



# The role of background algal symbionts as drivers of shuffling to thermotolerant Symbiodiniaceae following bleaching in three Caribbean coral species

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**Abstract** Reef-building corals host diverse dinoflagellate algal symbionts (Family Symbiodiniaceae) whose identity can influence host thermotolerance and whose relative abundance can be dynamic. Breakdown in this symbiosis during “bleaching” events can promote changes in symbiont communities in favour of thermotolerant types, particularly in the genus *Durusdinium*. We employed experimental bleaching to manipulate the symbiont communities of three common Caribbean reef-building species (*Montastraea cavernosa*, *Orbicella faveolata*, and *Siderastrea siderea*) and tested whether seasonal differences in the corals’ symbiont communities at the time of their collection affected their responses to manipulation. In *O. faveolata* and *S. siderea*, a minimum threshold of initial background proportion *Durusdinium trenchii* shaped recovery from bleaching with mainly *Durusdinium*. In contrast, in *M. cavernosa*, *Durusdinium* became highly dominant after recovery even when it was undetectable prior to bleaching. Seasonal changes were also detected in *M. cavernosa* and *S. siderea* dominated by *Cladocopium*, with significant increases and decreases, respectively, in symbionts per host cell in October (following annual temperature maxima) compared to the previous April

(following temperature minima). These results demonstrate how background symbionts and seasonal differences in symbiont density can affect the disturbance and recovery dynamics of algal symbiont communities in different coral species, and prompt further research into how seasonal changes in algal symbiosis might inform projected future bleaching, which is increasingly relevant in light of predicted winter warming and prolonged warm summer temperatures under climate change.

**Keywords** Coral bleaching · Symbiodiniaceae · Symbiont shuffling · *Durusdinium trenchii* · Thermotolerance · qPCR

## Introduction

Coral reef bleaching is defined as the loss of photosynthetic algal symbionts (Family Symbiodiniaceae), or their pigments, from reef-dwelling invertebrate hosts (Glynn 1996; LaJeunesse et al. 2018). This dysfunctional symbiosis (‘dysbiosis’, Palmer 2018) is typically driven by oxidative stress caused by photoinhibition of the algal symbionts usually as a result of sustained periods of anomalously high temperature, (Smith et al. 2005; Gustafsson et al. 2014), but can be modulated by the capacity of the coral host to reduce or mitigate that stress (Berkelmans and van Oppen 2006; Baird et al. 2009). Heat-induced bleaching is now the principal driver of scleractinian coral (‘coral’ hereafter) mortality worldwide, because bleaching events are becoming more frequent and more intense (Hughes et al. 2018). Annual severe bleaching is projected on 90% of the world’s coral reefs by 2055 (van Hooidonk et al. 2014) as rising sea surface temperatures increase the duration and frequency of marine heatwaves (Oliver et al. 2018; Fordyce et al. 2019). Exploring the drivers of thermal tolerance and potential for recovery of these

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symbioses following bleaching is therefore of paramount importance for the future of coral reefs.

Adults of some coral species can be flexible in their symbiotic associations, often hosting multiple different symbionts simultaneously (Baker 2003; Putnam et al. 2012; Ziegler et al. 2015), generally including a small number of high abundance taxa and a diversity of putative species at very low abundance (constituting less than 1% of the symbiont community) (Boulotte et al. 2016; Ziegler et al. 2018). At the broader genus level, ‘background’ may refer to any minority genus or more specifically those constituting less than 5–20% of the assemblage (Mieog et al. 2007; Silverstein et al. 2012). The loss of symbionts during bleaching may provide an opportunity for corals to recover with different symbiont communities (Buddemeier and Fautin 1993; Baker 2003), as a result of the proliferation of residual symbionts that remain in bleached coral tissue and/or the uptake of exogenous symbionts (typically referred to as ‘shuffling’ and ‘switching’ respectively, (Buddemeier and Fautin 1993; Baker 2003; Silverstein et al. 2012). Residual symbionts may include background symbionts even if their initial abundance prior to bleaching was very low (< 1%), presenting an opportunity for these populations to shift to dominance with associated increased functional importance to the holobiont; indeed, *Acropora millepora* hosting at least 0.3% *Durusdinium* generally became dominated by *Durusdinium* and suffered milder bleaching under heat stress compared to those hosting less than 0.3% *Durusdinium* (Bay et al. 2016). Because different Symbiodiniaceae can confer different phenotypes (e.g., thermal tolerance) to their hosts (Berkelmans and van Oppen 2006; Swain et al. 2017), these symbiont shifts can be of critical importance to the survival and persistence of individual colonies, and occasionally entire reef systems (Baker et al. 2004; Thornhill et al. 2006; LaJeunesse et al. 2009; Kemp et al. 2014; Claar et al. 2020; Palacio-Castro et al. 2023).

