REPORT

Reef habitats structure symbiotic microalgal assemblages in corals and contribute to differential heat stress responses

Sarah E. Leinbach[1] · Kelly E. Speare[2] ·
Marie E. Strader[3]

Abstract Coral-associated microbial symbionts, particularly dinoflagellates from the family Symbiodiniaceae, play a significant role in corals' ability to survive and recover from marine heatwaves and mass bleaching events. Yet, there remain limited data on the extent to which microalgal endosymbiont associations shift in situ during and after prolonged heat stress and over small spatial scales, potentially limiting the alteration of symbiont communities as a restoration tool. In 2019, Mo'orea, French Polynesia experienced a massive thermal anomaly accompanied by widespread coral bleaching and mortality. Using ITS2 amplicon sequencing, we assessed the possibility of microalgal assemblages explaining the observed variability in *Acropora hyacinthus* thermal tolerance and recovery dynamics between reef habitats. Our data reveal flexibility in *A. hyacinthus* symbiont associations, but show that these associations were strongly linked to both heat stress response and the reef habitat in which the colony resided, indicating a prominent role of local environments in shaping in hospite symbiont communities and, consequently, holobiont thermal tolerance. Notably, bleaching resistant colonies were invariably dominated by *Symbiodinium* during and after the bleaching event. Although we did not detect temporal changes in symbiont communities during recovery from thermal stress, this novel observation of *A. hyacinthus* in association with *Symbiodinium* suggests that heat stress may have facilitated a shift. Further, we identify symbiont type profiles that are potentially diagnostic of bleaching susceptibility. Our findings illuminate the extent of symbiont flexibility for this species and location, with important implications for coral reef recovery and management in a rapidly changing ocean.

Keywords Coral bleaching · Thermal stress · *Acropora hyacinthus* · ITS2 · Symbiodiniaceae · French Polynesia

✉ Sarah E. Leinbach
   sel0051@auburn.edu

1 Department of Biological Sciences, Auburn University, Auburn, AL, USA

2 Department of Ecology, Evolution, and Marine Biology, University of California Santa Barbara, Santa Barbara, CA, USA

3 Department of Biology, Texas A&M University, College Station, TX, USA

Introduction

Coral microbial symbionts play an integral role in the health, survival, and ecological functioning of their hosts (Bourne et al. 2016). Endosymbiotic dinoflagellate microalgae from the family Symbiodiniaceae are of particular importance as they facilitate a tightly regulated, mutualistic nutrient exchange that is crucial to coral holobiont metabolism and function (Rädecker et al. 2015). However, corals live close to their upper thermal physiological limits and anomalously warm seawater temperatures, or marine heatwaves (Oliver et al. 2021), resulting from anthropogenic climate change can disrupt this symbiotic relationship and lead to coral bleaching (Hoegh-Guldberg and Smith 1989). Given that marine heatwave-induced bleaching is projected to increase in the next century (Hughes et al. 2018), there is an urgent need to understand how coral–algal symbiotic relationships may be altered on the reef during or after bleaching events.

Diverse Symbiodiniaceae taxa are known to associate with coral hosts (LaJeunesse et al. 2018). These symbiont taxa exhibit varying tolerances to environmental stressors

and, as such, modulate coral host physiology and phenotype (Rowan 2004; Berkelmans and van Oppen 2006; Cunning et al. 2015). For instance, some species within *Durusdinium* and *Cladocopium* genera confer some degree of thermal bleaching resistance to their hosts, while others are associated with holobiont thermal sensitivity (Berkelmans and van Oppen 2006; Cunning et al. 2016; Howells et al. 2020). Corals also may harbor a single Symbiodiniaceae type or multiple taxa simultaneously (Thornhill et al. 2009; Silverstein et al. 2012), and emerging evidence points to symbiont type abundance and diversity as additional important factors that influence corals' health and response to stress (Kenkel and Bay 2018; Claar et al. 2020a; Howe-Kerr et al. 2020). For example, high algal symbiont alpha diversity has been implicated in poor host performance under stressful conditions, including elevated water temperatures, carbon dioxide levels, and inorganic nutrients (Claar et al. 2020a; Howe-Kerr et al. 2020). Therefore, connections between symbiont community composition and corals' responses to changing ocean conditions should be further considered when evaluating holobiont stress tolerance, especially in the context of prolonged marine heatwaves that contribute to mass bleaching.

The modification of Symbiodiniaceae communities has been proposed as a potential mechanism to bolster corals' resilience to environmental stressors, including temperature-induced bleaching (Buddemeier and Fautin 1993; Kinzie et al. 2001; Berkelmans and van Oppen 2006; Silverstein et al. 2015; Boulotte et al. 2016; Anthony et al. 2017; Voolstra et al. 2021). According to this idea, the proportional abundance of microalgal endosymbiont taxa can shift, either through resorting of taxa already present within the coral

tissues or uptake of exogenous symbiont cells, to favor types that are better suited to tolerate current levels of warming (Kinzie et al. 2001; Berkelmans and van Oppen 2006; Jones et al. 2008; Cunning et al. 2015; Boulotte et al. 2016). However, this is not a ubiquitous response. In fact, there are more examples of coral colonies not altering their dominant symbiont type in response to thermal stress, suggesting a strong role of host–symbiont genotype compatibility and calling into question how ecologically relevant alteration of Symbiodiniaceae assemblages within a colony is in situ (Goulet 2006; Sampayo et al. 2008; Stat et al. 2009; Thornhill et al. 2009; LaJeunesse et al. 2010; Smith et al. 2017). Hence, assessing in hospite microalgal assemblages and their potential to change through time is essential not only for understanding the coral holobiont's capacity to persist in the face of climate change, but also in determining the contribution of the coral–algal symbiosis to adaptation and/or acclimatization.

From December 2018 to May 2019, the island of Mo'orea, French Polynesia experienced a prolonged marine heatwave (Fig. 1b) accompanied by widespread coral bleaching and mortality (Speare et al. 2021). However, marked colony-level differences in bleaching response were observed in *Acropora hyacinthus* (Fig. 1c)*,* a key reef-builder in the Indo-Pacific Ocean that is highly sensitive to climate change (Veron 2000; Baird and Marshall 2002), with some individuals remaining unbleached ("resistant" colonies, Supplementary Fig. S1a) and others bleaching but later recovering after the thermal stress subsided ("recovered" colonies, Supplementary Fig. S1b) (Leinbach et al. 2021). Here, we leverage this natural, thermally induced bleaching event to compare Symbiodiniaceae communities (i.e., the total assemblage of
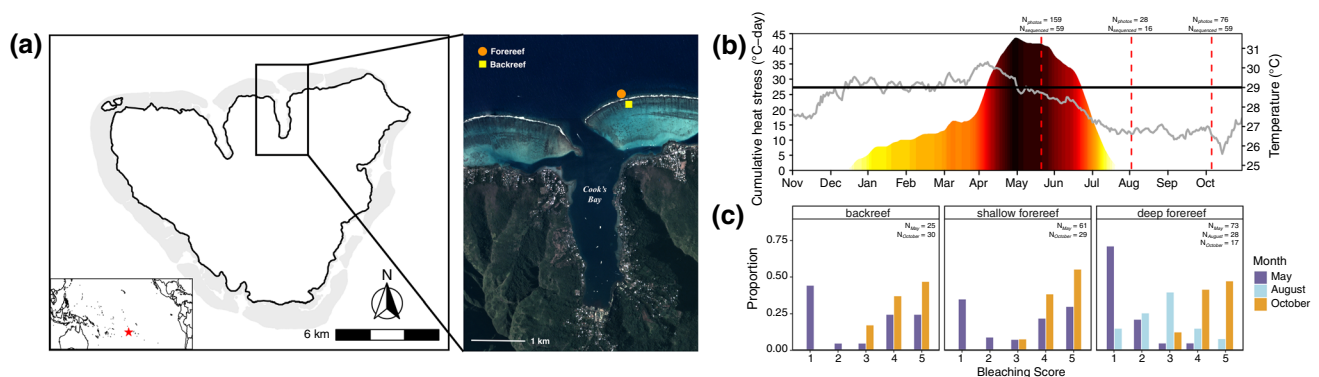

Fig. 1 Thermal stress and associated bleaching event in 2019 on the island of Mo'orea, French Polynesia. (**a**) Map of sampling locations in forereef and backreef habitats along the north shore of Mo'orea (red star, inset world map) (satellite imagery, Allen Coral Atlas 2022). (**b**) Observed sea surface temperatures from November 2018 to November 2019 (gray line) and bleaching threshold for corals in Mo'orea (black line; right axis). Vertical red dashed lines indicate sampling time points. Color gradient from yellow to black illustrates increasing cumulative heat stress (left axis) around the island. Sample sizes refer to the number of photographs taken and colonies successfully sequenced at each time point. (**c**) Bleaching severity in *Acropora hyacinthus* observed across reef habitats. A bleaching score of 1 indicates stark white bleaching and 5 indicates dark pigmentation (Supplementary Fig. S1c). Sample sizes refer to the number of colonies photographed and scored per month in each reef habitat

all symbiont types present in the coral host) between the two forenamed coral heat stress responses and across environmentally distinct reef habitats of *A. hyacinthus.* Associations between coral host and symbiont types can exhibit significant variation in response to abiotic factors and this partnership may be constrained by selective environmental variables, such as temperature and light intensity, that vary over small spatial scales across reef zones (Iglesias-Prieto et al. 2004; van Oppen et al. 2018; Dubé et al. 2021; Kriefall et al. 2022). We aimed to identify possible microalgal drivers for the observed variability in coral heat tolerance, including spatial and temporal changes in Symbiodiniaceae taxa. Addressing these questions will elucidate possible acclimatization mechanisms that coral survivors adopt when confronted with extreme heat stress.

