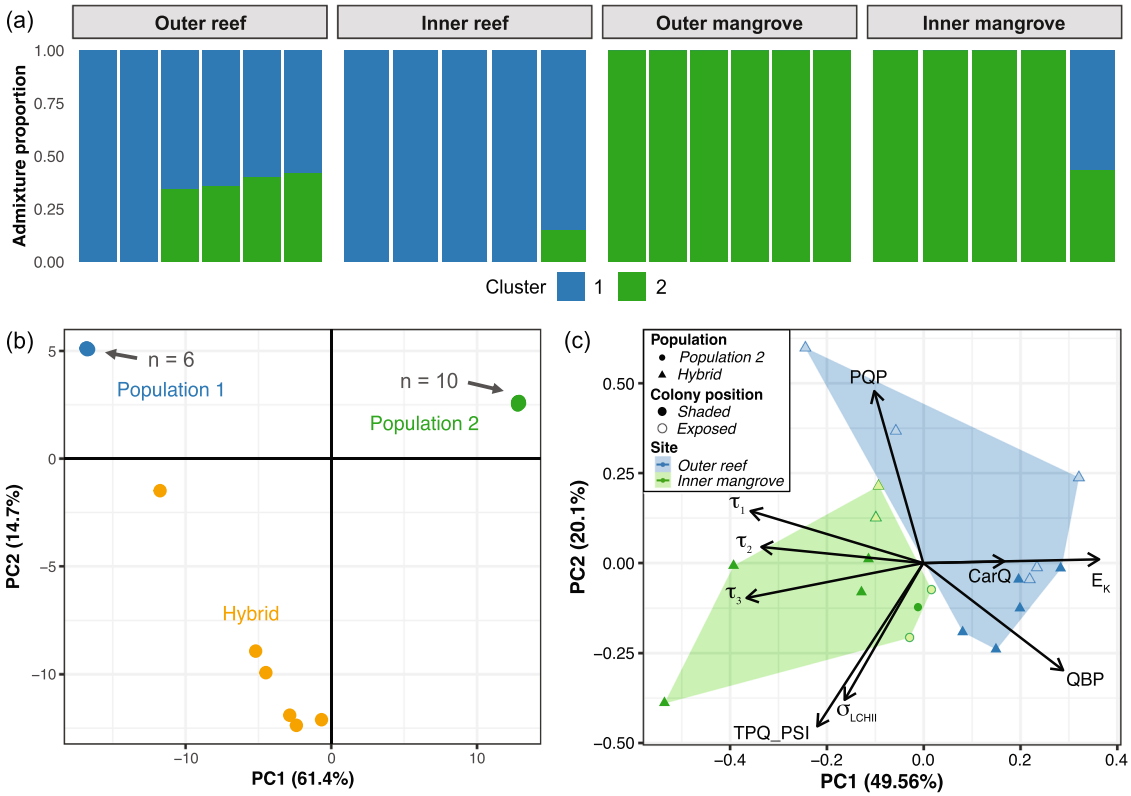

Fig. 2 **a** Individual cluster classifications of the coral host admixture proportions based on STRUCTURE and DAPC analysis. Each bar represents one individual. **b** Principal component analysis (PCA) of *Pocillopora acuta* across the three populations resulting from STRUCTURE and DAPC analysis. Variance explained by the first and second principal components is indicated on the axes. **c** PCA of 9 photophysiological parameters obtained with Light-Induced Fluorescence Transient-Fast Repetition Rate fluorometry (LIFT-FRRf). No individuals from lineage 1 were included in the photobiological analysis

"lineage 1", "lineage 2" and "hybrid") likely part of a known species complex (Smith et al. 2017).