Algal symbiont communities can also undergo seasonal changes in composition independently of bleaching (Chen et al. 2005; Ziegler et al. 2015), for example summertime increases in the relative abundance of *Durusdinium* in *Lepetoria phrygia* in Taiwan (Huang et al. 2020) and transient increases in the proportion of *Durusdinium trenchii* in the summer leading up to an autumn bleaching event (LaJeunesse et al. 2009), with communities generally reverting to their pre-disturbance composition over months to years in the absence of further heat stress (Thornhill et al. 2006; LaJeunesse et al. 2009).

In addition to differences in the identity of symbionts, total symbiont densities in corals also undergo seasonal fluctuations. Multi-year studies of Caribbean and Indo-Pacific coral species have shown increases in symbiont density and/or photochemical efficiency ( $F_v/F_m$ ) during winter, and decreases during the summer. Summertime

decreases occur independently of any visible signs of bleaching, suggesting an acclimatisation response to lower temperature and irradiance during the winter (Stimson 1997; Fagoonee et al. 1999; Fitt et al. 2000; Warner et al. 2002; Thornhill et al. 2011). Higher symbiont densities have also been implicated in decreased thermal tolerance, potentially due to carbon limitation of photosynthesis (reduced autotrophic capacity) (Wooldridge 2009, 2016), and/or increased production of reactive oxygen species in response to stress (Weis 2008; Cunning and Baker 2013). In fact, symbiont to host cell ratios may be useful proxies that contextualise symbiont density with respect to host tissue biomass (Cunning and Baker 2014). Thus, the first aim of the current study was to study the effects of seasonal changes on symbiont to host cell ratio and community composition.

The second aim was to investigate how seasonal changes in algal symbiont communities affected their ability to recover with different symbionts following bleaching. Although many factors, such as coral species (Goulet 2006; Baker and Romanski 2007), duration of heat stress, and recovery temperature (Cunning et al. 2015), have been tested in assessing the tendency for corals to change symbionts following bleaching, to our knowledge the effect of background symbionts in driving these changes has thus far only been reported in the Indo-Pacific species *Acropora millepora* (Bay et al. 2016). Competition studies between *Durusdinium* and other common genera inside octocoral hosts have suggested that population sizes following disturbance affect competitive outcomes between symbionts, with priority effects facilitating the initial proliferation of *Durusdinium* under stressful environmental conditions before they are excluded by photochemically superior competitors (McIlroy et al. 2019). However, these hypotheses have never been empirically tested and consequently, the question of whether seasonal changes in the abundance or proportion of *Durusdinium* affect the propensity for later shuffling/switching may be key to understanding recovery trajectories of corals following bleaching events.

Here, we compared seasonal differences in symbiont to host cell ratio and the proportion of *Durusdinium trenchii* in three common Caribbean reef-building coral species in Florida following annual temperature minima and maxima. We then subjected these corals to experimental bleaching and tested whether seasonal differences in algal symbiont communities affected the proportion of *Durusdinium* with which corals recovered following bleaching. Given the projected increase in long-lasting marine heatwaves that persist over multiple seasons (van Hooidonk et al. 2020; Cooley et al. 2022), and the increasingly important role of heat-tolerant (and often background) symbionts in warming oceans, developing our understanding of seasonal variation in symbiont community dynamics and the role of background

symbionts following bleaching and recovery may be of critical importance in understanding reef futures.