Methods

Study site and sample collection

Mo'orea, French Polynesia is a volcanic island in the Southern Pacific Ocean surrounded by a barrier reef system (Fig. 1a). Water temperature data (Fig. 1b) were collected at one site on the north shore outer reef, approximately 1 km west of Cook's Bay, as part of the Mo'orea Coral Reef Long Term Ecological Research (MCR LTER) core time series data collection (Leichter et al. 2020). A bottom-mounted thermistor (Seabird SBE 39) attached at 10 m depth recorded water temperatures at 20-min intervals. Cumulative heat stress (in °C-days) was calculated as a 12-week running sum of average daily temperatures exceeding 29 °C, the maximum monthly mean (MMM) and a noted bleaching threshold for corals in Mo'orea (Pratchett et al. 2013), from November 1, 2018, to October 31, 2019.

In May 2019, during the height of the bleaching event, SCUBA divers surveyed one site on the north shore of Mo'orea (17.4731° S, 149.8176°W (forereef) and 14.4751° S, 149.8170° W (backreef); Fig. 1a) to identify bleached and healthy *Acropora hyacinthus* coral colonies in three reef habitats: backreef (~3 m depth), shallow forereef (~5 m depth), and deep forereef (~14 m depth). Individual colonies were photographed, and small branches (~2–4 cm length) were collected from all *A. hyacinthus* colonies encountered and preserved in 100% ethanol. Colonies from the shallow and deep forereef habitats were tagged for future sampling. On the deep forereef in May 2019, we found no *A. hyacinthus* colonies without some degree of bleaching (Leinbach et al. 2021). By August 2019, all the previously tagged bleached colonies in the deep forereef had died. Despite this high mortality, August surveys on the deep forereef (~14 m depth), which occurred after the period of accumulated thermal stress (Fig. 1b), identified previously bleached, untagged

colonies that were observed to be visibly recovering from bleaching (Supplementary Fig. S1b). These new colonies were photographed, tagged, and sampled. Due to the high prevalence of bleaching at this site in May, we maintain that these previously untagged colonies were bleached during the bleaching event. In October, tagged colonies at both forereef depths were resampled and photographed. Untagged colonies in the backreef were also sampled and photographed. Bleaching severity and colony size for all sampled corals were determined using standardized photographs taken during the surveys. Each colony was assigned an integer score from 1 to 5 based on a visual evaluation of bleaching severity, where 1 indicates stark white bleaching and 5 indicates no bleaching with dark pigmentation (Fig. 1c, Supplementary Fig. S1c). The outline of each coral colony was traced in ImageJ to calculate planar surface area as an estimate of colony size (Schneider et al. 2012). See Supplementary Table S1 for more details on the number of colonies photographed, sampled, and sequenced from each reef habitat at each time point.

DNA extraction and ITS2 amplicon sequencing and analysis

Genomic DNA was extracted from samples (see Supplementary Tables S1 and S2 for more detailed sample sizes) using a sodium dodecyl sulfate (SDS) digestion protocol (Lundgren et al. 2013, Supplementary Methods) and cleaned with the Zymo Research Genomic DNA Clean and Concentrator-10 kit. For each sample, 900 ng of DNA was sent to the Georgia Genomics and Bioinformatics Core at the University of Georgia for sequencing. ITS2 amplicon libraries were generated using the Symbiodiniaceae-specific primers SYM_VAR_5.8S2 and SYM_VAR_REV (Hume et al. 2018) and sequenced on the Illumina MiSeq platform with 250-bp paired-end reads (Supplementary Methods).

To characterize Symbiodiniaceae taxa, raw reads from each sample were submitted directly to the analytical framework SymPortal (https://symportal.org) (Hume et al. 2019). SymPortal algorithmically searched for re-occurring sets of ITS2 sequences, called defining intragenomic variants (DIVs), and used their presence and abundance in each sample to predict ITS2 type profiles, which are representative of putative Symbiodiniaceae taxa. The final outputs from SymPortal used in downstream statistical analyses included files of ITS2 type profile sequence abundances for all coral samples and files separated by major Symbiodiniaceae genus of principal coordinate analysis (PCoA) coordinates conducted on Bray–Curtis indices (Supplementary Methods).

Statistical analyses

Statistical analyses of Symbiodiniaceae alpha and beta diversity were conducted on SymPortal outputs in R version 4.0.3. ITS2 type profile reads were normalized using trimmed mean of M-values (TMM) in the package edgeR (Robinson and Oshlack 2010) to account for differences in sequencing depth. The 21 resultant ITS2 type profiles from SymPortal were then collapsed into seven more conservative groupings based on PCoAs of their Bray–Curtis indices (Supplementary Fig. S2). We chose to further collapse the type profiles so as not to inadvertently overestimate Symbiodiniaceae diversity. The groupings were determined based on their distribution along PC1. All subsequent analyses were conducted on the collapsed ITS2 type profiles.

Alpha diversity was measured by calculating ITS2 type profile richness for each sample. Generalized linear mixed-effects models (GLMMs) were employed to examine the effects of heat stress response, reef habitat, colony health (defined as "bleached" or "healthy"), and month on richness, with a random effect of colony identity included. A linear mixed-effects model (LME) was used to analyze the relationship between richness and colony size. Poisson regressions were also utilized to investigate richness differences over time in colonies that were sampled over multiple months.

Multivariate statistics were used to examine beta diversity, specifically community structure, defined as the relative abundance of sequencing reads for each collapsed ITS2 type profile. Permutational analyses of variance (PERMANO-VAs), via the *adonis* function in the package vegan (Okansen et al. 2020), were utilized to explore how coral heat stress response, reef habitat, colony health, and month impacted symbiont community structure. Additional iterations of these analyses were conducted on individual colonies that were sampled over multiple time points (referred to as "paired colonies") to assess any changes in Symbiodiniaceae community within an individual over time. Pairwise comparisons were performed using the function *pairwiseAdonis* after any significant PERMANOVA results. Multivariate dispersion was quantified (function *betadisper*) using Bray–Curtis dissimilarities for community structure data. Differences in dispersion (i.e., if *betadisper* is significant) between samples can confound PERMANOVA results, resulting in a type I error when comparing symbiont communities. To ensure significant PERMANOVA results indicated true community differences, a bootstrapped sensitivity analysis was executed on any PERMANOVA results that showed significant heterogeneity of dispersion (Claar et al. 2020b; Supplementary Methods). All tests passed the sensitivity test.

Community structure data were visualized with non-metric multidimensional scaling (NMDS), using Bray–Curtis dissimilarities. Venn diagrams were created with the Eulerr package (Larsson 2018) to visualize shared Symbiodiniaceae ITS2 type profiles between heat stress responses, reef habitats, and colony health statuses. All model outputs and results are listed in Supplementary Table S3.

Results

Amplicon sequencing of 134 samples from 110 individual *A. hyacinthus* colonies yielded 12,491,776 sequencing reads, 8,379,219 of which passed the quality filtering in SymPortal (67.08%) (Supplementary Table S2). In total, we detected 21 ITS2 type profiles within our samples, which we further collapsed into seven more conservative type profiles (Supplementary Fig. S2). These ITS2 type profiles included representatives from three Symbiodiniaceae genera: *Symbiodinium*, *Cladocopium*, and *Durusdinium*.

