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Transcriptomic response of *Acropora cervicornis* following transplantation to a marginal, nearshore environment

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As reef-building coral cover has declined worldwide, coral restoration has become a widespread response towards repopulating degraded reefs. *In-situ* nurseries have provided refugia for the regrowth of several coral species, yet long-term success following outplanting remains highly variable, particularly when corals are introduced into novel or marginal environments. Additionally, while growth and survivorship are commonly used to evaluate restoration success, molecular responses may also provide critical insights into the capacity of corals to acclimatize following transplantation. Here, we examined host and algal symbiont gene expression in the critically endangered reef-building coral *Acropora cervicornis* following transplantation from an offshore nursery in Key Biscayne, Florida to a nearshore, urbanized habitat in the Port of Miami, Florida. Three nursery-propagated genotypes were outplanted in June 2021 and sampled after four months at both sites for transcriptomic analysis (n=12 after quality filtering). Transplanted corals exhibited significant shifts in host gene expression relative to nursery controls, with 961 host and symbiont genes significantly upregulated and 165 significantly downregulated. Upregulated host genes were predominantly associated with the environmental stress response, including heat shock proteins, unfolded protein binding, apoptotic processes, detoxification pathways, and innate immune signaling. Weighted gene co-expression network analysis identified two host modules positively associated with the nearshore outplant site and were enriched for pathways related to protein folding, immune activity, and cellular reorganization. These results demonstrate that *A. cervicornis* outplanted to a nearshore, urbanized environment exhibits sustained activation of stress- and immune-related molecular pathways months after transplantation, which is consistent with a stress-response profile that may reflect ongoing acclimatization. Integrating molecular diagnostics with environmental monitoring may refine genotype and site selection to enhance restoration outcomes.

KEYWORDS
coral nursery, coral restoration, Florida's coral reef, transcriptomics, urban corals

1 Introduction

The staghorn coral, *Acropora cervicornis*, once dominated Florida's Coral Reef (FCR) (Aronson and Precht, 2006), forming dense thickets due to its fast-growing and branching morphology and providing ecosystem services such as shoreline protection, essential fish habitat, and rapid reef accretion (Gladfelter, 1982; Lirman et al., 2010). A major disease outbreak in the 1980s led to a drastic decline in their abundance, and subsequent stress events, including marine heatwaves, cold-water events, and predation have prevented their recovery (Aronson and Precht, 2006; Schopmeyer et al., 2012). As such, *A. cervicornis* became federally listed on the Endangered Species Act in 2006, and coral restoration efforts have prioritized this species' propagation and outplanting (Hogarth, 2006; Young et al., 2012).

In order to propagate this species in *in-situ* nurseries, fragments of wild colonies have been collected from remaining populations in their greatly reduced range (Lirman et al., 2014; Schopmeyer et al., 2017). Conditioning and grow-out in these nurseries, has been prioritized to both protect this species and enhance productivity of fragments through common gardening practices by restoration practitioners (Rinkevich, 2014; Schopmeyer et al., 2012). However, despite over thirty years of restoration with this keystone reef species, their projected long-term survivorship in Florida remains limited in the face of abiotic environmental stressors such as marine heatwaves (Van Hooidonk et al., 2016; van Woesik et al., 2021; Ware et al., 2020). Indeed, *A. cervicornis* and its sibling species *A. palmata* were recently declared functionally extinct in Florida following the fourth global coral bleaching event (Manzello et al., 2025), requiring drastic action to preserve remaining individuals. Conserving the remaining wild and nursery populations of *A. cervicornis* and increasing their abundance, genetic diversity, and resilience therefore continue to be priorities for management agencies, researchers, and restoration practitioners alike.

In coral restoration efforts, while site selection for outplanting has traditionally been limited to the species' native habitat, relocation to more stressful environments has been proposed as an intervention for assisted acclimatization (Baums et al., 2019). As reef environments continue to degrade, it is important for these nursery-propagated corals to demonstrate the ability to survive in environmentally variable and/or novel environments. Historically, *A. cervicornis* was found in high abundance on reef crests and midslope zones (Cramer et al., 2020), but observations show wild colonies establishing outside these niches, indicating potential for recovery in non-native environments (Wirt et al., 2013). In the northern extent of FCR and at its latitudinal limit, high-density thickets of *A. cervicornis* have been found near urbanized areas (D'Antonio et al., 2016; Vargas-Ángel et al., 2003; Walker et al., 2012). Additionally, key predictors of this species' occurrence include moderate turbidity and multi-annual thermal ranges of 4–5 °C (van Woesik et al., 2020), suggesting a shift toward more stressful conditions. Testing transplantation into nearshore, urbanized sites is therefore critical to assess the acclimatization capacity of *A. cervicornis*, as well as evaluating whether urbanized habitats serve as useful locations for *in-situ* nurseries and stress-hardening sites.

One such urban environment is the Port of Miami, connecting Biscayne Bay to the western Atlantic through constructed waterways which hold large reef-building coral species that have naturally recruited on seawalls, riprap, and pilings (Enochs et al., 2023). This environment has proven to be a refuge for coral no longer seen in high abundance on nearby natural reefs, with significantly higher coral cover and diversity despite experiencing greater fluctuations in temperature, salinity, pH, and photosynthetically active radiation (Enochs et al., 2023). A transcriptomic comparison of *Pseudodiploria strigosa* from the Port of Miami and a natural reef revealed elevated gene expression related to the innate immune response and heterotrophy, highlighting molecular mechanisms which may be needed for acclimatization to such a variable environment (Rubin et al., 2021).

A. cervicornis exhibits notable phenotypic plasticity, enabling acclimatization and adaptation across diverse reef environments. Transplant studies in the Florida Keys and Miami highlighted genotypic variation in morphological traits and bleaching susceptibility, with immune-related genetic markers predicting survivorship (Drury and Lirman, 2021; Million et al., 2022). In Bonaire, physiological and epigenetic differences arose among clonemates living in different habitat types (Hackerott et al., 2023). Laboratory experiments revealed gene expression plasticity under combined thermal and acidification stress, with significant co-expression of genes involved in structural cellular organization (Dilworth et al., 2024). Despite these studies, how *A. cervicornis* gene expression responds to environmental stress associated with urbanized, coastal areas remains poorly understood.