## Materials and methods

### Colony selection and core collection

To select colonies for study, we pre-screened samples from 54 colonies (all > 30 cm in diameter) of *Montastraea cavernosa*, *Orbicella faveolata*, and *Siderastrea siderea* at depths of 7.5–8.5 m depth from Emerald Reef (25.406 to 25.407 N, 80.058 to 80.060 W), off Key Biscayne, SE Florida, USA. We characterised the algal symbiont communities in each colony (see *DNA extraction and analyses*, below), and selected the 10 colonies of each species containing no detectable *Durusdinium*, or failing that, containing the lowest proportions of *Durusdinium* (30 colonies in total). Although genotypes were not explicitly identified in this study, selected colonies were at least 5 m apart to decrease the chances of sampling clonemates (Baums et al. 2006). From each colony, two cores, each 2.5 cm diameter and 2 cm deep, were removed using a submersible drill (Nemo Power Tools Ltd.) fitted with a diamond core drill bit (Montana Brand Tools). To standardise irradiance and minimise variation in symbiont communities due to intra-colonial niche partitioning (Rowan et al. 1997), cores ( $N=60$  in total) were only extracted from the uppermost surfaces of colonies. Holes in colonies resulting from coring were filled with a two-part epoxy putty to promote healing. Cores were collected in March–April 2019 (hereafter referred to as the ‘April’ batch), and another set of 60 cores was collected from the same 30 colonies in October 2019 (referred to as the ‘October’ batch).

### Laboratory maintenance of corals

Cores were attached to ceramic plugs using cyanoacrylate ‘Reef Glue Gel’ (Boston Aqua Farms) and from each batch of 60 cores, 1–2 cores of each colony ( $N=45$  cores total, across 3 species) were assigned to the bleaching treatment, and the remaining 5 cores of each species ( $N=15$  total) were used as non-bleached controls (Table S1). Mounted cores were maintained in plastic egg-crates in ~300L indoor, flow-through, fibreglass tanks in the Marine Technology and Life Science Seawater (MTLSS) complex at the University of Miami’s Rosenstiel School of Marine, Atmospheric, and Earth Science, supplied with seawater at 27 °C ( $\pm 1$  °C) from nearby Bear Cut that had been sand-filtered to 10 microns (which removes larger particles but not Symbiodiniaceae (Littman et al. 2008)). The 45 heat-stressed cores from each batch were kept in one tank and the 15 control cores in another, with cores rotated within tanks during each

weekly cleaning to reduce any potential confounding effects of tank position. This experimental design was chosen in the knowledge that cores would be exposed to viable exogenous Symbiodiniaceae cells both in the filtered seawater supplied to aquaria, and via the continual release of Symbiodiniaceae from other corals in the same aquarium (Yamashita et al. 2011). For this reason, the origin (exogenous or endogenous) of recovered symbiont populations cannot be resolved here but this remains tangential to the conclusions of this study.

Two 500 gph pumps were used to circulate water within each tank, and corals were maintained on a 12 h:12 h light:dark cycle using three Hydra 52HD lights (Aqua Illumination, C2 Development Inc.) at 20% intensity across all wavelengths, which delivered approximately 125  $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$  PAR, measured using an Apogee MQ-210X light meter) across each tank. Corals were fed twice weekly with 4 g of resuspended zooplankton and phytoplankton (‘Reef-Roids’, Polyplab, Kansas USA).

### Heat stress

After 3–5 weeks of acclimation to laboratory conditions, experimental cores were exposed to a heat stress protocol. On day 1 of heat stress, the temperature was raised (using in-tank heaters) to 32 °C; this rapid temperature ramp rate followed previous methods for successful symbiont manipulations in these species (Cunning et al. 2015). After 15 days of heat stress at 32 °C ( $\pm 0.5$  °C), photochemical efficiency measurements were taken using an imaging pulse amplitude modulated (I-PAM) fluorometer (Walz, Effeltrich, Germany). Corals were dark-adapted for 30 min (Warner et al. 2002), then received a saturating pulse at 2,800  $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$  at 460 nm for 800 ms. The maximum quantum yield of symbionts’ PSII was quantified as  $F_v/F_m$  (Warner et al. 1996). I-PAM measurements were always taken in the early evening to control for diel variation in photochemical efficiency (Warner and Berry-Lowe 2006). After 15 days, if  $F_v/F_m$  was either < 0.25 or < 50% of the coral’s pre-heat stress  $F_v/F_m$ , corals were placed into a glass ‘recovery’ aquarium within the fibreglass tank, which was maintained at a sub-bleaching but warm temperature of 29 °C ( $\pm 0.5$  °C) to promote shifts towards *Durusdinium* dominance (Cunning et al. 2015). Corals that maintained  $F_v/F_m$  values above these thresholds were maintained under heat stress, and I-PAM measurements were taken every two days until  $F_v/F_m$  thresholds were met. After 25 days (April batch) or 22 days (October batch) of heat stress, the temperature was raised to 33 °C ( $\pm 0.5$  °C) to induce sufficient  $F_v/F_m$  declines in any remaining corals. In total, the mean Degree Heating Weeks (DHW) to which all heat-stressed corals were exposed (Liu et al. 2014) was 8.6 DHW (April batch) and 9.8 DHW (October batch).