Symbiont communities varied across reef habitats

Acropora hyacinthus colonies in the backreef, shallow forereef, and deep forereef were characterized by distinctive symbiont communities (PERMANOVA, $p = 0.001$; Fig. 2b; Supplementary Table S3a, b). Overall, colonies in the shallow forereef were almost exclusively associated with *Symbiodinium* A1 and colonies in the deep forereef were predominantly associated with *Cladocopium* C3ae (Fig. 2). Backreef colonies hosted highly variable symbiont associations, with many colonies (32/44, 72.72%) hosting more than one ITS2 type profile (Fig. 2a, d), often at high abundances. Furthermore, several backreef colonies (14/44, 31.82%) contained representatives from all three Symbiodiniaceae genera. A smaller proportion of colonies (9/44, 20.45%) associated with multiple ITS2 type profiles within the same genus. Backreef coral colonies exhibited significantly higher alpha diversity than both the shallow and deep forereef habitats (GLMM, $p_{shallow} = 0.0054$, $p_{deep} = 0.0014$; Fig. 2a; Supplementary Table S3l). There was no significant difference in alpha diversity between the two forereef depths (GLMM, $p = 0.84$) and the majority of forereef colonies housed only one ITS2 type profile, although mixed communities were observed (18/57, 31.58% in the shallow forereef; 7/33, 21.21% in the deep forereef) (Fig. 2a; Supplementary Table S4a). Coral colonies in the shallow forereef were dominated by *Symbiodinium* A1. However, 2/57 (3.51%) colonies were dominated by *Cladocopium* C3ae and 8/57 (14.04%) colonies contained observable levels of *Durusdinium* D1. Mixed-genera symbiont assemblages were observed in 17/57 (29.83%) samples and four of these housed multiple ITS2 type profiles from the same genera. In the deep forereef, *Cladocopium* C3ae was the predominant type profile in 30/33 (90.91%) colonies, with the remaining three samples hosting a *Durusdinium* D1 majority (Fig. 2d). Five
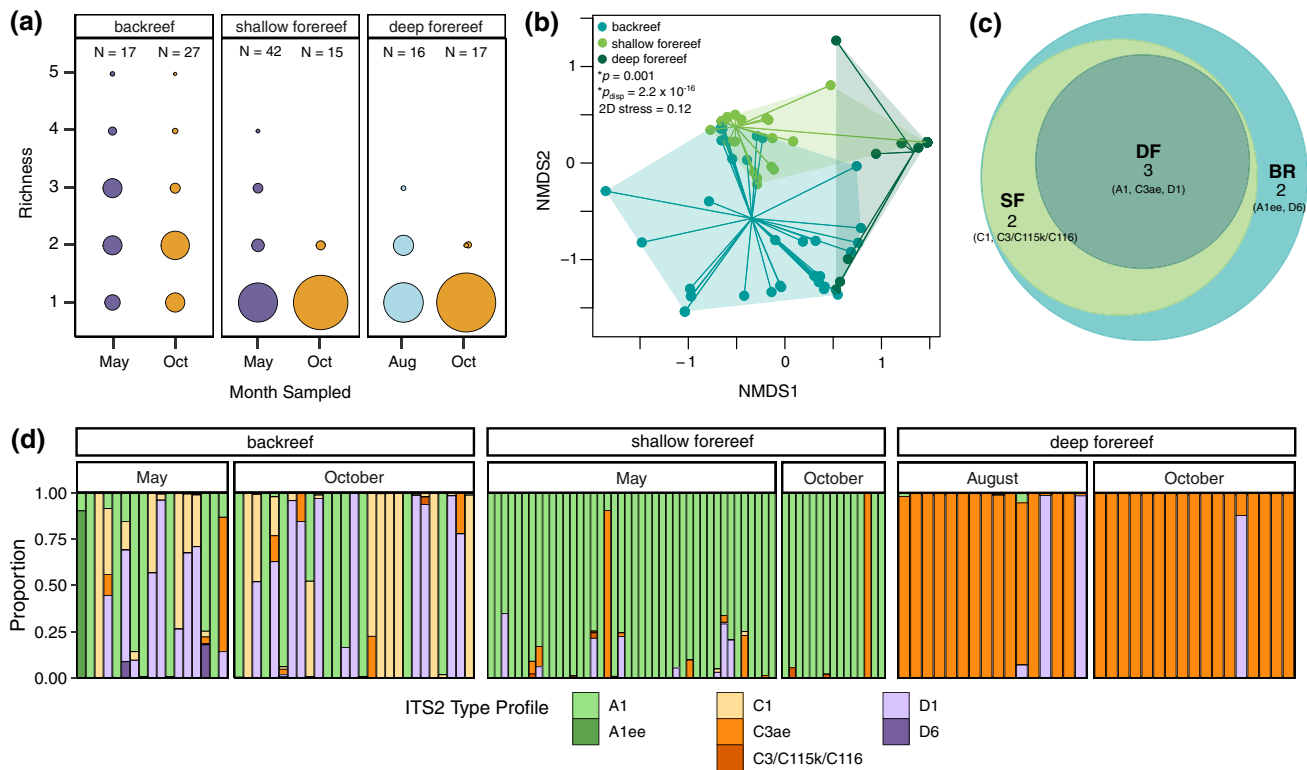
Fig. 2 Symbiodiniaceae communities across three reef habitats. (**a**) ITS2 type profile richness per colony across reef habitats and sampling time points. Size of each circle is scaled to the proportion of colonies in each reef habitat–month combination that host a given number of ITS2 type profiles. (**b**) Non-metric multidimensional scaling (nMDS) of symbiont community structure based on ITS2 type profiles. Statistical significance for PERMANOVA (p) and multivariate dispersion (p_{disp}) is denoted with an asterisk. (**c**) Venn diagram of the number and identity of ITS2 type profiles present in colonies found in each reef habitat. (**d**) Normalized relative proportion of ITS2 type profiles from colonies across backreef, shallow forereef, and deep forereef habitats over the sampling time points

of the *Cladocopium*-dominated colonies in August (5/16, 31.25%) supported mixed-genera symbiont assemblages and one colony housed Symbiodiniaceae from all three observed genera (Fig. 2d). Colonies in the backreef contained two unique ITS2 type profiles (A1ee, D6) that were not found in forereef colonies (Fig. 2c).

Within each reef habitat, we observed no significant shifts in Symbiodiniaceae community composition over time (PERMANOVAs, $p_{backreef} = 0.85$, $p_{shallow} = 0.52$, $p_{deep} = 0.23$; Fig. 2d; Supplementary Table S3c). Additionally, during each sampling time point, symbiont community structure in corals across reef habitats remained significantly different from each other (PERMANOVA, $p_{May} = 0.001$, Supplementary Fig. S3a; $p_{October} = 0.001$, Supplementary Fig. S3b). Although colony size differed significantly between reef habitats—on average, backreef colonies were significantly smaller than forereef colonies from both depths, and deep forereef colonies were significantly smaller than shallow forereef colonies (Supplementary Table S3o)—it did not influence ITS2 type profile richness (GLMM, $p = 0.91$; Supplementary Fig. S4).

Relationship between symbiont assemblages and coral health depended on reef habitat

Healthy and bleached coral colonies sampled at the height of the thermal anomaly in May showed no significant difference in symbiont community structure (PERMANOVA, $p = 0.18$; Fig. 3b). However, we found divergent patterns when considering the backreef and shallow forereef separately. In the backreef, healthy and bleached colonies did not support significantly different symbiont communities (PERMANOVA, $p = 0.81$; Fig. 3d; Supplementary Fig. S5b). Healthy backreef corals generally contained fewer profiles than bleached colonies, but this trend was not significant (GLMM, $p = 0.25$; Fig. 3a; Supplementary Table S4b) and the majority of colonies (13/17, 76.47%) housed more than one ITS2 type profile (Figs. 3a, d). Conversely, in the shallow forereef, healthy and bleached corals' symbiont communities were significantly different (PERMANOVA, $p = 0.001$; Fig. 3d; Supplementary Fig. S5a). Healthy shallow forereef colonies also hosted significantly fewer ITS2 type profiles compared to bleached conspecifics (GLMM, $p = 0.00085$; Fig. 3a; Supplementary Table S4b). All healthy
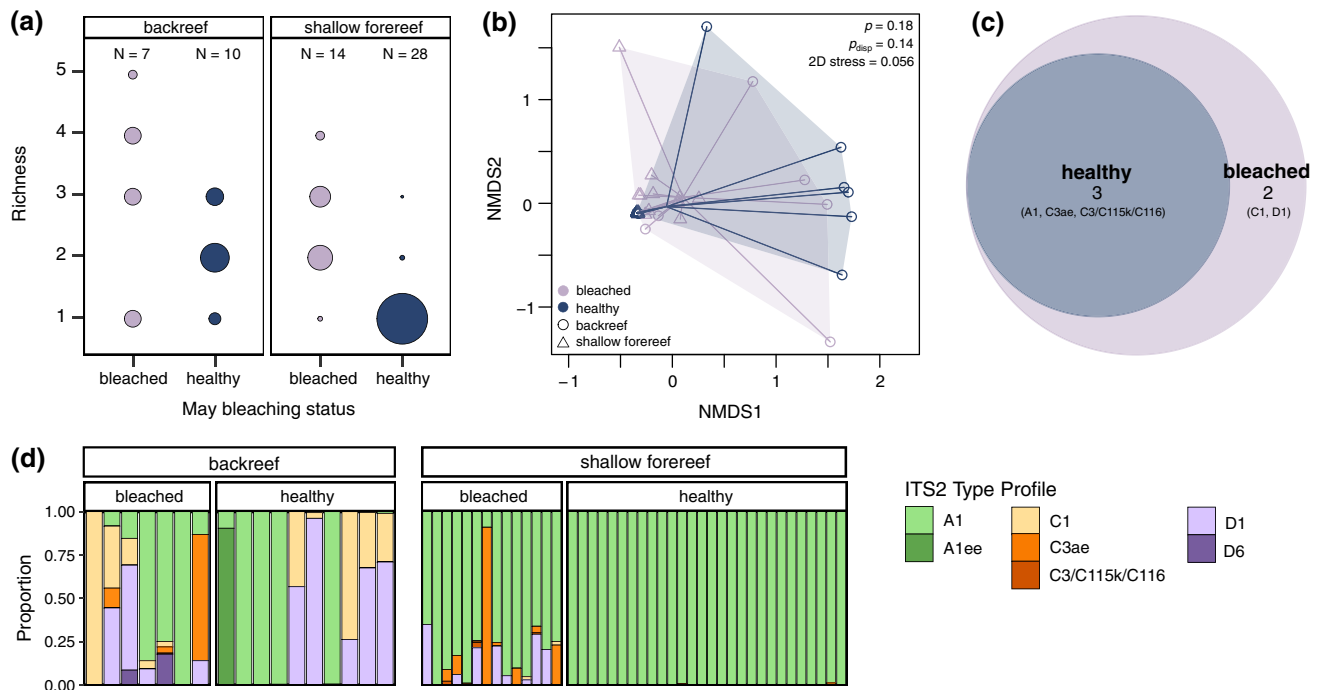
Fig. 3 Symbiodiniaceae communities in healthy and bleached colonies sampled during May in the backreef and shallow forereef. (**a**) ITS2 type profile richness per colony for healthy and bleached colonies found in two reef habitats. Size of each circle is scaled to the proportion of colonies in each reef habitat-bleaching status combination that host a given number of ITS2 type profiles. (**b**) Non-metric multidimensional scaling (nMDS) of symbiont community structure based on ITS2 type profiles. Statistical significance for PERMANOVA (p) and multivariate dispersion (p_{disp}) is denoted with an asterisk. (**c**) Venn diagram of the number and identity of ITS2 type profiles present in healthy and bleached colonies from the shallow forereef in May. (**d**) Normalized relative proportion of ITS2 type profiles from bleached and healthy colonies in the backreef and shallow forereef habitats