Documenting the response of *A. cervicornis* transplanted from an *in-situ* nursery into a marginal habitat is an important step in evaluating this species' capacity for acclimatization in an era of global change and increasing urbanization. Here, we investigated the transcriptomic responses of both the coral host and its algal endosymbionts following the introduction of nursery-propagated *A. cervicornis* to a novel, highly urbanized environment. We specifically aimed to document the sustained, long-term response (on a scale of months), as many studies within this genus focused on acute stress response (hours, days, or weeks). We hypothesized that corals transplanted to the Port of Miami would exhibit a transcriptional shift toward enhanced stress-mitigation and immune signatures. We predicted these shifts would converge with the upregulation of immune-related genes seen in native urban colonies of *P. strigosa* (Rubin et al., 2021), the increased expression of the environmental stress response in nearshore transplanted *Porites astreoides* (Kenkel and Matz, 2016), and upregulation of heat-shock proteins documented in *A. hyacinthus* in thermally variable tidal pools (Palumbi et al., 2014).

2 Methods

2.1 Coral collection and sampling

On June 23, 2021, 13 colonies (each ~20 cm diameter) of *A. cervicornis* were outplanted to riprap boulders within the mouth of the Port of Miami (25.765861, -80.138361, ~3 m depth) following

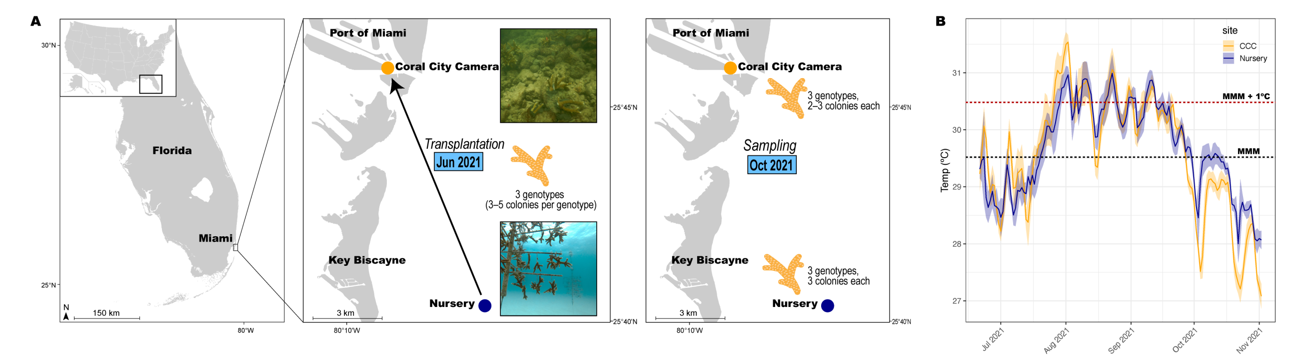

FIGURE 1
(A) Map of *in-situ* nursery, where *A. cervicornis* genotypes were propagated for several years prior to the study (dark blue circle), and the Coral City Camera (CCC) site within the Port of Miami (yellow circle). Two inset images depict differing environments; coral nursery trees in an open sandy area at a depth of ~8 m, and CCC site composed of riprap boulders, rubble, and sand at a depth of ~3 m. Two maps represent the transplantation time point (June 2021) and the sampling time point (October 2021). **(B)** Average daily *in-situ* temperatures (shading represents standard deviation) for the nursery and CCC. The horizontal dashed black line represents the maximum monthly mean (MMM) from NOAA's Coral Reef Watch for the region (29.5°C). The horizontal dashed grey line represents the bleaching threshold as defined by NOAA's Coral Reef Watch (MMM + 1°C, 30.5°C).

collection and fragmentation from the *in-situ* coral nursery off Key Biscayne, Florida (Figure 1A; 25.676306, -80.098694, ~8 m depth). The 13 colonies represented three genotypes, locally named Cheetos-B (*n*=5), Miami Beach-C (*n*=3), and Sunny Isles-E (*n*=5), which were originally sourced from three different reefs in Miami-Dade County at least two years prior. The site chosen within the Port of Miami will be referred to herein as the Coral City Camera (CCC) site, as corals were outplanted within view of the 24 hour live-streaming underwater camera (Octopus, View into the Blue) hosted online (https://www.coralcitycamera.com).

On October 26, 2021, four months after transplantation, nine tissue samples (~1 cm) were collected from fragments at the CCC site (*n*=3 per genotype across the twelve surviving colonies, Supplementary Table 1); one port-native colony of *A. cervicornis* (genotype locally named "Ventura") was also sampled. Due to the mortality of one colony of Miami Beach-C, in order to obtain three replicate tissue samples, one colony was sampled from twice. On November 3, 2021, nine samples were collected from the same three genotypes held at the Key Biscayne nursery (*n*=3 per genotype). All tissue samples were immediately preserved in Zymo DNA/RNA Shield (Cat #R1100-250) and kept at –80°C until DNA and RNA extractions were performed.

2.2 Temperature measurements

As *A. cervicornis* is sensitive to thermal stress and temperature is an important abiotic factor that influences their resilience (Manzello et al., 2025), one temperature logger was deployed at each site (HOBO Water Temperature Data logger, Onset – Key Biscayne Nursery, 8m depth; Tilt current meter, Lowell Instruments – CCC, 3m depth) in early 2021 to track any temperature stress experienced following transplantation. Temperatures were recorded every 2 hours for the duration of the study. To obtain sea surface temperature (SST)-derived maximum monthly means (MMMs) for the nursery and CCC, the 'raster' package from R (Hijmans and van Etten, 2012) was used to extract the values from the NOAA 1981–2012 5-km Coral Reef Watch climatology data product (v3.1) at the sites' coordinates, from the NOAA NESDIS STAR file share website (https://www.star.nesdis.noaa.gov/pub/sod/mecb/crw/data/5km/v3.1_op/climatology/nc/). The MMM for the nursery was 29.53°C and was 29.54°C for CCC. To assess the accumulation of thermal stress for both sites, degree-heating-weeks (DHW) were calculated as the summation of the degrees exceeding the MMM+1°C across a twelve-week period (Gleeson and Strong, 1995; Liu et al., 2003).

2.3 RNA-Seq library preparation, sequencing, and bioinformatics

Total RNA was extracted using the Zymo MagBead DNA/RNA extraction kit (Cat #R2130). RNA quality was assessed using a Nanodrop 1000 and concentrations were determined with a Qubit Fluorometer 2.0. Samples were then prepared as Lexogen QuantSeq 3'mRNA-Seq cDNA libraries (Cat #015), pooled, and sequenced on a NOVAseq S2 flow cell at Lexogen Facilities (Vienna, Austria).