During this controlled bleaching protocol, small (~2 mm diameter) tissue biopsies were preserved in 1% SDS (sodium dodecyl sulphate) in DNAB (Baker and Cuning 2016) at four time points: ‘Before heat stress’ (cores of both treatments were sampled just before the onset of heat stress), ‘After heat stress’ (experimental cores were sampled when they were removed from heat stress and control cores were sampled when heat stress had ended for all cores), ‘1 month recovery’ (bleached cores were sampled one month after they had been taken out of heat stress), and ‘2 month recovery’ (all cores were sampled at the end of the experiment, on average one month after the ‘1 month recovery’ sampling).

### DNA extraction and analyses

Aliquots of tissue samples were subjected to a modified organic extraction protocol (Baker et al. 1997) and quantitative PCR was performed using Taqman Environmental Master Mix (QuantStudio 3, Applied Biosystems) and symbiont genus-specific primers and probes targeting the actin gene (Cuning and Baker 2013; Cuning et al. 2015). To date, the only species of *Durusdinium* that has been reported in the Caribbean and western Atlantic is *D. trenchii* (Correa et al. 2009; Pettay et al. 2015) but we specify *Durusdinium* to the genus level in the figures presented in order to maintain consistency with other symbiont genera (of which there are multiple local species (LaJeunesse 2002)). VIC dye was used for the *Cladocopium* probe, whilst all other probes used a FAM dye. *Cladocopium* and *Durusdinium* targets were multiplexed together in the same well. Data were corrected for differences in DNA extraction efficiency, actin gene copy number, and dye fluorescence (Table S2) using the stepOneR package (Cuning 2018). Amplifications were filtered to include only those in which both technical replicates amplified with  $C_t$  values < 40.

Whilst the use of genus-level qPCR-based assays does not allow for finer-scale symbiont identification, these methods were used in this study to rapidly and cheaply quantify changes in the relative abundances of symbiont genera, in particular of *Durusdinium*, for which there is only one species (*D. trenchii*) present in the western Atlantic (Pettay et al. 2015). Other studies have estimated very high sensitivities of qPCR methods for detecting the presence of extremely rare ‘background’ *Durusdinium* at proportions as low as 0.003%, albeit using multicopy target loci (Mieog et al. 2007; Correa et al. 2009).

### Statistical analyses

Data were analysed in RStudio V4.2.1 (R Core Team 2022). Linear mixed effects models with colony as a random effect, and batch and proportion *Durusdinium* as fixed effects, were fit to pre-heat stress S:H data using the ‘lme4’