Coral photobiological-based phenotype

To identify photobiological phenotypes between the reef and mangrove habitats, we conducted a multivariate analysis of parameters between the outer reef and inner mangrove site at the lowest light concentration. Collectively, the first two principal components accounted for 69.66% of the total variance in photo-physiological parameters. We found significant differences in photo-physiology looking at both the lineage level (PERMANOVA, $F_{(1,16)}=0.90$, $p=0.008$) and colony position ($F_{(1,16)}=1.83$, $p=0.008$), with colony included as a random factor. With clone removal, we found a significant interaction between lineage level and colony position (PERMANOVA, $F_{(1,11)}=0.68$, $p=0.038$) (Fig. S9ab). No individuals from lineage 1 were included in the photobiological analysis as distinct lineages were identified after this analysis was performed. Additionally, photobiological phenotype clusters differed significantly between individuals sampled from the outer reef and inner mangrove site (PERMANOVA, $F_{(1,15)}=6.91$, $p<0.001$) and between shaded and exposed regions of the colony (PERMANOVA, $F_{(1,15)}=2.64$, $p=0.007$), with colony as a random factor. The interaction between site and colony position also had a significant effect on the photobiological phenotypes (PERMANOVA, $F_{(1,15)}=2.52$, $p=0.011$) (Fig. 2c). Reef samples primarily cluster according to light harvesting potential (E_K), whereas mangrove samples cluster according to the light utilisation capacity, including the time constants (turnover) of electron carrier components (τ_1, τ_2, τ_3). Slower electron turnover times between electron donor-acceptors (τ_1 and τ_2) observed in the mangrove specimens and higher E_K values observed in the reef corals indicate differing photosynthetic strategies adopted by the symbionts in the two habitats.

Symbiodiniaceae diversity

Pocillopora acuta symbiont composition was primarily driven by lineage (PERMANOVA, $F_{(2,93)}=146.87$, $p<0.001$). Amongst individuals belonging to lineage 1, the ITS2 profile C1d/C42.2/C1-C1bl-C3cg-C1b-C45c was dominant. Additionally, one individual contained

C1d-C1bl-C42.2-C1-C3cg-C1b and one individual contained C1d/C1/C42.2/C3-C1b-C3cg-C45c-C115k-C1au-C41p, both with the C1d majority sequence. Corals from lineage 2 were almost exclusively associated with *Durusdinium* (ITS2 profile D1bt/D6/D4-D1-D1cf-D1bs-D1ce-D1dr). Interestingly, the largest diversity in Symbiodiniaceae profiles was observed for hybrid individuals. Two hybrid individuals (eight samples) contained the same ITS2 type profile D1bt/D6/D4-D1-D1cf-D1bs-D1ce-D1dr, while the other individuals contained *Cladocopium* dominated profiles, i.e. C1d/C42.2/C1-C1bl-C3cg-C1b-C45c, C1d/C1/C42.2-C3cg-C1b-C115k-C45c-C42ap, C1d/C1/C42.2/C3-C1b-C3cg-C45c-C115k-C1au-C41p and C1d-C42.2-C1-C1k-C1b-C3cg (Fig. 3). The two *Durusdinium* dominated individuals were sampled from the inner mangrove, while the other samples originated from the reef, predominantly the outer reef site.

Individuals from lineage 1 were dominated by *Cladocopium* symbionts (99.91% relative abundance), while individuals from lineage 2 were predominantly associated with *Durusdinium* (99.96% relative abundance). Background levels (< 1% of total sequence abundance) of additional Symbiodiniaceae genera, i.e. *Breviolum*, *Durusdinium* and *Fugacium*, were detected in some of the samples belonging to lineage 1 (Table S4; Fig. S10). For lineage 2, differences in Symbiodiniaceae sequence composition were evident between shaded and exposed locations within the coral (PERMANOVA, $F_{(1,38)} = 2.893$, $p = 0.014$, respectively; Fig. S11). Interestingly, out of the 40 samples from lineage 2, five out of the six samples that contained *Cladocopium* sequences were found in the shaded regions collected from the inner mangrove site (Fig. 3). Five of these six samples contained the *Cladocopium* C1d sequence (four from the shaded region and one from the exposed region).