corals in the shallow forereef were dominated by *Symbiodinium* A1, whereas bleached corals tended to primarily affiliate with *Symbiodinium* A1 but also contained *Durusdinium* D1 and *Cladocopium* type profiles at lower abundance (Fig. 3d).

There was one unique type profile found only in healthy colonies (A1ee) and one unique type profile found only in bleached colonies (D6) (Supplementary Fig. S5c). Among backreef colonies, one ITS2 type profile was unique to healthy colonies (A1ee), and three were unique to bleached colonies (C3ae, C3/C115k/C116, D6) (Supplementary Fig. S5d). On the shallow forereef, there were no unique type profiles in healthy colonies and bleached colonies housed two unique ITS2 type profiles (C1, D1) (Fig. 3c).

Symbiont communities differed between coral heat stress responses

We found significant differences in symbiont community composition and structure between the two observed heat stress responses: resistance and recovery (PERMANOVA, $p = 0.001$; Fig. 4b). Resistant colonies, which were found exclusively in the shallow forereef, were consistently dominated by *Symbiodinium* A1, whereas recovered corals, which we documented in both the shallow and deep forereef,

displayed more flexibility in symbiont association. Recovered colonies were largely dominated by *Cladocopium* C3ae (32/36, 88.89%), but some colonies were found instead to host *Symbiodinium* A1 (1/36, 2.78%) or *Durusdinium* D1 (3/36, 8.33%) (Fig. 4d). There was no significant difference in alpha diversity between heat stress responses (GLMM, $p = 0.20$; Fig. 4a; Supplementary Table S4c). Recovered colonies hosted two unique ITS2 type profiles (C1, D1) and resistant colonies hosted one unique type profile (C3/C115k/C116) (Fig. 4c).

Tagging of some resistant and recovered coral colonies allowed us to investigate if there were differences within an individual colony between sampling time points. We found no significant change in symbiont community structure within an individual throughout the study period (PERMANOVAs, $p_{recovered} = 0.71$, $p_{resistant} = 0.48$; Fig. 5; Supplementary Table S4d). Except for one individual (colony ID 324, Fig. 5a), all colonies were dominated by the same ITS2 type profile in both of their respective sampling time points.
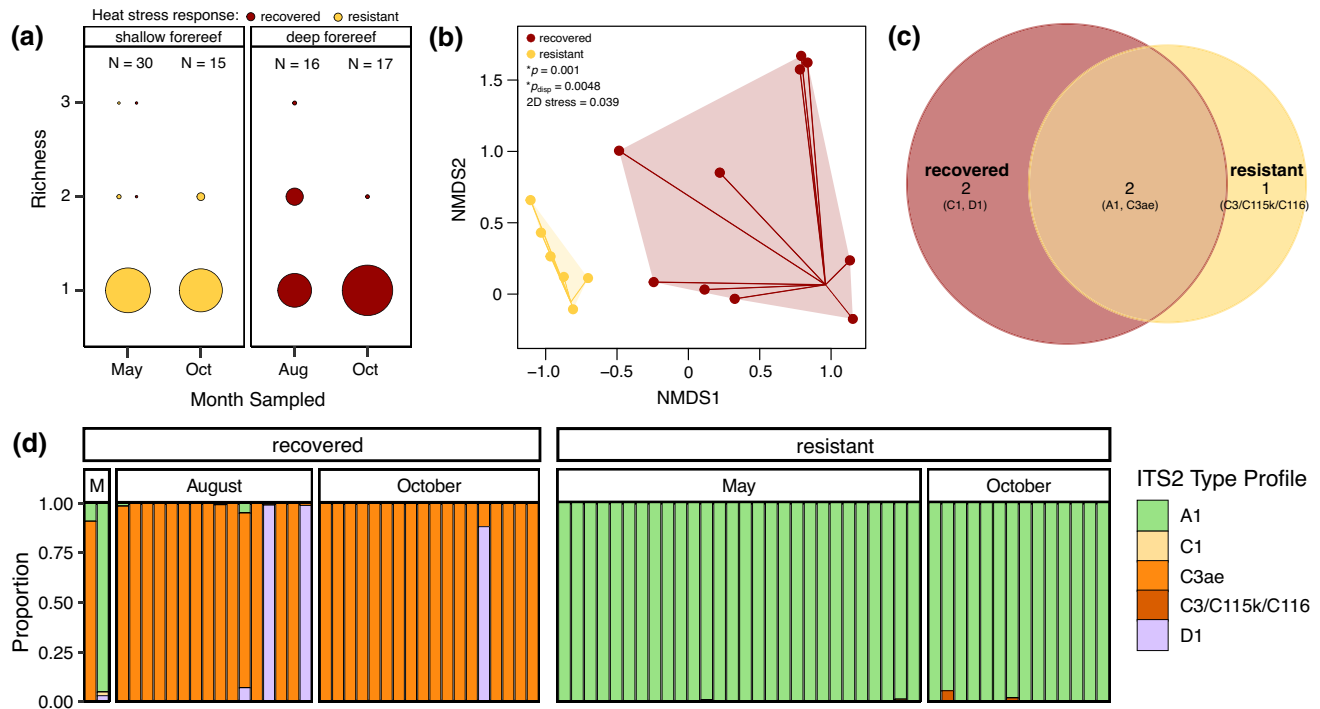
Fig. 4 Symbiodiniaceae communities in recovered and resistant colonies. (**a**) ITS2 type profile richness per colony across reef habitats and sampling time points. Size of each circle is scaled to the proportion of colonies in each reef habitat–month combination that host a given number of ITS2 type profiles. (**b**) Non-metric multidimensional scaling (nMDS) of symbiont community structure based on ITS2 type profiles. Statistical significance for PERMANOVA (*p*) and multivariate dispersion (p_{disp}) is denoted with an asterisk. (**c**) Venn diagram of the number and identity of ITS2 type profiles present in resistant and recovered colonies. (**d**) Normalized relative proportion of ITS2 type profiles from resistant and recovered colonies over the sampling time points. M represents May
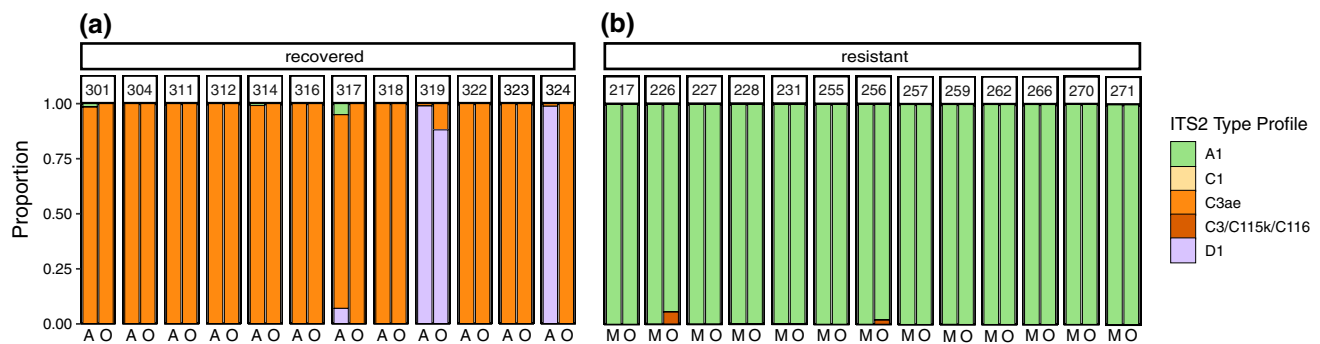