The full bioinformatics pipeline can be found on GitHub (https://github.com/ademerlis/AcerCCC/). Raw sequences were processed using TrimGalore v0.6.10 (Krueger, 2016) to remove low-quality base pair assignments, Illumina adapters, and poly-A tails. Then, concatenated genomes from FASTA files of *A. cervicornis* (Locatelli et al., 2024) and *Symbiodinium* clade A3 (Shoguchi et al., 2018) were used as the index for sequence alignments using Bowtie2 v2.5.2 (Langmead and Salzberg, 2012). SAMtools v1.3 (Danecek et al., 2021) was used to quantify gene counts, and cross-mapping between host and symbiont reads were addressed by discarding multi-mapped reads during the filtering step. Lastly, genome and transcriptome annotations for *A. cervicornis* and *Symbiodinium* clade A3 were created using protocols in the GitHub repositories '*annotatingTranscriptomes*' (Matz, 2015) and '*emapper_to_GOMWU_KOGMWU*' (Matz, 2018), which employ eggnog-Mapper (Huerta-Cepas et al., 2017). The first step generates functional annotations on predicted protein sequences from each genome, and the second step produces gene-to-GO (gene ontology) term mapping tables necessary for GO enrichment analysis.

Seven out of nineteen samples were removed from downstream analyses due to low percentage alignment (<20%) or for violating

the default sample array distance criterion using the '*arrayQualityMetrics()*' R function (Kauffmann et al., 2009), including the port-native colony, which had an overall alignment rate of 40% (Supplementary Table 1). Of the remaining twelve samples, sequencing yielded an average (± standard error) of 20.8 ± 0.7 million reads per sample. After trimming and cleaning, this was reduced to 18.6 ± 1.1 million reads per sample. The average read alignment was 10.7 ± 0.7 million reads per sample, and the average alignment rate was 57 ± 0.9% (Supplementary Table 1). This rate reflects several contributing factors. The draft *Symbiodinium* clade A3 assembly (Shoguchi et al., 2018) was generated from short-read Illumina sequencing and contains scaffolding gaps that limit mapping of symbiont-derived reads. Residual symbiont diversity not captured by the single reference genome (e.g., within-genus genomic divergence) may further reduce mapping efficiency. Lastly, non-target RNA from microorganisms associated with the coral holobiont, which is a common contributor to reduced alignment rates in coral transcriptome studies, likely also accounts for a portion of unmapped reads. After filtering out genes (isogroups) with low counts, 21,814 genes remained for *A. cervicornis*, and 31,202 genes remained for *Symbiodinium*.

2.4 Differential gene expression analysis

Read counts were imported into R v4.2.1 and analyzed for differential gene expression using DESeq2 v1.36.0 (Love et al., 2014). Genes with low counts (<10 across all samples) were removed, and the DESeq2 model was created with the design: ~ Genotype + Location. The model was then transformed using a variance-stabilized transformation for expression visualizations (Love et al., 2014). The '*apeglm*' method was used for effect size shrinkage of log-fold change (Zhu et al., 2019). The number of differentially expressed genes (DEGs) at a false discovery rate (FDR) adjusted p-value cut-off of 0.05 was determined using the Wald test for location: CCC versus nursery corals. Volcano plots were generated using the '*EnhancedVolcano*' package (Blighe et al., 2024). Principal coordinates analysis of Manhattan distance was generated using the '*ape*' package (Paradis and Schliep, 2018). Formal analysis of variance of distance matrices for Genotype + Location was run using a PERMANOVA with $1e^6$ permutations using the *vegan* package (Oksanen, 2016).

2.5 Functional enrichment analysis

Gene ontology (GO) enrichment analysis was conducted on the significantly differentially expressed genes for both host and symbiont genes, and significant WGCNA gene modules for host genes only, as there were not enough significant DEGs for symbiont gene co-expression analysis. This was conducted using the R package '*TopGO*' to identify significantly enriched GO terms (herein referred to as "child" GO terms) using the "weight01" algorithm for the Fisher's Exact Test, and an alpha value of 0.01 (Alexa and Rahnenfuhrer, 2017). The GO terms from this analysis were then grouped into broader categories ("Parent" GO terms) using the "GOslim" function in the R package *GSEABase* with the reference database "GOslim generic obo" (Gentleman, 2017; Roper et al., 2025).

2.6 Weighted gene co-expression network analysis

Weighted gene co-expression network analysis (WGCNA) was performed using the *A. cervicornis* host genes to identify modules of co-expressed transcripts and determine the correlation of those modules with location (Langfelder and Horvath, 2008). Genes with counts <10 in 90% of samples were removed, and remaining data were normalized via variance stabilized transformation in DESeq2 (Love et al., 2014). One additional outlier was identified and removed for the *A. cervicornis* dataset based on the standardized threshold of whole network signed connectivity (-2.5). A soft-threshold power of 26 was selected based on the soft-threshold R^2 value cut-off of 0.9. Gene co-expression modules were selected using a cut height of 0.99 on the topological overlap matrix and a minimum module size of 100 genes. Then, a cut height of 0.6 was selected for merging modules, resulting in 10 modules. Eigengene expression of these modules was correlated to the location the coral was sampled (either nursery or CCC), using a Pearson correlation at an alpha of 0.05. For each module, the hub gene was identified, which is the gene with the highest module membership and greatest trait correlation. If the hub gene was unannotated, its genetic sequence was queried in InterPro to identify any functional protein signatures (Blum et al., 2025).

2.7 Genus-level Symbiodiniaceae assemblages

As coral environmental tolerance depends heavily on the interaction between the coral host and its algal symbionts (family Symbiodiniaceae), we also determined the symbiont community composition of *A. cervicornis* at two time points via two methodologies. First, during the bioinformatics pipeline, sequence alignment tests were performed to evaluate dominant symbiont genera by aligning sample reads to a reference containing Symbiodiniaceae 28S sequences across the four main genera, with at least four references per genus (*Symbiodinium* spp., *Breviolum* spp., *Cladocopium* spp. and *Durusdinium* spp.) (Studivan et al., 2023). Additionally, outplants were revisited in September 2022, 15 months after transplantation, and small tissue biopsies (*n*=6–13 per genotype, ~0.5 cm) were collected from two genotypes (Cheetos-B and Sunny Isles-E) for analysis using qPCR following established protocols (Baker and Ross Cunning, 2015; Cunning and Baker, 2013).