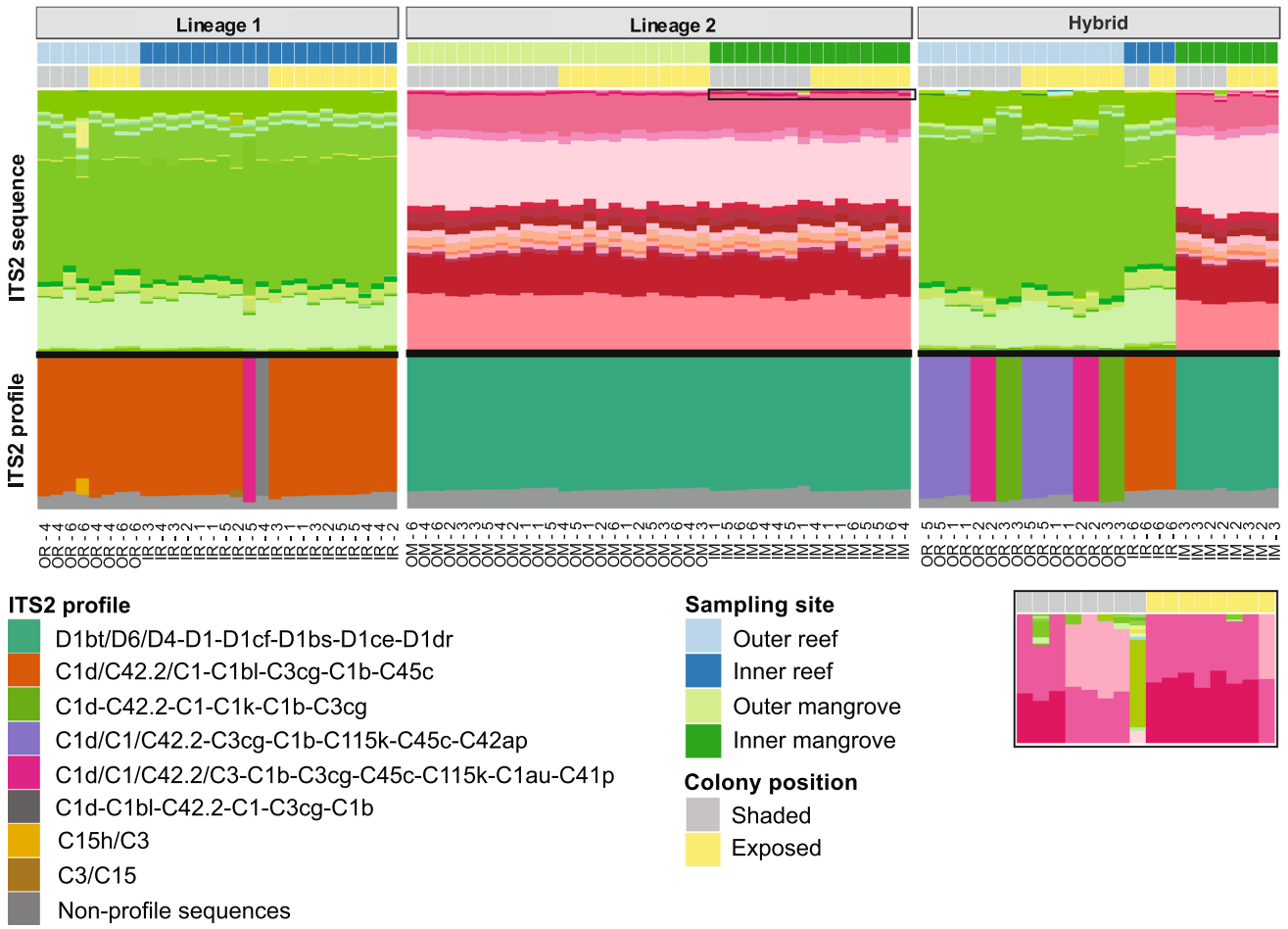

Fig. 3 Relative ITS2 sequence abundance (top, above solid black line) and predicted major ITS2 profiles (bottom) for individuals of *Pocillopora acuta* across the three putative lineages. *Cladocopium* sequences are in green and *Durusdinium* sequences in red. The blue and green coloured bars on top show the sampling site of the coral colony. Grey and yellow bars on top indicate shaded and exposed regions of the colony sampled, respectively. The x-axis labels represent the colony the sample is taken from (OR = outer reef; IR = inner reef; OM = outer mangrove; IM = inner mangrove). Inset shows the background sequences of lineage 2 containing *Cladocopium* sequences (top 1% of the graph is shown)

On the other hand, colony position did not have a significant effect on the symbiont community composition from lineage 1 and the hybrid lineage (PERMANOVA, $F_{(1,26)} = 2.400$, $p = 0.056$; PERMANOVA, $F_{(1,26)} = 0.0033$, $p = 0.920$, respectively).

Host–symbiont combinations across populations

The relationship between the coral host and its associated symbiont community was further explored by Procrustes analysis. There was a significant correlation between the coral host Euclidean distance matrix and the symbiont ITS2 generalised UniFrac distance (PROTEST, $r = 0.85$, $p = 0.001$). This correlation emphasises the important interaction between symbiont type and coral population structure (Fig. S12).

Discussion

The adverse effects of climate change on tropical reef ecosystems heighten the task of identifying tolerant coral communities that have greater capacity to withstand future environmental change (Schoepf et al. 2023). These coral communities have been proposed as important refugia (Camp et al. 2016; Burt et al. 2020) and source biodiversity in adaptive management strategies (Caruso et al. 2021; Savary et al. 2021; Schoepf et al. 2023) ranging from coral transplantation to microbial manipulation (Camp 2022). The suitability of these resilient corals for various interventions is influenced by both the genetic and phenotypic plasticity of the individual.