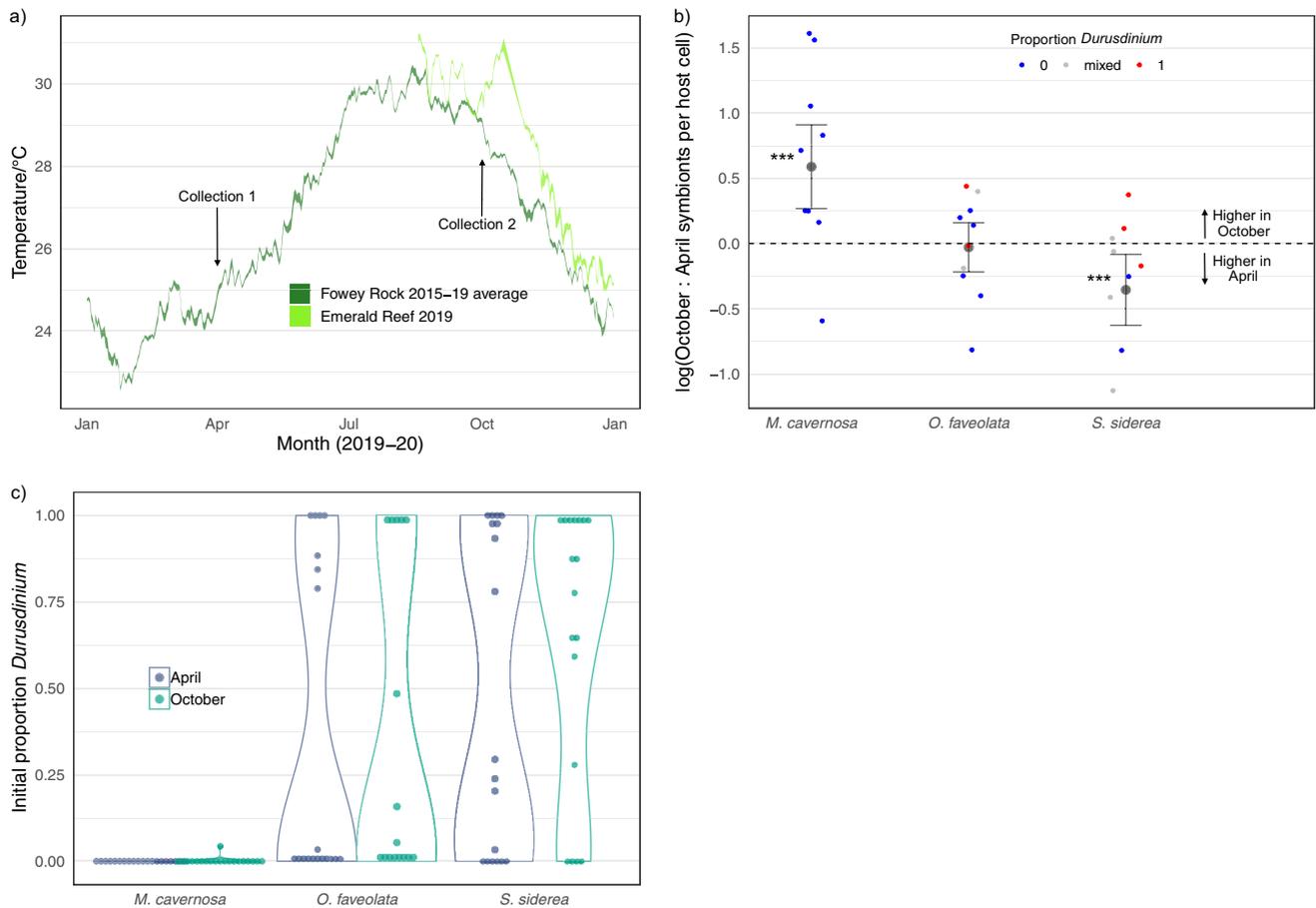
package (Bates et al. 2015). Generalised mixed effects models with binomial error distributions, including colony as a random effect and the pre-heat stress proportion of *Durusdinium*, were fit to the post-heat stress proportion of *Durusdinium* (with batch included as an additional fixed effect in some models), also using the ‘lme4’ package (Bates et al. 2015). Parameter estimates and associated confidence intervals were estimated from mixed effects models using the ‘emmeans’ package (Lenth 2022), whilst the significance of fixed effects in models was tested using partial F-tests in the ‘lmerTest’ package (Kuznetsova et al. 2017).

By fitting a predictive quasibinomial model of the proportion *Durusdinium* hosted after heat stress relative to the initial proportion *Durusdinium* hosted, a shuffling metric was derived to represent the magnitude of shuffling to *Durusdinium*, following Cuning et al. (2018). No *Durusdinium* were detected in any *M. cavernosa* cores before heat stress, so this shuffling metric was calculated as the change in the proportion of *Durusdinium*. It should be restated that although shifts in symbiont assemblages are described here using a ‘shuffling metric’, the origins of recovered symbionts (endogenous symbiont population growth via ‘shuffling’ or uptake of exogenous symbionts via ‘switching’) cannot be disentangled. All data and statistical analyses are available at [github.com/DaisyBuzzoni/seasonal\\_shuffling](https://github.com/DaisyBuzzoni/seasonal_shuffling).