Fig. 5 Normalized relative proportion of ITS2 type profiles from paired (**a**) recovered (N = 12 pairs) and (**b**) resistant colonies (N = 13 pairs). M—May sampling time point, A—August sampling time point, O—October sampling time point. These resistant and recovered colonies were sampled on the shallow and deep forereef, respectively

Discussion

We examined Symbiodiniaceae assemblages in *Acropora hyacinthus* colonies displaying two distinct heat stress responses and assessed the temporal stability of these relationships, including how they differ across reef habitats, in the context of a mass bleaching event. Previous studies have classified *Acropora* species as flexible with respect to

Symbiodiniaceae associations (i.e., as symbiont generalists) (van Oppen et al. 2001; Putnam et al. 2012; Kriefall et al. 2022). Our results support this idea, as we found *Acropora hyacinthus* in Mo'orea harbored microalgal endosymbionts from multiple ITS2 type profiles distributed across three genera, including some colonies hosting multiple genera simultaneously. Our findings also reveal that, despite coral host–Symbiodiniaceae flexibility within a reefscape,

dominant Symbiodiniaceae type profile was strongly linked to both reef habitat and holobiont propensity for thermal resistance or recovery. Further, there was covariance between these different responses to the heat anomaly and the reef habitat in which the colonies were found; resistant colonies were exclusively found in the shallow forereef, while recovered colonies were almost exclusively found in the deep forereef. Therefore, we are unable to disentangle the relative contribution of reef habitat and bleaching history to *A. hyacinthus* in hospite microalgal assemblages, but our results suggest a prominent role of local environmental conditions in structuring symbiont communities and, in turn, host response to heat stress.

Intraspecific coral holobiont responses to heat stress can vary across reef habitats and are influenced by abiotic factors including light intensity, water temperature and temperature variability, and water flow (McClanahan et al. 2005; Hoogenboom et al. 2017; Schoepf et al. 2020). We documented divergent patterns of bleaching severity and recovery in *A. hyacinthus*, with colonies residing in the deep forereef exhibiting more extensive bleaching and mortality than those in the backreef and shallow forereef (Fig. 1c). Observations of prior bleaching events in Mo'orea noted similar spatially heterogenous bleaching susceptibilities. For example, during bleaching events in 1994, 2002, and 2007, coral assemblages at shallow depths displayed less severe bleaching than those at deeper depths (Penin et al. 2007, 2013). Previous studies ascribed these results to an interplay between hydrodynamic conditions and differential acclimatization and/or adaptation of coral–algal symbioses, but did not investigate specific mechanisms (Penin et al. 2007, 2013). We extend these conclusions by demonstrating that *A. hyacinthus* colonies hosted distinct symbiont communities within each reef habitat (Fig. 2). *Acropora hyacinthus* acquires its symbionts via horizontal transmission and thus may be able to form symbioses with the endosymbionts best adapted to local environmental conditions (Buddemeier and Fautin 1993; Van Oppen et al. 2001; Quigley et al. 2017). Because Symbiodiniaceae types can confer different physiological traits to the coral host, this resultant symbiont zonation may enable coral holobionts to survive over a gradient of environmental conditions, in particular light, temperature, and nutrient availability, that can vary over small spatial scales (Rowan 2004; Frade et al. 2008; Dubé et al. 2021; Kriefall et al. 2022).

The deep forereef (~ 14 m depth) receives the lowest irradiance out of all three reef habitats we sampled (Dubé et al. 2021), and colonies located there were predominantly associated with *Cladocopium* C3ae (Fig. 2d). Some *Cladocopium* species are known to be more photosynthetically efficient than other Symbiodiniaceae and are thus frequently observed in symbiosis with coral colonies at depth, where light intensity is lower (Cooper et al. 2011; Eckert et al. 2020; Wall et al. 2020). Alternatively, in the shallow forereef (~ 5 m depth), which is characterized by a higher irradiance (Dubé et al. 2021), the vast majority of colonies were dominated by *Symbiodinium* A1. Some *Symbiodinium* species are capable of several photoprotective mechanisms, including the production of UV-adsorbing mycosporine-like amino acids (MAAs) and upregulation of alternative photosynthetic electron pathways (Banaszak et al. 2000; Reynolds et al. 2008), explaining why *Symbiodinium* is chiefly found in coral hosts in shallow waters where light levels are high (Rowan and Knowlton 1995; Reynolds et al. 2008). Backreef environments are characterized by high irradiance, temperature, temperature fluctuation, and nitrogen concentration (Kriefall et al. 2022), and as such, they may present the most stressful conditions for corals. A prior investigation of *A. hyacinthus* in Mo'orea before the 2019 thermal anomaly found that the backreef constrained Symbiodiniaceae diversity compared to the forereef (Kriefall et al. 2022), whereas we observed the opposite trend, suggesting that the heat stress and concordant bleaching event may have disrupted coral–algal associations. We found significantly higher alpha diversity in colonies on the backreef compared to both forereef depths (Fig. 2a) and highly variable symbiont community compositions (Fig. 2d). Such symbiont variation could be a form of bet-hedging, allowing corals to exploit different physiological traits of multiple symbiont taxa and thus enhance survival in the dynamic backreef environment (Loram et al. 2007; Torda et al. 2017). Because backreef colonies were significantly smaller than those on the forereef (Supplementary Fig. S4; Supplementary Table S3o), it is possible that they were younger and had not yet finished the winnowing process to establish a dominant symbiont type. Although some colonies were below the accepted size threshold for maturity in *A. hyacinthus* (~ 7 cm diameter) (Wallace 1985), we found no correlation between colony size and number of ITS2 type profiles (Supplementary Fig. S4), indicating that the increased alpha diversity of backreef colonies is linked to some other factor, such as environmental conditions, not an artifact of coral life stage.

Symbiont zonation, in addition to reflecting environmental constraints, is also related to host genetic structuring (Bongaerts et al. 2010; Brazeau et al. 2013). The reef-wide patterns of Symbiodiniaceae community diversity and composition we observed may thus reflect underlying host differentiation, which we did not address in this study. Kriefall et al., however, found high gene flow between adjacent reef habitats and no evidence for *A. hyacinthus* genetic structuring in Mo'orea (Kriefall et al. 2022). They also found no evidence for host genetic variation correlating with symbiont associations. Cryptic species of *A. hyacinthus* have also been uncovered throughout the Pacific Ocean, including in Samoa, Palau, Australia, and Japan (Ladner and Palumbi 2012; Fifer et al. 2022), but no such finding has yet come

to light in Mo'orea. If there is indeed no genetic partitioning within our study system, this points to an underlying environmental driver of symbiont structuring and suggests that the distinct symbiont communities we observed between heat stress responses partitioned by depth and reef habitat may be an emergent property of reef-wide distribution of symbionts that are adapted to their environment.

At the height of the bleaching event in May 2019, all colonies within a reef habitat hypothetically experienced similar thermal stress, yet we observed significantly different Symbiodiniaceae community structures between healthy and bleached *A. hyacinthus* colonies on the shallow forereef (Fig. 3d; Supplementary S5a), suggesting that factors beyond the prevailing reef habitat conditions mediate the distribution of in hospite symbiont communities. Bleached colonies harbored higher alpha diversity compared to healthy conspecifics and housed symbiont communities that more closely resembled the variable mixed assemblages found in backreef colonies (Figs. 3a, d). This pattern could potentially be explained by the Anna Karenina principle (AKP), which posits that stressors induce stochastic changes in microbial community composition, leading to microbiomes of dysbiotic individuals exhibiting higher dispersion than those in healthy individuals (Zaneveld et al. 2017). Bleached backreef colonies also tended to host more ITS2 type profiles than healthy backreef colonies (Fig. 3a), but we did not detect significant differences in symbiont diversity or structure between them. This may be due to the decreased statistical power resulting from a smaller sample size for backreef colonies compared to shallow forereef colonies; thus, the AKP may be operating in the backreef as well as the shallow forereef and could, to some degree, explain differences in symbiont communities in our study compared to those documented by Kriefall et al. (2022). The thermal anomaly and subsequent bleaching in 2019 may have impaired host mechanisms to regulate and constrain symbiont assemblages (Moeller and Peay 2016; Zaneveld et al. 2017; Howe-Kerr et al. 2020), leading to increased variation and diversity in symbiont communities in bleached individuals. Alternatively, antagonistic interactions between diverse symbionts could have destabilized the coral–algal symbiosis and led to the observed bleaching (Miller 2007; Kenkel and Bay 2018; McIlroy et al. 2020), although our study is unable to disentangle whether the observed symbiont community variability is the result of thermal stress or the cause of differential bleaching phenotypes within a reef habitat. Because we observed both bleached and healthy individuals within a reef habitat, this points to additional factors influencing heat stress response and symbiont community composition, such as host microhabitat occupation, host genotype, or differential gene regulatory pathways involved in thermal physiology and symbiosis (Ganot et al. 2011; Barshis et al. 2013; Hoogenboom et al. 2017; Kavousi et al. 2020; Dilworth et al.