Woody Isles as an extreme and marginal coral habitat

The Woody Isles mangrove lagoon is considered a marginal and extreme system due to lower coral cover and diversity than the neighbouring Low Isles reef and more variable and extreme environmental parameters (Camp et al. 2019; Haydon et al. 2021; Schoepf et al. 2023). The abiotic data we retrieved between February 2022 and 2023 confirmed previous findings of low pH and highly variable temperature (Camp et al. 2019; Haydon et al. 2021). The two temperature loggers (HOBO MX2501 and back-up) show the same trend and recorded temperatures of 35 °C which is warmer than most studies from other coral associated mangroves (Camp et al. 2019; Stewart et al. 2021, 2022). Average temperatures were slightly higher on the reef site (27.0 °C vs. 26.7 °C), while diel variation was much larger for the mangrove site (15.1–35.0 °C) compared to the reef (20.7–31.6 °C) which is in accordance with Stewart et al. (2021). pH was significantly lower in the mangrove habitat, and the mean pH values from this study are comparable to other co-existing mangrove-coral (CMC) habitats (Stewart et al. 2022). As noted in the supplementary methods, the extreme low pH of 5.83 was returned at the edge of the thermal limits of the instrument (temperature: 34.98 °C) and should be considered with caution, as it is more extreme than previous CMC studies which found minimum pH values of 7.48–7.79 (Camp et al. 2019; García-Troche et al. 2021; Stewart et al. 2021, 2022). However, these values are within the pH range found for (soils of) mangrove lagoons more broadly (Lim et al. 2012; Dookie et al. 2022).

Pocillopora acuta genetic structure within Woody Isles mangrove lagoon

Local hydrology, bathymetry and reproductive mode can influence coral connectivity and thereby impact gene flow and admixture between sites (Ayre and Hughes 2000; van Oppen et al. 2011; Sammarco et al. 2012). Here, we identified two lineages with high genetic differentiation based on fixation indices. The observed limited admixture in our study reflects low levels of gene flow between the lineages across the sampling sites. Interestingly, STRUCTURE and DAPC analyses provide evidence of admixture between the lineages (i.e. hybrids). These hybrid individuals were primarily sampled from the outer reef site and showed highest diversity in Symbiodiniaceae ITS2 profiles. Differences in morphological characteristics combined with high F_{ST} values amongst the collected coral specimens suggest the presence of a species complex, in line with previous research by Smith et al. (2017). In contrast to Smith et al. (2017), this study has shown distinct lineages that are not occurring sympatrically, but instead favour different ecological niches (reef vs. mangrove). Further morphological and genetic analyses are required to resolve possible speciation of *P. acuta*.

The amount of genetic differentiation found between our populations is higher than F_{ST} values found across other gradients (F_{ST} between 0.0005 and 0.22) (Combosch and Vollmer 2011; Robitzch et al. 2015; Gélin et al. 2017b; Buitrago-López et al. 2023). This is likely influenced by the extreme gradients present, difference in reproductive mode and barriers to larval dispersal across our study site. Our results suggest that the presence of two distinct genetic lineages might be driven by adaptation to different ecological niches (Combosch and Vollmer 2011; Warner et al. 2015). We also found several individuals from the inner reef that were closely related (Fig. S7), which is skewing the F_{ST} values to be uncharacteristically high given the high relatedness (majority full siblings) (Waples and Anderson 2017), impacting our results.

The Woody Isles mangrove lagoon can become closed off from the neighbouring reef at low tides. This restricted water exchange with the surrounding area might limit gene flow as the mangrove lagoon is more dependent on flow