3 Results

3.1 Greater heat accumulation at urbanized, nearshore relocation site

Daily temperature measurements indicated that overall thermal conditions were similar between sites, as the mean temperatures were 29.5°C for both sites. From June to November, the temperatures ranged from 26.2–31.9°C for CCC, and 26.9–31.5°C for the

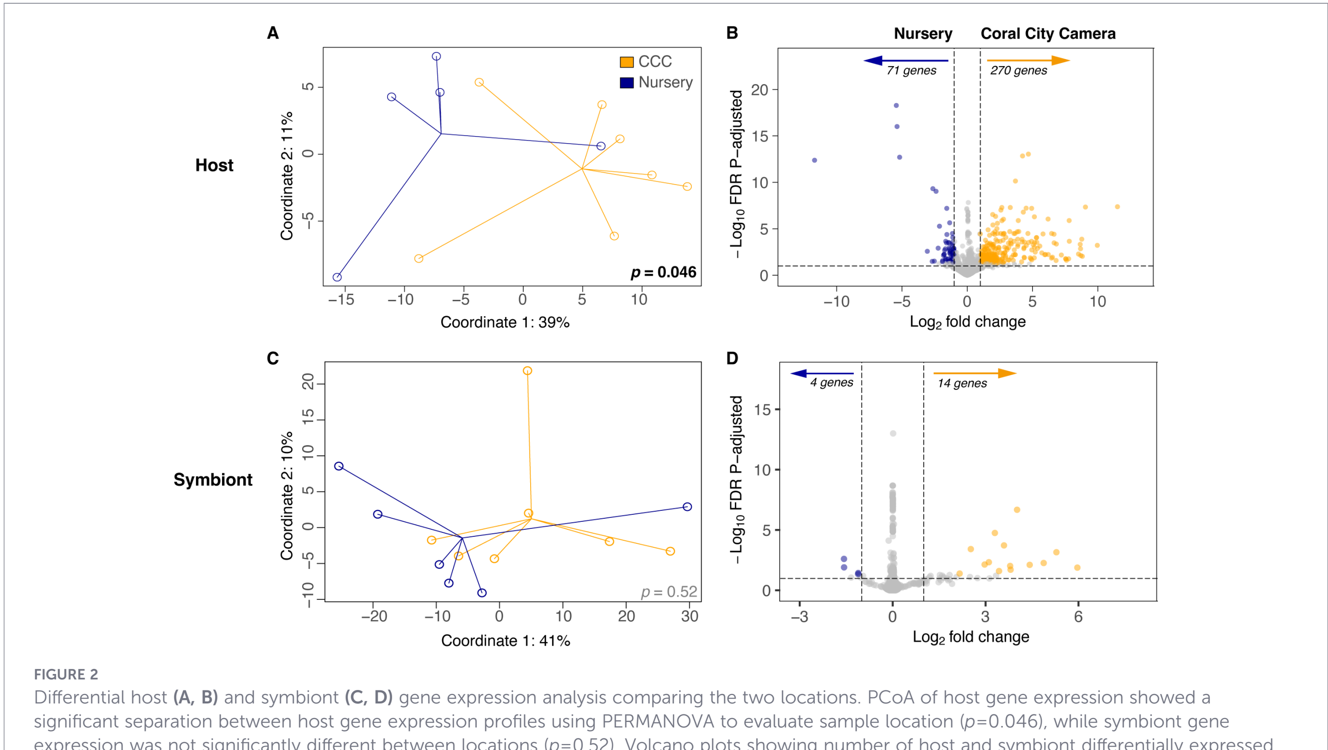

FIGURE 2
Differential host **(A, B)** and symbiont **(C, D)** gene expression analysis comparing the two locations. PCoA of host gene expression showed a significant separation between host gene expression profiles using PERMANOVA to evaluate sample location (p=0.046), while symbiont gene expression was not significantly different between locations (p=0.52). Volcano plots showing number of host and symbiont differentially expressed genes (FDR-adjusted p-value < 0.05, L2FC > |1|) upregulated in CCC samples (orange) and nursery samples (navy blue). Dashed lines intersect with FDR-adjusted p-value and L2FC threshold.

nursery. However, CCC experienced temperatures exceeding the maximum monthly mean of 29.5°C by more than 2 C for approximately two weeks in August. While both sites exceeded 31 C, only CCC surpassed 31.5 C, experiencing an accumulation of 4.82 DHW, while the nursery experienced 4.17 DHW (Figure 1B). Despite this elevated thermal exposure, CCC outplants did not exhibit bleaching during the summer monitoring period (Supplementary Figure 1).

3.2 Distinct host and symbiont gene expression patterns between source and relocated corals

Principal coordinates analysis (PCoA) and two-way PERMANOVA testing location (nursery or CCC) and genotype revealed significant differences in host gene expression profiles. The strongest separation occurred along PC axis 1, which explained 39% of the total variance among samples (PERMANOVA, Location: p=0.046; Figure 2A). Most differentially expressed genes (DEGs) in the host were upregulated in CCC corals relative to nursery corals (Figure 2B). A total of 819 host DEGs were identified, of which 404 were annotated. The most strongly upregulated host gene was annotated as being involved in granuloma formation (log2 fold change [L2FC] = 11.5, FDR-adjusted p<0.001). Additional upregulated host genes included a tumor necrosis factor (TNF) receptor-associated factor (L2FC=7.8, p<0.001), cytochrome P450 (L2FC=2.3, p<0.001), a C-type lectin (L2FC=1.5, p=0.002), and a gene associated with cytoplasmic sequestration of NF-κB (L2FC=2.7, p<0.001). Additionally, three DEGs were associated with unfolded protein binding, four with apoptosis-related processes, and four with heat shock proteins (Supplementary Table 2).

In contrast, although symbiont gene expression also showed the greatest variation along PC1 (41% of variance explained by location), higher variability among nursery samples resulted in no significant difference between sites (PERMANOVA, Location: p = 0.51; Figure 2C). 307 DEGs were identified, of which 70 were annotated. The most strongly upregulated gene encoded a centrosomal protein (L2FC=4.4, p = 0.008). Other upregulated genes included one associated with medium-chain acyl-CoA dehydrogenase activity (L2FC=3.6, p<0.001) and a NAD-dependent protein deacetylase of the SIR2 family (L2FC=3.0, p = 0.007) (Figure 2D).