2021). Nonetheless, our results contribute to the expanding number of studies illustrating the AKP in the context of endosymbiotic dinoflagellates (Claar et al. 2020a, 2020b; Howe-Kerr et al. 2020).

Projections for the survival of future coral reefs often hinge upon colonies harboring thermally tolerant *Durusdinium* symbionts (Berkelmans and van Oppen 2006). However, our study adds to the growing body of literature demonstrating that enhanced bleaching tolerance is not universally associated with *Durusdinium* (Abrego et al. 2008; Howe-Kerr et al. 2020; Howells et al. 2020). We found that colonies resistant to bleaching in the shallow forereef were invariably dominated by *Symbiodinium* A1 (Fig. 4d). *Symbiodinium* A1 produces UV-protective MAAs and low amounts of hydrogen peroxide, a causative agent of coral bleaching, at elevated temperatures (Banaszak et al. 2000; Suggett et al. 2008), which could potentially contribute to the lack of bleaching we observed in the resistant colonies living on the shallow forereef. This is an interesting finding considering that *Symbiodinium* A1 generally enters into symbiosis with corals opportunistically, and thus resembles parasitism rather than mutualism (Stat et al. 2008). In previous experimental work that manipulated coral–algal combinations in *Acropora millepora,* colonies hosting *Symbiodinium* A1 had the lowest thermotolerance and fitness (Mieog et al. 2009). Conversely, *Symbiodinium* A1-A1v was the dominant symbiont type profile in *Acropora pulchra* thriving in a thermally extreme lagoon in New Caledonia (Camp et al. 2020), *Millepora* spp. in Belize dominated by *Symbiodinium* resisted bleaching (Schwiesow et al. 2021), and *Porites divaricata* in the Caribbean hosting *Symbiodinium* were able to swiftly acclimate to repeat bleaching (Grottoli et al. 2014). These contrasting reports suggest that the physiological costs and benefits of hosting *Symbiodinium* could be species- and/or location-specific and highlight the complexity of coral–algae symbiotic relationships, especially as they relate to thermal tolerance. We recommend that future studies further investigate the physiological ramifications of hosting *Symbiodinium* and its potential role in bleaching resistance.

Restructuring of symbiont communities or shifts in dominant symbiont type have been observed as a response to heat stress and proposed as a mechanism of host plasticity and adaptation (Buddemeier and Fautin 1993; Jones et al. 2008; Grottoli et al. 2014; Cunning et al. 2015). However, we did not observe significant temporal changes in symbiont community composition within colonies that varied in their heat stress responses or reef habitat locations during or after the thermal anomaly (Figs. 2, 4, 5). Although other studies have similarly reported temporally stable symbiont assemblages in *A. hyacinthus* after bleaching (Thomas et al. 2019), our study cannot definitively rule out the possibility that corals hosted different Symbiodiniaceae types before the bleaching

event, as we did not monitor *A. hyacinthus* prior to peak thermal stress. Earlier surveys in Mo'orea conducted in 2013 found the majority of *A. hyacinthus* colonies in the backreef and forereef were dominated by *Cladocopium*, with only a very small proportion of colonies dominated by *Symbiodinium* (Kriefall et al. 2022). This is in stark contrast to our results, suggesting that the 2019 thermal anomaly, or another thermal event between 2013 and 2019, may have induced changes in symbiont communities or selected for colonies hosting *Symbiodinium*. Although we did not observe bleaching in the resistant forereef colonies, it is possible that a shift may have occurred without visible bleaching or before the sampling time point in May (Thornhill et al. 2006; LaJeunesse et al. 2009). *Symbiodinium* is commonly identified in corals recovering from bleaching or thermal stress (Toller et al. 2001), and thus, the resistant colonies we observed in the field could have potentially experienced bleaching outside the scope of our sampling regime.

Conclusions

Acropora spp. are considered to be thermally sensitive relative to other coral genera (Loya et al. 2001; Putnam et al. 2012); however, we identified individuals able to resist or recover from heat stress incurred by a severe thermal anomaly that resulted in high coral mortality (Leinbach et al. 2021; Speare et al. 2021). Intraspecific variation in coral–algal symbioses and bleaching susceptibility underpin coral adaptive potential, and surviving individuals can be harnessed for assisted evolution intervention methods used in reef restoration and management (Quigley et al. 2018; Suggett and van Oppen 2022). Understanding the spatial and temporal dynamics of coral–Symbiodiniaceae associations during and after bleaching events is crucial in identifying host–symbiont pairs that are both more tolerant to projected temperature increases and well suited for their surrounding reef habitat. Our work demonstrating flexibility of *Acropora hyacinthus* microalgal symbiont associations across a reefscape, but fidelity within a reef habitat and colony, indicates that these associations are at least partly influenced by local environmental conditions and ultimately contribute to response to heat stress. We also documented no significant temporal shifts in symbiont assemblages, including no reversion back to pre-bleaching communities (Kriefall et al. 2022), despite the cessation of thermal stress for several months, suggesting that novel coral–algal relationships may be maintained after thermal stress. At the site level, we observed a diverse pool of Symbiodiniaceae associating with *A. hyacinthus* colonies, including observations of symbioses with multiple Symbiodiniaceae taxa simultaneously. This suggests that it may be possible to enhance *A. hyacinthus* thermal tolerance, within the constraints of

host–symbiont genotype compatibility, through the manipulation of symbiont types or diversity, where types could be selected based on holobiont thermal tolerance observed in each reef habitat. Moreover, we identified ITS2 type profiles that were specifically associated with resistant and recovered colonies, and healthy and bleached colonies. These symbiont associations may be diagnostic of heat stress response or bleaching susceptibility and could conceivably be developed into biomarkers for coral resilience or employed to augment thermal tolerance.

Although our study was limited to three reef habitats within one site in Mo'orea, it provides fundamental yet critical insight into natural symbiont dynamics in the field. In hospite symbiont assemblages are shaped by a complex interplay between prevailing local environmental conditions, acute and chronic stressors, symbiont physiology, and host factors. Future work should investigate symbiont flexibility and fidelity over larger spatial and temporal scales, and further characterize symbiont physiology and its relationship to thermal tolerance, especially in *Symbiodinium*, to provide a more nuanced view of host–symbiont combinations and their ability to withstand environmental perturbations, such as bleaching. The extent to which humans are able to manipulate specific symbiont types or assemblages represents a valuable path of future inquiry and action for coral reef management efforts, with the goal of promoting resistance and resilience to the anticipated impacts of anthropogenic global change.

Declarations

Conflict of interests The authors declare that there is no conflict of interest.

References

Abrego D, Ulstrup KE, Willis BL, Van Oppen MJH (2008) Species-specific interactions between algal endosymbionts and coral hosts define their bleaching response to heat and light stress. Proc R Soc B Biol Sci 275:2273–2282

Allen Coral Atlas (2022) Imagery, maps and monitoring of the world's tropical coral reefs.

Anthony K, Bay LK, Costanza R, Firn J, Gunn J, Harrison P, Heyward A, Lundgren P, Mead D, Moore T, Mumby PJ, van Oppen MJH, Robertson J, Runge MC, Suggett DJ, Schaffelke B, Wachenfeld D, Walshe T (2017) New interventions are needed to save coral reefs. Nat Ecol Evol 1:1420–1422

Baird AH, Marshall PA (2002) Mortality, growth and reproduction in scleractinian corals following bleaching on the Great Barrier Reef. Mar Ecol Prog Ser 237:133–141

Banaszak AT, LaJeunesse TC, Trench RK (2000) The synthesis of mycosporine-like amino acids (MAAs) by cultured, symbiotic dinoflagellates. J Exp Mar Bio Ecol 249:219–233

Barshis DJ, Ladner JT, Oliver TA, Seneca FO, Traylor-Knowles N, Palumbi SR (2013) Genomic basis for coral resilience to climate change. Proc Natl Acad Sci U S A 110:1387–1392

Berkelmans R, van Oppen MJH (2006) The role of zooxanthellae in the thermal tolerance of corals: a "nugget of hope" for coral reefs in an era of climate change. Proc R Soc B Biol Sci 273:2305–2312

Bongaerts P, Riginos C, Ridgway T, Sampayo EM, van Oppen MJH, Englebert N, Vermeulen F, Hoegh-Guldberg O (2010) Genetic divergence across habitats in the widespread coral *Seriatopora hystrix* and its associated *Symbiodinium*. PLoS ONE 5:e10871

Boulotte NM, Dalton SJ, Carroll AG, Harrison PL, Putnam HM, Peplow LM, Van Oppen MJH (2016) Exploring the *Symbiodinium* rare biosphere provides evidence for symbiont switching in reef-building corals. ISME J 10:2693–2701

Bourne DG, Morrow KM, Webster NS (2016) Insights into the coral microbiome: underpinning the health and resilience of reef ecosystems. Annu Rev Microbiol 70:317–340

Brazeau DA, Lesser MP, Slattery M (2013) Genetic structure in the coral, *Montastraea cavernosa*: assessing genetic differentiation among and within mesophotic reefs. PLoS ONE 8:e65845