## Results

### Symbiont communities differed between April and October

The mean number of symbionts per coral cell (S:H ratio) increased in *Montastraea cavernosa* between April 2019 (after the seasonal temperature minimum in January/February) and October 2019 (after the seasonal maximum in August/September) ( $t = 3.78$ ,  $p = 0.0008$ ), decreased in *S. siderea* colonies ( $t = -3.99$ ,  $p = 0.0005$ ), and did not change significantly in *O. faveolata* ( $t = -1.10$ ,  $p = 0.284$ ) (Fig. 1b). The increase in S:H observed in *M. cavernosa* represents an increase in *Cladocopium* symbionts (since no *Durusdinium* were present), yet the decrease in S:H between April and October in *S. siderea* corals varied depending on dominant symbiont genus (significant April/October \* symbiont genus interaction,  $t = 3.09$ ,  $p = 0.005$ ); Fig. 1b indicates that the decrease in S:H in *S. siderea* from April to October was driven more by colonies that consistently hosted *Cladocopium*, than by those consistently hosting *Durusdinium*. However, this seasonal decrease in S:H in *S. siderea* colonies dominated by *Cladocopium* did not translate to a significant change in *Cladocopium:Durusdinium* when considering all *S. siderea* colonies, including those hosting mixed communities; no change was detected in the proportion of



**Fig. 1** Seasonal differences in initial symbiont communities. **a** Temperature data from Emerald Reef measured with a Hobo logger (Onset Computer Corporation) deployed on the reef from August–December 2019, and approximated for previous months from NOAA temperature data measured at Fowey Rocks (9 km south of Emerald) between 2015 and 2019. Line width indicates standard error of mean daily recorded temperatures. **b** October 2019: April 2019 ratio of symbionts per host cell for each coral colony shown on a  $\log_{10}$  scale. Small points represent individual colonies whilst large points and

error bars represent predicted October:April odds ratios and 95% confidence intervals. Colonies were grouped into categories of pre-heat stress proportion *Durusdinium*; colonies with replicate cores from both April and October hosting >95% are shown in red, those hosting <5% are shown in blue and all other colonies are shown in grey **c** Points represent the proportion of *Durusdinium* in each coral core after collection from the reef, binned into 0.033 increments in proportion. Violin plots represent probability density distributions

*Durusdinium* in cores of *M. cavernosa* ( $z=0$ ,  $p=1$ ), *O. faveolata* ( $z=1.19$ ,  $p=0.235$ ) or *S. siderea* ( $z=1.69$ ,  $p=0.091$ ) between April and October (Fig. 1c).

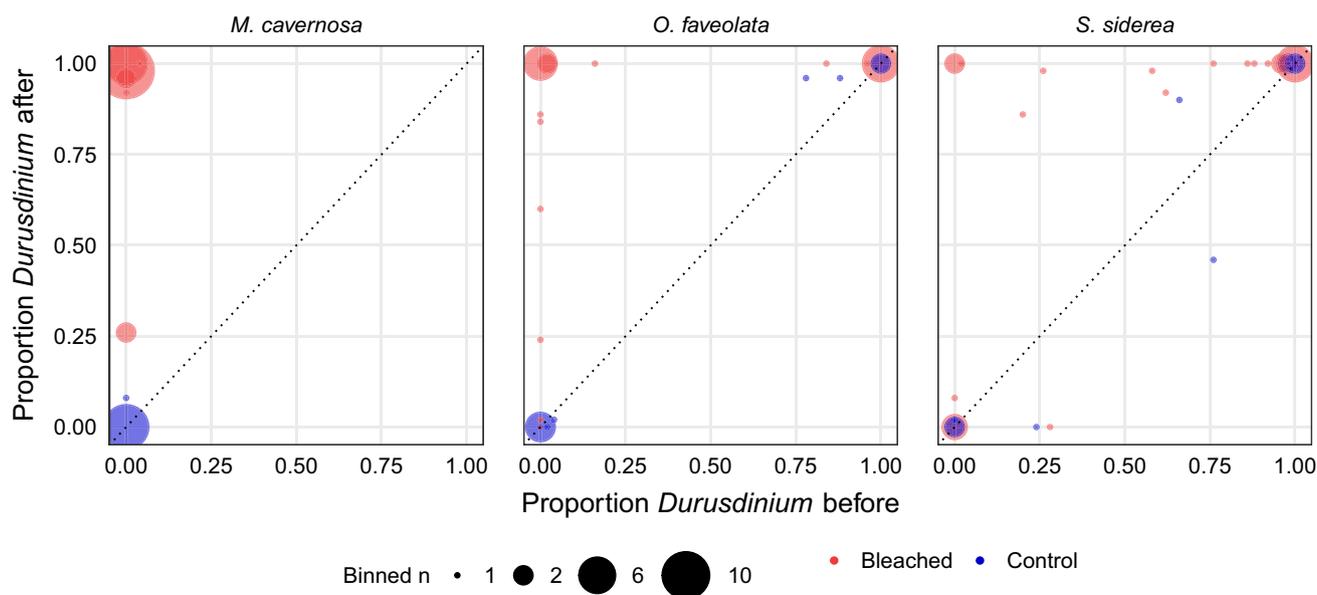
### Shifts in favour of *Durusdinium* depend on coral species but not on season