Gene Ontology (GO) enrichment analysis of host DEGs identified 365 genes associated with the functional enrichment category, "Biological Process," 53 with "Molecular Function," and 30 with "Cellular Component." The most highly enriched parent GO terms included anatomical structure development, cell differentiation, regulation of DNA-templated transcription, and signaling. Additional enriched terms were related to chromatin organization, programmed cell death, and protein folding (Supplementary Table 3). Child GO terms reflected cellular responses to heat, hypoxia, and unfolded protein stress, as well as structural and cellular functions, including epithelial tube morphogenesis and transcriptional regulation (Figure 3). For the algal endosymbiont, GO enrichment analysis yielded a single significantly enriched "Cellular Component" term, actin cortical patch.

3.3 Two significant co-expression gene modules associated with location

Weighted gene co-expression network analysis (WGCNA) of host genes identified ten highly co-expressed modules, two of which

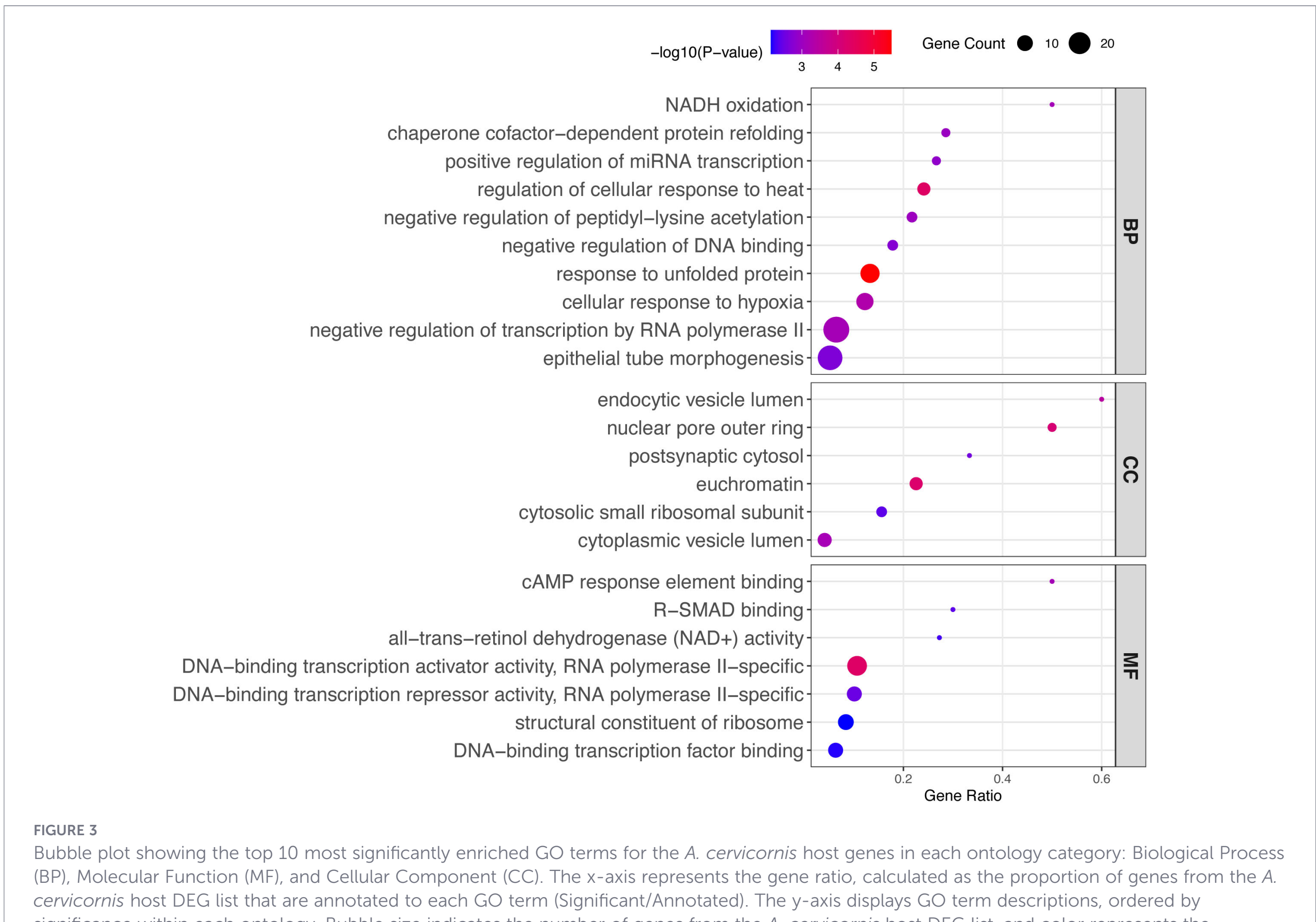

FIGURE 3
Bubble plot showing the top 10 most significantly enriched GO terms for the *A. cervicornis* host genes in each ontology category: Biological Process (BP), Molecular Function (MF), and Cellular Component (CC). The x-axis represents the gene ratio, calculated as the proportion of genes from the *A. cervicornis* host DEG list that are annotated to each GO term (Significant/Annotated). The y-axis displays GO term descriptions, ordered by significance within each ontology. Bubble size indicates the number of genes from the *A. cervicornis* host DEG list, and color represents the statistical significance of enrichment, log-transformed *p*-value calculated using Fisher's exact test with the weight01 algorithm.

were significantly correlated with site (Figure 4A). Both the "darkmagenta" and "mediumpurple3" modules showed strong positive correlations with CCC samples (darkmagenta: Pearson's r=0.80, p=0.003; mediumpurple3: r=0.63, p=0.039). The "darkmagenta" module contained 658 genes, with a FAD-dependent oxidoreductase identified as the hub gene. The "mediumpurple3" module comprised 751 genes, however, its hub gene lacked functional annotation. InterPro analysis failed to detect conserved protein domains or assign functional annotations, suggesting this gene may represent a lineage-specific or uncharacterized protein. Module eigengene expression values were higher in CCC samples for both modules, although neither difference was statistically significant due to high variability among CCC individuals (darkmagenta: p=0.055; mediumpurple3: p =0.16; Figure 4B).