Buddemeier RW, Fautin DG (1993) Coral bleaching as an adaptive mechanism. Bioscience 43:320–326

Camp EF, Suggett DJ, Pogoreutz C, Nitschke MR, Houlbreque F, Hume BCC, Gardner SG, Zampighi M, Rodolfo-Metalpa R, Voolstra CR (2020) Corals exhibit distinct patterns of microbial reorganisation to thrive in an extreme inshore environment. Coral Reefs 39:701–716

Claar DC, McDevitt-Irwin JM, Garren M, Vega Thurber R, Gates RD, Baum JK (2020a) Increased diversity and concordant shifts in community structure of coral-associated Symbiodiniaceae and bacteria subjected to chronic human disturbance. Mol Ecol 29:2477–2491

Claar DC, Tietjen KL, Cox KD, Gates RD, Baum JK (2020b) Chronic disturbance modulates symbiont (Symbiodiniaceae) beta diversity on a coral reef. Sci Rep 10:4492

Cooper TF, Ulstrup KE, Dandan SS, Heyward AJ, Kühl M, Muirhead A, O'Leary RA, Ziersen BEF, van Oppen MJH (2011) Niche specialization of reef-building corals in the mesophotic zone: metabolic trade-offs between divergent *Symbiodinium* types. Proc R Soc B Biol Sci 278:1840–1850

Cunning R, Silverstein RN, Baker AC (2015) Investigating the causes and consequences of symbiont shuffling in a multi-partner reef coral symbiosis under environmental change. Proc R Soc B Biol Sci 282:20141725

Cunning R, Ritson-Williams R, Gates RD (2016) Patterns of bleaching and recovery of *Montipora capitata* in Kane'ohe Bay, Hawai'i, USA. Mar Ecol Prog Ser 551:131–139

Dilworth J, Caruso C, Kahkejian VA, Baker AC, Drury C (2021) Host genotype and stable differences in algal symbiont communities explain patterns of thermal stress response of *Montipora capitata* following thermal pre-exposure and across multiple bleaching events. Coral Reefs 40:151–163

Dubé CE, Ziegler M, Mercière A, Boissin E, Planes S, Bourmaud CAF, Voolstra CR (2021) Naturally occurring fire coral clones demonstrate a genetic and environmental basis of microbiome composition. Nat Commun 12:6402

Eckert RJ, Reaume AM, Sturm AB, Studivan MS, Voss JD (2020) Depth influences symbiodiniaceae associations among *montastraea cavernosa* corals on the Belize barrier reef. Front Microbiol 11:518

Fifer JE, Yasuda N, Yamakita T, Bove CB, Davies SW (2022) Genetic divergence and range expansion in a western North Pacific coral. Sci Total Environ 813:152423

Frade PR, Bongaerts P, Winkelhagen AJS, Tonk L, Bak RPM (2008) In situ photobiology of corals over large depth ranges: a multivariate analysis on the roles of environment, host, and algal symbiont. Limnol Oceanogr 53:2711–2723

Ganot P, Moya A, Magnone V, Allemand D, Furla P, Sabourault C (2011) Adaptations to endosymbiosis in a cnidarian-dinoflagellate association: differential gene expression and specific gene duplications. PLoS Genet 7:e1002187

Goulet TL (2006) Most corals may not change their symbionts. Mar Ecol Prog Ser 321:1–7

Grottoli AG, Warner ME, Levas SJ, Aschaffenburg MD, Schoepf V, Mcginley M, Baumann J, Matsui Y (2014) The cumulative impact of annual coral bleaching can turn some coral species winners into losers. Glob Chang Biol 20:3823–3833

Hoegh-Guldberg O, Smith GJ (1989) The effect of sudden changes in temperature, light and salinity on the population density and export of zooxanthellae from the reef corals *Stylophora pistillata* Esper and *Seriatopora hystrix* Dana. J Exp Mar Bio Ecol 129:279–303

Hoogenboom MO, Frank GE, Chase TJ, Jurriaans S, Álvarez-Noriega M, Peterson K, Critchell K, Berry KLE, Nicolet KJ, Ramsby B, Paley AS (2017) Environmental drivers of variation in bleaching severity of *Acropora* species during an extreme thermal anomaly. Front Mar Sci 4:376

Howe-Kerr LI, Bachelot B, Wright RM, Kenkel CD, Bay LK, Correa AMS (2020) Symbiont community diversity is more variable in corals that respond poorly to stress. Glob Chang Biol 26:2220–2234

Howells EJ, Bauman AG, Vaughan GO, Hume BCC, Voolstra CR, Burt JA (2020) Corals in the hottest reefs in the world exhibit symbiont fidelity not flexibility. Mol Ecol 29:899–911

Hughes TP, Anderson KD, Connolly SR, Heron SF, Kerry JT, Lough JM, Baird AH, Baum JK, Berumen ML, Bridge TC, Claar DC, Eakin CM, Gilmour JP, Graham NAJ, Harrison H, Hobbs JPA, Hoey AS, Hoogenboom M, Lowe RJ, McCulloch MT, Pandolfi JM, Pratchett M, Schoepf V, Torda G, Wilson SK (2018) Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. Science 359:80–83

Hume BCC, Ziegler M, Poulain J, Pochon X, Romac S, Boissin E, de Vargas C, Planes S, Wincker P, Voolstra CR (2018) An improved primer set and amplification protocol with increased specificity and sensitivity targeting the *Symbiodinium* ITS2 region. PeerJ 2018:e4816

Hume BCC, Smith EG, Ziegler M, Warrington HJM, Burt JA, LaJeunesse TC, Wiedenmann J, Voolstra CR (2019) SymPortal: A novel analytical framework and platform for coral algal symbiont

next-generation sequencing ITS2 profiling. Mol Ecol Resour 19:1063–1080

Iglesias-Prieto R, Beltrán VH, LaJeunesse TC, Reyes-Bonilla H, Thomé PE (2004) Different algal symbionts explain the vertical distribution of dominant reef corals in the eastern Pacific. Proc R Soc B Biol Sci 271:1757–1763

Jones AM, Berkelmans R, Van Oppen MJH, Mieog JC, Sinclair W (2008) A community change in the algal endosymbionts of a scleractinian coral following a natural bleaching event: field evidence of acclimatization. Proc R Soc B Biol Sci 275:1359–1365

Kavousi J, Denis V, Sharp V, Reimer JD, Nakamura T, Parkinson JE (2020) Unique combinations of coral host and algal symbiont genotypes reflect intraspecific variation in heat stress responses among colonies of the reef-building coral. Montipora Digitata Mar Biol 167:23

Kenkel CD, Bay LK (2018) Exploring mechanisms that affect coral cooperation: symbiont transmission mode, cell density and community composition. PeerJ 2018:e6047

Kinzie RA, Takayama M, Santos SR, Coffroth MA (2001) The adaptive bleaching hypothesis: experimental tests of critical assumptions. Biol Bull 200:51–58

Kriefall NG, Kanke MR, Aglyamova GV, Davies SW (2022) Reef environments shape microbial partners in a highly connected coral population. Proc R Soc B Biol Sci 289:20212459

Ladner JT, Palumbi SR (2012) Extensive sympatry, cryptic diversity and introgression throughout the geographic distribution of two coral species complexes. Mol Ecol 21:2224–2238

LaJeunesse TC, Smith RT, Finney J, Oxenford H (2009) Outbreak and persistence of opportunistic symbiotic dinoflagellates during the 2005 Caribbean mass coral "bleaching" event. Proc R Soc B Biol Sci 276:4139–4148

LaJeunesse TC, Smith R, Walther M, Pinzón J, Pettay DT, McGinley M, Aschaffenburg M, Medina-Rosas P, Cupul-Magaña AL, Pérez AL, Reyes-Bonilla H, Warner ME (2010) Host-symbiont recombination versus natural selection in the response of coral-dinoflagellate symbioses to environmental disturbance. Proc R Soc B Biol Sci 277:2925–2934

LaJeunesse TC, Parkinson JE, Gabrielson PW, Jeong HJ, Reimer JD, Voolstra CR, Santos SR (2018) systematic revision of Symbiodiniaceae highlights the antiquity and diversity of coral endosymbionts. Curr Biol 28:2570–2580

Larsson J (2018) Area-proportional Euler and Venn diagrams with circles or ellipses. https://cran.r-project.org/package=eulerr

Leichter J, Seydel K, Gotschalk C (2020) MCR LTER: Coral reef: Benthic water temperature, ongoing since 2005. Environ Data Initiat 10:109–123

Leinbach SE, Speare KE, Rossin AM, Holstein DM, Strader ME (2021) Energetic and reproductive costs of coral recovery in divergent bleaching responses. Sci Rep 11:23546

Loram JE, Trapido-Rosenthal HG, Douglas AE (2007) Functional significance of genetically different symbiotic algae Symbiodinium in a coral reef symbiosis. Mol Ecol 16:4849–4857

Loya Y, Sakai K, Yamazato K, Nakano Y, Sambali H, Van Woesik R (2001) Coral bleaching: the winners and the losers. Ecol Lett 4:122–131