regimes and timings than the deeper reef sites. In contrast, the reef sites are less hydrodynamically restricted to neighbouring locations. Higher connectivity to the metapopulation could explain the higher proportion of hybrid individuals found amongst reef samples, specifically the outer reef (Underwood et al. 2020). Generally, brooding coral species exhibit higher genetic differentiation and population structure across sites compared to broadcast spawning corals due to reduced larval dispersal (Prata et al. 2024). *Pocillopora acuta* has a proposed mixed reproductive strategy (brooding and spawning) and can produce both sexual and asexual offspring (Schmidt-Roach et al. 2014; Smith et al. 2019), which seems to differ between geographic regions (Torda et al. 2013a, 2013b; Thomas et al. 2014; Gélin et al. 2017a) and along disturbance gradients (Torres et al. 2020). Lower coral cover in the extreme mangrove lagoon could increase the number of asexually brooded larvae under mate scarcity (Schmidt-Roach et al. 2014; Smith et al. 2019), explaining the two clones found in the inner mangrove. However, overall, only a low number of clones were found in our study (2 out of 23 individuals). The low number of clonal individuals in *P. acuta* is consistent with Torda et al. (2013a, 2013b) where < 7% of the *P. acuta* individuals sampled on the GBR (therein: *P. damicornis* type β (Baums et al. 2014)) were asexually produced. Future studies incorporating hydrological processes within and between the mangrove and reef system could allow us to model larval dispersal and further explain the admixture observed between populations.

Corals from extreme mangrove lagoons are being targeted for use in active restoration practices, such as outplanting, or assisted evolution due to their stress-tolerant nature (Camp 2022). However, recent research highlights the need for caution as there may be inherent trade-offs in these stress-tolerant communities that could potentially undermine their future competitive adaptability and success (Scucchia et al. 2023). For instance, corals show decreased calcification rates (20–30%) and enhanced respiration rates (35%) at mangrove sites compared to their congeners at adjacent reef habitats (Camp et al. 2019). Additionally, genetic diversity and skeleton density can become reduced in mangrove corals (Scucchia et al. 2023). Due to the distinctiveness of the lineages found here, moving mangrove corals to the reef has additional considerations, such as genetic monitoring, as part of the intervention (Baums 2008). Despite the fact that the long-term success of mangrove corals in active coral restoration may not be guaranteed under future conditions, these extreme habitats provide important knowledge on resilient coral species and mechanisms to survive in hostile conditions and they underpin the need to preserve the genetic diversity across reef systems (Scuccia et al. 2023).

Functional and genetic diversity of Symbiodiniaceae within *Pocillopora acuta*

The strong host genetic structure between lineage 1 and lineage 2 (across reef to mangrove habitats) is congruent with the macroscale Symbiodiniaceae community (Davies et al. 2023) shifting from *Cladocopium* to *Durusdinium*, respectively. Functional differences were also evident with an interaction between sites and colony positions, suggesting that the symbionts of *P. acuta* are exposed to a range of light conditions across multiple spatial scales. These functional differences were still significant when colony was included as a random factor, suggesting the sampling environment as the main driver of the observed photobiological differences. *Durusdinium* within mangrove *P. acuta* exhibits a strong reliance on non-photochemical quenching (NPQ; 1-Q) in summer months observed in the Woody Isles mangrove lagoon (Haydon et al. 2021). We find slow electron turnover times for *Durusdinium* in the mangrove in comparison with *Cladocopium* on the reef. Reliance on NPQ coupled with slower electron turnover times could point towards low-light adaptation (Hennige et al. 2008; Suggett et al. 2015). The distinct photosynthetic strategy and potential low-light adaptation of the symbionts housed within mangrove corals might impact their bleaching resilience when transferred to a bright and exposed site (Rowan et al. 1997). However, a previous study showed that symbiont physiological performance remained stable when transplanted from mangrove to reef (Haydon et al. 2021). Alternatively, photo-physiological signatures of *Durusdinium* and *Cladocopium* might be related to nutrient availability which can impact resource availability for cellular machinery used in photosynthesis (Raven et al. 1999). The acquisition of micro-nutrients is species-specific and temperature dependent for Symbiodiniaceae and coral (Reich et al. 2020; Camp et al. 2022; Grima et al. 2022). Further work with increased sample size is required to resolve the environmental drivers of the distinct photo-physiological signatures of *Durusdinium* and *Cladocopium*.

Host–symbiont combinations across Low Isles reef and Woody Isles mangrove lagoon

This study expands on previous work (Camp et al. 2019; Haydon et al. 2021, 2023; Ros et al. 2021) to demonstrate that the host population is uniquely structured in the mangrove lagoon, which is congruent with distinct Symbiodiniaceae communities that are conserved across inner and outer mangrove locations. Despite being less than 100 m away, the inner reef site had distinct host and Symbiodiniaceae genetic structure to the mangrove lagoon sites, demonstrating the unique diversity housed within the extreme system. Habitat characteristics (e.g. higher thermal maxima observed in the

mangrove) may contribute to this distinction as *Durusdinium* is considered to have higher thermal tolerance (Palacio-Castro et al. 2023) and may therefore be better suited to the mangrove conditions. However, other corals within the mangrove system associate with *Cladocopium* (e.g. *Porites lutea* with *Cladocopium* C15 (Camp et al. 2019)). Thus, there are species-specific differences in Symbiodiniaceae associations between the two habitats, which has also been documented at other sites (Camp et al. 2020).