Within the "darkmagenta" module, 354 genes were annotated. Highly upregulated genes included those associated with heat shock proteins, apoptotic processes, cytochrome P450, and G-protein–coupled GABA receptor activity (Supplementary Table 4). GO enrichment analysis identified 248 genes associated with "Biological Process," 19 with "Molecular Function," and 6 with "Cellular Component." The most represented parent GO terms were cell differentiation and anatomical structure development, with additional significant enrichment in immune system processes, lipid metabolic processes, cytoskeleton organization, and signaling pathways (Figure 4C).

The "mediumpurple3" module contained fewer annotated genes, with 58 associated with "Biological Process" and three with "Molecular Function." Genes upregulated in CCC corals included a *PIH1* domain-containing protein, matrix metalloproteinase-28, genes involved in protein folding, and a C-type lectin (Supplementary Table 4). Although fewer GO terms were significantly enriched relative to the "darkmagenta" module, the dominant parent terms again included cell differentiation and anatomical structure development, followed by protein maturation, cell motility, and protein folding (Figure 4C). The child GO terms which drove these parent term assignments included the G-protein coupled receptor signaling pathway and mRNA catabolism (Supplementary Figure 2).

3.4 Genus-level Symbiodiniaceae assemblages

Sequence alignment tests using 28S Symbiodiniaceae references determined exclusive alignment to the genus *Symbiodinium*, except for the port-native colony, Ventura, which did not algin to any reference 28S sequences. Additionally, qPCR determined that two genotypes, Cheetos-B and Sunny Isles-E, predominantly hosted the genus *Symbiodinium*, while the port-native colony, Ventura, predominantly hosted the genus *Durusdinium* (Supplementary Figure 3), 15 months after transplantation.

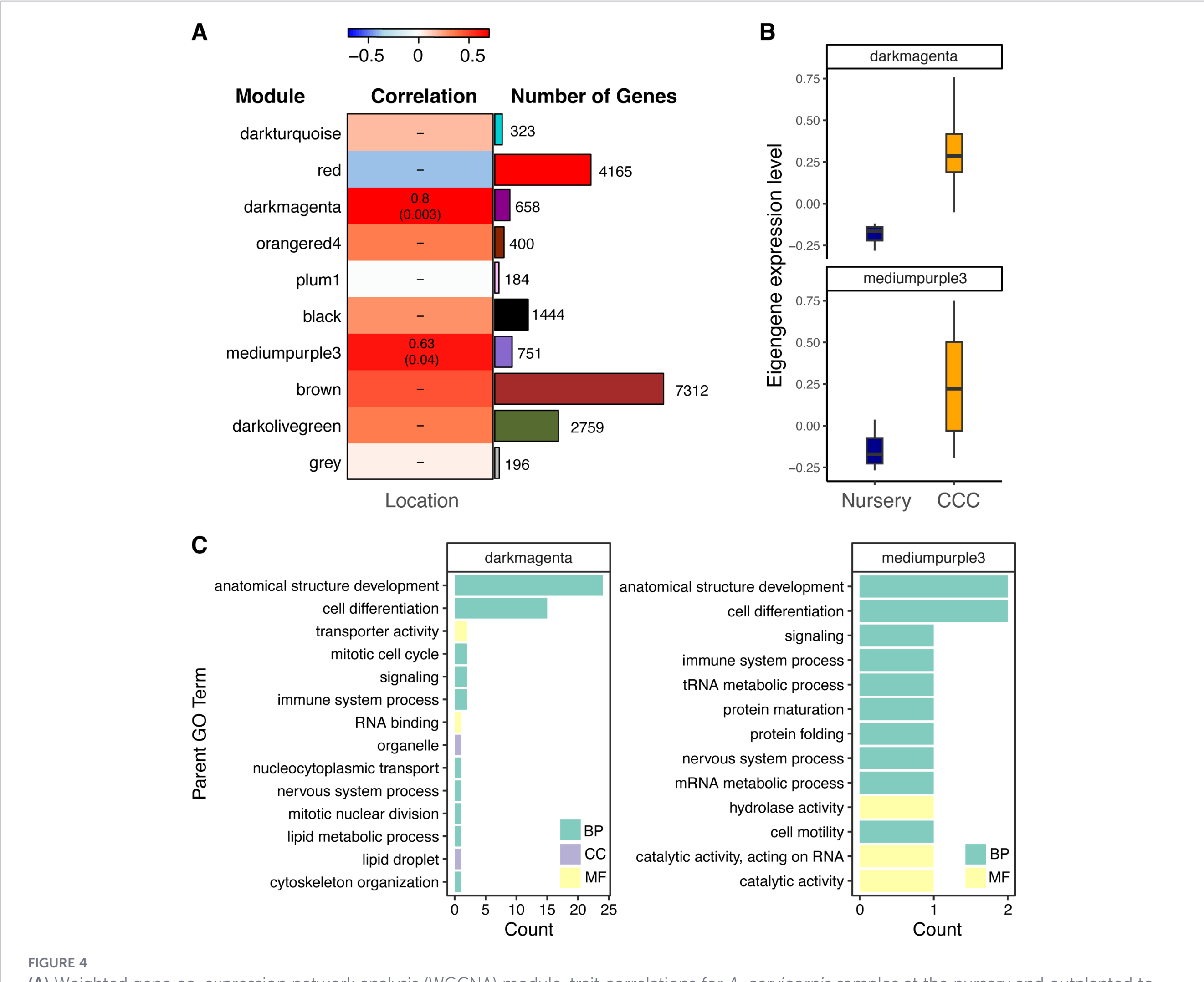

FIGURE 4
(A) Weighted gene co-expression network analysis (WGCNA) module-trait correlations for *A. cervicornis* samples at the nursery and outplanted to the CCC site. Blue boxes indicate a negative correlation with transplantation to the CCC site, and red boxes indicate a positive correlation with transplantation to the CCC site. The number in each box indicates Pearson's correlation for each module, where only significant correlations are plotted with correlation strengths (p<0.05). The barplot indicates the number of genes which make up that module. **(B)** Boxplot of nursery (dark blue) versus CCC (orange) sample module eigengene expression levels for the two significantly correlated gene modules, "darkmagenta" and "mediumpurple3". **(C)** Bar plots for the functional enrichment analysis of the "darkmagenta" and "mediumpurple3" gene modules, using the GOSlim (Parent GO) terms to explain function in each ontology category: Biological Process (BP), Molecular Function (MF), and Cellular Component (CC).