Lundgren P, Vera JC, Peplow L, Manel S, van Oppen MJH (2013) Genotype - environment correlations in corals from the Great Barrier Reef. BMC Genet 14:9

McClanahan TR, Maina J, Moothien-Pillay R, Baker AC (2005) Effects of geography, taxa, water flow, and temperature variation on coral bleaching intensity in Mauritius. Mar Ecol Prog Ser 298:131–142

McIlroy SE, Wong JCY, Baker DM (2020) Competitive traits of coral symbionts may alter the structure and function of the microbiome. ISME J 14:2424–2432

Mieog JC, Olsen JL, Berkelmans R, Bleuler-Martinez SA, Willis BL, van Oppen MJH (2009) The roles and interactions of symbiont, host and environment in defining coral fitness. PLoS ONE 4:e6364

Miller TEX (2007) Does having multiple partners weaken the benefits of facultative mutualism? A test with cacti and cactus-tending ants. Oikos 116:500–512

Moeller H, Peay K (2016) Competition-function tradeoffs in ectomycorrhizal fungi. Peer J 4:e2270

Okansen J, Guillaume Blanchet F, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2020) Vegan: Community Ecology Package. R package version 2.5–7. https://cran.r-project.org/package=vegan

Oliver ECJ, Benthuysen JA, Darmaraki S, Donat MG, Hobday AJ, Holbrook NJ, Schlegel RW, Sen Gupta A (2021) Marine heatwaves. Ann Rev Mar Sci 13:313–342

Penin L, Adjeroud M, Schrimm M, Lenihan HS (2007) High spatial variability in coral bleaching around Moorea (French Polynesia): patterns across locations and water depths. Comptes Rendus - Biol 330:171–181

Penin L, Vidal-Dupiol J, Adjeroud M (2013) Response of coral assemblages to thermal stress: are bleaching intensity and spatial patterns consistent between events? Environ Monit Assess 185:5031–5042

Pratchett MS, McCowan D, Maynard JA, Heron SF (2013) Changes in bleaching susceptibility among corals subject to ocean warming and recurrent bleaching in Moorea. French Polynesia Plos One 8:e70443

Putnam HM, Stat M, Pochon X, Gates RD (2012) Endosymbiotic flexibility associates with environmental sensitivity in scleractinian corals. Proc R Soc B Biol Sci 279:4352–4361

Quigley KM, Bay LK, Willis BL (2017) Temperature and water quality-related patterns in sediment-associated Symbiodinium communities impact symbiont uptake and fitness of juveniles in the genus Acropora. Front Mar Sci 4:401

Quigley KM, Bay LK, Willis BL (2018) Leveraging new knowledge of Symbiodinium community regulation in corals for conservation and reef restoration. Mar Ecol Prog Ser 600:245–253

Rädecker N, Pogoreutz C, Voolstra CR, Wiedenmann J, Wild C (2015) Nitrogen cycling in corals: the key to understanding holobiont functioning? Trends Microbiol 23:490–497

Reynolds JMC, Bruns BU, Fitt WK, Schmidt GW (2008) Enhanced photoprotection pathways in symbiotic dinoflagellates of shallow-water corals and other cnidarians. Proc Natl Acad Sci U S A 105:13674–13678

Robinson MD, Oshlack A (2010) A scaling normalization method for differential expression analysis of RNA-seq data. Genome Biol 11:R25

Rowan R (2004) Thermal adaptation in reef coral symbionts. Nature 430:742

Rowan B, Knowlton N (1995) Intraspecific diversity and ecological zonation in coral-algal symbiosis. Proc Natl Acad Sci U S A 92:2850–2853

Sampayo EM, Ridgway T, Bongaerts P, Hoegh-Guldberg O (2008) Bleaching susceptibility and mortality of corals are determined by fine-scale differences in symbiont type. Proc Natl Acad Sci U S A 105:10444–10449

Schneider CA, Rasband WS, Eliceiri KW (2012) NIH Image to ImageJ: 25 years of image analysis. Nat Methods 9:671–675

Schoepf V, Jung MU, McCulloch MT, White NE, Stat M, Thomas L (2020) Thermally variable, Macrotidal reef habitats promote rapid recovery from mass coral bleaching. Front Mar Sci 7:245

Schwiesow MW, Samayoa AM, Torres J, Leimbach A, Santiago-Rivera G, Tepper CS (2021) Symbiodinium distribution patterns in Millepores in the Caribbean: south water cay, Belize and san Salvador, the Bahamas. Mar Sci 9:1–10

Silverstein RN, Correa AMS, Baker AC (2012) Specificity is rarely absolute in coral–algal symbiosis: implications for coral response to climate change. Proc R Soc B Biol Sci 279:2609–2618

Silverstein RN, Cunning R, Baker AC (2015) Change in algal symbiont communities after bleaching, not prior heat exposure, increases heat tolerance of reef corals. Glob Chang Biol 21:236–249

Smith EG, Vaughan GO, Ketchum RN, McParland D, Burt JA (2017) Symbiont community stability through severe coral bleaching in a thermally extreme lagoon. Sci Rep 7:2428

Speare KE, Adam TC, Winslow EM, Lenihan HS, Burkepile DE (2021) Size-dependent mortality of corals during marine heatwave erodes recovery capacity of a coral reef. Glob Chang Biol 00:1–17

Stat M, Morris E, Gates RD (2008) Functional diversity in coral-dinoflagellate symbiosis. Proc Natl Acad Sci U S A 105:9256–9261

Stat M, Loh WKW, LaJeunesse TC, Hoegh-Guldberg O, Carter DA (2009) Stability of coral-endosymbiont associations during and after a thermal stress event in the southern great barrier reef. Coral Reefs 28:709–713

Suggett DJ, van Oppen MJH (2022) Horizon scan of rapidly advancing coral restoration approaches for 21st century reef management. Emerg Top Life Sci 14:125–136

Suggett DJ, Warner ME, Smith DJ, Davey P, Hennige S, Baker NR (2008) Photosynthesis and production of hydrogen peroxide by *Symbiodinium* (Pyrrhophyta) phylotypes with different thermal tolerances. J Phycol 44:948–956

Thomas L, López EH, Morikawa MK, Palumbi SR (2019) Transcriptomic resilience, symbiont shuffling, and vulnerability to recurrent bleaching in reef-building corals. Mol Ecol 28:3371–3382

Thornhill DJ, LaJeunesse TC, Kemp DW, Fitt WK, Schmidt GW (2006) Multi-year, seasonal genotypic surveys of coral-algal symbioses reveal prevalent stability or post-bleaching reversion. Mar Biol 148:711–722

Thornhill DJ, Xiang Y, Fitt WK, Santos SR (2009) Reef endemism, host specificity and temporal stability in populations of symbiotic dinoflagellates from two ecologically dominant Caribbean corals. PLoS ONE 4:e6262

Toller WW, Rowan R, Knowlton N (2001) Repopulation of zooxanthellae in the Caribbean corals *Montastraea annularis* and *M. faveolata* following experimental and disease-associated bleaching. Biol Bull 201:360–373

Torda G, Donelson JM, Aranda M, Barshis DJ, Bay L, Berumen ML, Bourne DG, Cantin N, Foret S, Matz M, Miller DJ, Moya A, Putnam HM, Ravasi T, Van Oppen MJH, Thurber RV, Vidal-Dupiol J, Voolstra CR, Watson SA, Whitelaw E, Willis BL, Munday PL (2017) Rapid adaptive responses to climate change in corals. Nat Clim Chang 7:627–636

van Oppen MJH, Palstra FP, Piquet AMT, Miller DJ (2001) Patterns of coral-dinoflagellate associations in *Acropora*: significance of local availability and physiology of *Symbiodinium* strains and host-symbiont selectivity. Proc R Soc B Biol Sci 268:1759–1767

van Oppen MJH, Bongaerts P, Frade P, Peplow LM, Boyd SE, Nim HT, Bay LK (2018) Adaptation to reef habitats through selection on the coral animal and its associated microbiome. Mol Ecol 27:2956–2971

Veron JE (2000) Acropora hyacinthus. In: Veron JE (ed) Corals of the World. Australian Institute of Marine Sciences, Australian, pp 404–405

Voolstra CR, Suggett DJ, Peixoto RS, Parkinson JE, Quigley KM, Silveira CB, Sweet M, Muller EM, Barshis DJ, Bourne DG, Aranda M (2021) Extending the natural adaptive capacity of coral holobionts. Nat Rev Earth Environ 2:747–462

Wall CB, Kaluhiokalani M, Popp BN, Donahue MJ, Gates RD (2020) Divergent symbiont communities determine the physiology and nutrition of a reef coral across a light-availability gradient. ISME J 14:945–958

Wallace CC (1985) Reproduction, recruitment and fragmentation in nine sympatric species of the coral genus *Acropora*. Mar Biol 88:217–233

Zaneveld JR, McMinds R, Thurber RV (2017) Stress and stability: applying the Anna Karenina principle to animal microbiomes. Nat Microbiol 2:17121

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.