Pocilloporid corals have co-evolved with *Cladocopium* symbionts during the late Pliocene and early Pleistocene (~3 mya) (Turnham et al. 2021; Johnston et al. 2022). Pocilloporids can be associated with multiple symbiont genera, indicating flexible host–symbiont associations (Cunning et al. 2013). We found small abundances of C1d sequences (belonging to *Cladocopium pacificum* (Turnham et al. 2021)) in the inner mangrove individuals that were dominated by *Durusdinium*. This cohabitation of *Durusdinium* and *Cladocopium pacificum* is almost exclusively found when shaded parts of the colonies are sampled suggesting within-colony light gradients as a driver of the observed Symbiodiniaceae intra-colony variance (Lewis et al. 2022). Our finding suggests the possibility of a tripartite symbiosis and perhaps co-phylogeny between *Cladocopium*, *Durusdinium* and Pocilloporid coral hosts, though symbiont mixtures are generally considered rare for *Pocillopora* (Turnham et al. 2023). *Cladocopium pacificum* (C1d) sequences were also found in *Cladocopium* dominated sequences across lineage 1 and hybrid individuals. As *P. acuta* initially obtains symbionts from their parents, the diverging symbiont community structure across Woody Isles mangrove and the Low Isles reef habitats is consistent with the reproductively isolated coral populations.

The competitive outcome between co-existing symbiont genera and formation of available ecological niches can be influenced by various factors, e.g. light (Sampayo et al. 2007; Lewis et al. 2022), nutrient availability (McIlroy et al. 2020; Camp et al. 2022) and sea surface temperatures (McIlroy et al. 2020; Glynn et al. 2023). Mutualistic partners can be outcompeted or reduced to 'background' levels due to differences in competitive traits (McIlroy et al. 2019, 2020). A transplantation study showed that Symbiodiniaceae communities remained stable after transplanting *P. acuta* corals from mangrove to reef and reef to mangrove (Haydon et al. 2021). This suggests strong priority effects for the resident symbiont communities may be inhibiting a shift to dominance of additional compatible symbiont genera through niche pre-emption (Fukami 2015). Future experiments involving the experimental bleaching of corals to create vacant niches and subsequent transplantation between reef and mangrove systems may provide valuable insights into the strength of such priority effects and the potential for symbiont shuffling post-transplantation. These experiments offer an opportunity to further investigate and understand the dynamics and implications of coral–symbiont associations in different ecological contexts.

Conclusion

Increasing thermal bleaching events and other natural and anthropogenic stressors are leading to global coral reef declines. Due to the importance of these ecosystems for marine organisms and human populations, the need to identify and analyse resilient coral communities is of critical importance. Here, we found evidence for a species complex driven by ecological niches, suggested by two lineages and potential hybrid individuals present across the sampling sites. Coral lineages harboured distinct symbiont communities and showed separate photobiological phenotypes across the outer reef and inner mangrove lagoon. This genetic distinctiveness could have consequences for their use in active restoration practices. Local-scale conservation efforts should focus on preserving and capturing the unique genetic diversity housed within single coral species to ensure functional diversity of coral ecosystems in the future (Gélin et al. 2017a; Buitrago-López et al. 2023).

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Author contributions Chiara M Duijser, Emma F Camp and Matthew R Nitschke designed the study. Chiara M Duijser collected the coral samples and ran the photo-physiology assays, with Emma F Camp deploying the environmental sensors. Chiara M Duijser did the DNA extractions and the bioinformatics supported by Sage H Rassmussen and Matthew R Nitschke. Chiara M Duijser and Emma F Camp led the writing with significant editorials from Sage H Rassmussen and Matthew R Nitschke. All authors read and approved the final manuscript.

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Data availability The data and scripts to reproduce the analyses can be found online at https://github.com/ChiaraDuijser/host-symbiont_interactions_environmental_gradient. The raw sequence data for symbiont genetic analysis are available at the Sequence Read Archive (SRA) of NCBI, accession number: PRJNA1200712.

Declarations

Competing interests The authors have no competing interests to declare.

Ethical approval Field work was conducted at Low Isles under permit G18/40023.1 issued by Great Barrier Reef Marine Park Authority.

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