4 Discussion

4.1 Relocated corals up-regulate stress response and immune genes

This study aimed to characterize the host and symbiont transcriptomic response of nursery-propagated *A. cervicornis* following transplantation to the highly urbanized, marginal habitat of the Port of Miami. By comparing these outplants to their nursery-maintained conspecifics, we sought to determine if relocated corals would display molecular signals congruent with the environmental stress response and immunity over a four-month period. *A. cervicornis* outplants at CCC exhibited a significant transcriptional shift from nursery-maintained conspecifics. The predominant up-regulation of stress mitigation and immune genes indicates that transplants maintained a sustained transcriptional signal in response to the Port of Miami environment. The activation of similar mechanisms has been previously linked to acclimatization across a variety of sites and environmental conditions (Bay and Palumbi, 2015; Palumbi et al., 2014; Thomas et al., 2018). The persistence of this signal four months later suggests a continuous response to chronic stressors, but further research is necessary to determine if this signal leads to long-term acclimatization to the novel environment, and whether there are genotypic differences in acclimatization potential.

Many of the genes upregulated in CCC corals are central to the environmental stress response, including heat shock proteins (HSPs) and components of the unfolded protein response (Dixon et al., 2020; Kenkel and Matz, 2016). These transcriptional signatures are widely implicated in coral responses to thermal stress and bleaching, where they function to stabilize protein structure and maintain cellular homeostasis under elevated temperatures (Barshis et al., 2013; Desalvo et al., 2010). This signal of gene expression may reflect a greater gene expression plasticity that has been linked to

greater stress tolerance in other coral species, including acroporids (Bay and Palumbi, 2017; Kenkel and Matz, 2016). The temperatures experienced at CCC are sublethal for *A. cervicornis* in this region (DeMerlis et al., 2022), and the absence of visual thermal stress (e.g., paling or bleaching) in outplants suggests that the observed molecular shifts may facilitate physiological adjustment to this marginal environment. Survivorship of outplants after four months was 92%, indicating that these processes are at least consistent with short-term persistence. However, it is important to note that sustained upregulation of these genes could also reflect chronic or sublethal physiological stress rather than acclimatization. Without long-term monitoring, it remains unclear whether this transcriptional state represents a stable, acclimatized phenotype or a costly energetic trade-off. Future research tracking individual genotypes over multiple seasons is required to determine if these transcriptional signals translate to sustained fitness and long-term restoration success.

Host genes driving the WGCNA modules that were significantly correlated with location were predominantly associated with protein folding, apoptosis, immune activity, and detoxification, indicating a coordinated regulation of defense machineries. The hub gene of the "darkmagenta" module, FAD-dependent oxidoreductase, represents a broad enzyme family involved in redox reactions that manage oxidative stress (Williams et al., 2021). Significant upregulation of oxidoreductases, along with peroxidases and HSPs, have been identified as biomarkers of heat stress in several coral species (Han et al., 2024). This is further supported by the enrichment of the "darkmagenta" module for heat shock responses, apoptotic processes, cytochrome P450 activity, and immune signaling. Cytochrome P450 enzymes have been implicated in coral acclimatization under thermally variable conditions, suggesting a potential pathway through which *A. cervicornis* transplanted to CCC may attempt to cope with elevated or fluctuating environmental stressors (Palumbi et al., 2014).

Genes within the "mediumpurple3" module also point to stress-induced cellular reorganization. Matrix metalloproteinase-28, which was highly upregulated in CCC corals, is known to degrade extracellular matrix components during injury repair in cnidarians (DuBuc et al., 2014; Shimizu et al., 2002). Additionally, *PIH1* domain–containing proteins have been shown to modulate apoptosis and interact with *Hsp90* in chromatin remodeling complexes (Eckert et al., 2010; Inoue et al., 2010). Our study identified enriched GO terms that previously predicted *A. hyacinthus* survival following transplantation to a more thermally variable environment, including response to wounding, cell differentiation, and extracellular matrix organization (Bay and Palumbi, 2017). Together, these patterns may suggest that CCC corals were reallocating cellular resources toward mitigation, repair, and transcriptional reprogramming.

Several of the most highly upregulated host genes in CCC corals were associated with innate immune responses, including granuloma formation, TNF signaling, C-type lectins, and NF-κB regulation. Granuloma formation represents an aggregation of immune cells in response to inflammation (Shah et al., 2017), while TNF signaling can initiate apoptosis and programmed cell death (Palmer and Traylor-Knowles, 2012). In corals, TNF pathways have been implicated in bleaching-associated symbiont loss and the removal of damaged host cells (Helgoe et al., 2024; Quistad et al., 2014). C-type lectins play a key role in pathogen recognition and non-self differentiation (Rathinam et al., 2024). NF-κB is a central transcriptional regulator in corals that links innate immunity with environmental stress responses and the coral-algal symbiosis (Emery et al., 2024; Mansfield et al., 2017; Williams et al., 2018). The activation of the innate immune response may be vital for surviving marginal environments with more diverse microbial communities, including bacterial pathogens (Ziegler et al., 2016), or it could also indicate an increased exposure to pathogen loads or inflammation. As Miami's coastal waters experience frequent urban runoff and sewage leaks (Troxell et al., 2024), corals surviving near these outflows must acclimatize to these contaminants. While gene expression shifts may be the first step in this process, the coral holobiont likely also undergoes microbiome shifts, as previously documented (Roitman et al., 2020).

As symbiont identity can modulate host gene expression and stress tolerance, we sought to address the influence of transplantation on symbiont gene expression (Avila-Magaña et al., 2021; Barfield et al., 2018; Glynn et al., 2025). However, many genes were unannotated due to limitations in the current annotation methodologies. Of the annotated genes, a centrosomal protein, a SIR2–family NAD–dependent deacetylase, and medium-chain acyl-CoA dehydrogenase activity were highly upregulated. In other organisms, these proteins' functions have been linked to cell cycle dynamics, structural reorganization, and metabolic sensing of cellular stress (Ausseil et al., 2000; North and Verdin, 2004; Pan et al., 2022). The enriched GO term, actin cortical patch, further suggests cytoskeletal organization and cell-cycle regulation (Moseley and Goode, 2006). Overall, our limited symbiont results are congruent with other transcriptomic studies. While *Symbiodinium* expression shifts are comparatively lower in magnitude compared to the coral host, the differentially expressed genes encode similar protective and metabolic functions, such as antioxidants and molecular chaperones (Gierz et al., 2017). These intracellular signals suggest environmental changes are impacting the organization of symbionts within their host symbiosomes, potentially leading to downstream modifications in symbiont community composition (Anthony et al., 2023).

4.2 Host genotype likely contributes to expression variability

Although strong site-level patterns were detected, substantial variability was evident between individuals, particularly among CCC samples. While we were unable to explicitly test for genotype-level effects due to reduced sample size following quality and outlier filtration, prior work has demonstrated that host genotype is a primary driver of immune and stress-related gene expression variation in both *A. cervicornis* and *A. palmata* across reef environments (Villafranca et al., 2025; Young et al., 2024). It is likely that genotypic differences also contributed to the dispersion observed in the PCoAs and in module eigengene expression, but additional study would be required to fully disentangle genotype-by-environment interactions. Furthermore, as this study included only three genotypes, it does not represent a baseline for the species as a whole.

4.3 Symbiont composition and stability

All nursery-propagated *A. cervicornis* genotypes in this study hosted symbionts within the genus *Symbiodinium*, consistent with Florida populations of this species predominantly associating with the species *S. fitti* (Drury and Lirman, 2021; Lirman et al., 2014; O'Donnell et al., 2018). Although the thermally tolerant *Durusdinium trenchii* has been documented in nearshore *A. cervicornis* (Baums et al., 2010; Berkelmans and Van Oppen, 2006; Cunning et al., 2015), the genus *Durusdinium* was not detected in our transplanted corals even after one year post-transplantation. Notably, a native *A. cervicornis* colony at the CCC site did predominantly host the genus *Durusdinium* based on qPCR results, but this individual was excluded from gene expression analyses due to a low alignment rate using the concatenated host and symbiont genome. The inability of this port-native colony's reads to align to any tested algal reference 28S sequence, including of the genus *Durusdinium*, further illustrates how reference mismatch can substantially reduce overall mapping efficiency. This supports the interpretation that a portion of unmapped reads in our dataset may reflect holobiont reads that lack a suitable reference.

As recent evidence supports the enhanced thermal tolerance for *A. palmata* hosting *Durusdinium* in Florida compared to those hosting *Symbiodinium* (Karp et al., 2025), this relationship may also be important for *A. cervicornis.* Port-native colonies of *P. strigosa* that upregulated genes involved in immune system processes in a previous study were dominated by *Durusdinium* compared to offshore conspecifics (Rubin et al., 2021), suggesting that the conditions of this environment confer a shift in symbiont community composition. The persistence and resilience of urban-native *A. cervicornis* colonies in commercial ports in southeast Florida, and their capacity to host *Durusdinium*, suggest that symbiont flexibility may also play an important role in long-term survival in these urbanized, nearshore environments.

4.4 Environmental parameters of the Port of Miami governing coral resilience

Thermal conditions differed modestly, but CCC experienced greater cumulative heat stress and a greater range in temperatures compared to the nursery. This is in agreement with previous work characterizing multiple sites within the Port of Miami, demonstrating that the region experiences greater thermal variability, with greater extremes in both high and low temperatures compared to a nearby natural reef site (Enochs et al., 2023). However, temperature is not the only parameter governing the stressful habitats of the Port of Miami. While not measured in this study, we hypothesize that other environmental drivers may play a role in the transcriptomic differences observed. The region is characterized by higher light exposure, higher nutrient concentrations, lower salinity, greater acidity, increased turbidity, and increased water flow (Enochs et al., 2023). These interacting stressors have been shown to exacerbate coral physiological stress (Page et al., 2025; Palacio-Castro et al., 2021; Tisthammer et al., 2024). Yet, the persistence of a diversity of coral species and size classes suggests historical and ongoing recruitment and survivorship in the Port of Miami. However, the longevity of the responses we observed in this study several months after transplantation could indicate an energetic cost, and this important caveat requires further study in the growth and metabolism of transplanted corals.

The capacity for transcriptional plasticity and the duration for which a genotype can endure this response are likely to become highly selective traits for coral restoration efforts in a changing climate. Given the recent functional extinction of *A. cervicornis* in much of its historical range due to the 2023 mass bleaching event (Manzello et al., 2025), restoration efforts will require more targeted strategies, including sourcing genotypes from environmentally extreme habitats, increasing genotypic diversity in outplants, and optimizing the timing of transplantation to reduce cumulative stress exposure. Integrating molecular diagnostics with environmental monitoring will be essential for identifying genotypes and sites that maximize long-term restoration success.

Data availability statement

All code, results files, and annotated transcriptomes are publicly available on GitHub and are archived on Zenodo (DeMerlis, 2025; Studivan, 2026a, Studivan, 2026b). Sequence data are available on NCBI under BioProject PRJNA1333470.

Ethics statement

Ethical approval was not required for the study involving animals in accordance with the local legislation and institutional requirements because approval is not required for corals.

Author contributions

AD: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. CF: Methodology, Project administration, Resources, Writing – review & editing. DH: Investigation, Methodology, Project administration, Resources, Writing – review & editing. RK: Data curation, Formal analysis, Investigation, Resources, Validation, Visualization, Writing – review & editing. LI: Data curation, Formal analysis, Methodology, Resources, Writing – review & editing. NA: Data curation, Formal analysis, Methodology, Resources, Writing – review & editing. KW: Conceptualization, Data curation, Formal analysis, Investigation, Supervision, Validation, Writing – review & editing. MS: Conceptualization, Data curation, Formal analysis,

Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – review & editing. MJ: Data curation, Methodology, Resources, Writing – review & editing. AB: Investigation, Methodology, Project administration, Resources, Writing – review & editing. DL: Data curation, Methodology, Project administration, Resources, Supervision, Writing – review & editing. NT-K: Conceptualization, Funding acquisition, Methodology, Project administration, Resources, Software, Supervision, Writing – review & editing. IE: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – review & editing.

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Conflict of interest

Author CF is affiliated with Coral Morphologic, an organization involved in coral-related commercial and outreach activities.

The remaining author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2026.1796814/full#supplementary-material

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