The proportion of *Durusdinium* before bleaching and after recovery differed between coral species (Figs. 1c and 2) (when corals collected in April and October were pooled due to minimal seasonal changes in proportion *Durusdinium*, Fig. 1b). The shuffling index for experimental corals after two months of recovery (where a value of 1 indicates shuffling to complete *Durusdinium* dominance) was 0.927 for *M. cavernosa*, 0.938 for *O. faveolata* and 0.760 for *S. siderea*

(Fig. 3a). For corals not subjected to heat stress (controls), shuffling indices (where a value of 0 indicates no change in community composition) were 0.009, 0.017 and  $-0.170$  for *M. cavernosa*, *O. faveolata* and *S. siderea*, respectively. There was no significant difference in the magnitude of shuffling between April and October for *M. cavernosa* ( $t=1.668$ ,  $p=0.107$ ), *O. faveolata* ( $t=0.415$ ,  $p=0.683$ ), or *S. siderea* ( $t=0.029$ ,  $p=0.977$ ), (Fig. S1).

### Initial presence or minimum proportion of *Durusdinium* drives magnitude of symbiont shifts, depending on coral species

By the end of heat stress, some shuffling towards *Durusdinium* had already occurred in *O. faveolata* and *S. siderea*,



**Fig. 2** Proportion of symbionts that were identified as *Durusdinium* in cores (April and October batches combined) before heat stress and after two months of recovery following heat stress in **a** *Montastraea*

*cavernosa*, **b** *Orbicella faveolata*, and **c** *Siderastrea siderea*. Data are grouped into 0.02 (proportion *Durusdinium*) bins

but not in *M. cavernosa* (Fig. 3a) (excluding one *M. cavernosa* colony which hosted no detectable *Cladocopium* at the end of heat stress, Fig. 3c). Fig. S2b indicates that S:H only recovered after two months of recovery (and partially recovered after one month in *S. siderea*), suggesting symbiont shuffling after heat stress represents differential symbiont loss rather than symbiont recovery. However, despite the delay in shifts towards higher proportions of *Durusdinium* in *M. cavernosa*, the magnitude of the shift two months after heat stress was not significantly different to that seen in *O. faveolata* (Fig. 3a).

In order to better distinguish the role of background *Durusdinium* on the timing and trajectory of symbiont shuffling, corals were grouped by species and by initial *Durusdinium* proportion (Fig. 3b, c). No significant differences were found between *O. faveolata* and *S. siderea*, in the change in the proportion of *Durusdinium* following recovery ( $t=0.971$ ,  $p=0.333$ ), and these two species are therefore pooled in Fig. 3b due to small group sample sizes. *O. faveolata* and *S. siderea* cores that initially hosted some *Durusdinium* (<50%) recovered after two months with significantly higher proportions of *Durusdinium* than those that initially hosted no (0%) *Durusdinium* ( $z=2.284$ ,  $p=0.022$ ) (Fig. 3b), despite enduring comparable symbiont losses and recovering symbionts only after two months of recovery (Fig. S2a). In fact, most *O. faveolata* and *S. siderea* colonies that hosted no pre-heat stress *Durusdinium* recovered with <50% *Durusdinium*, whilst 34 of the 35 remaining colonies that hosted any pre-heat stress *Durusdinium* (as little as 0.04%) recovered after two months with near

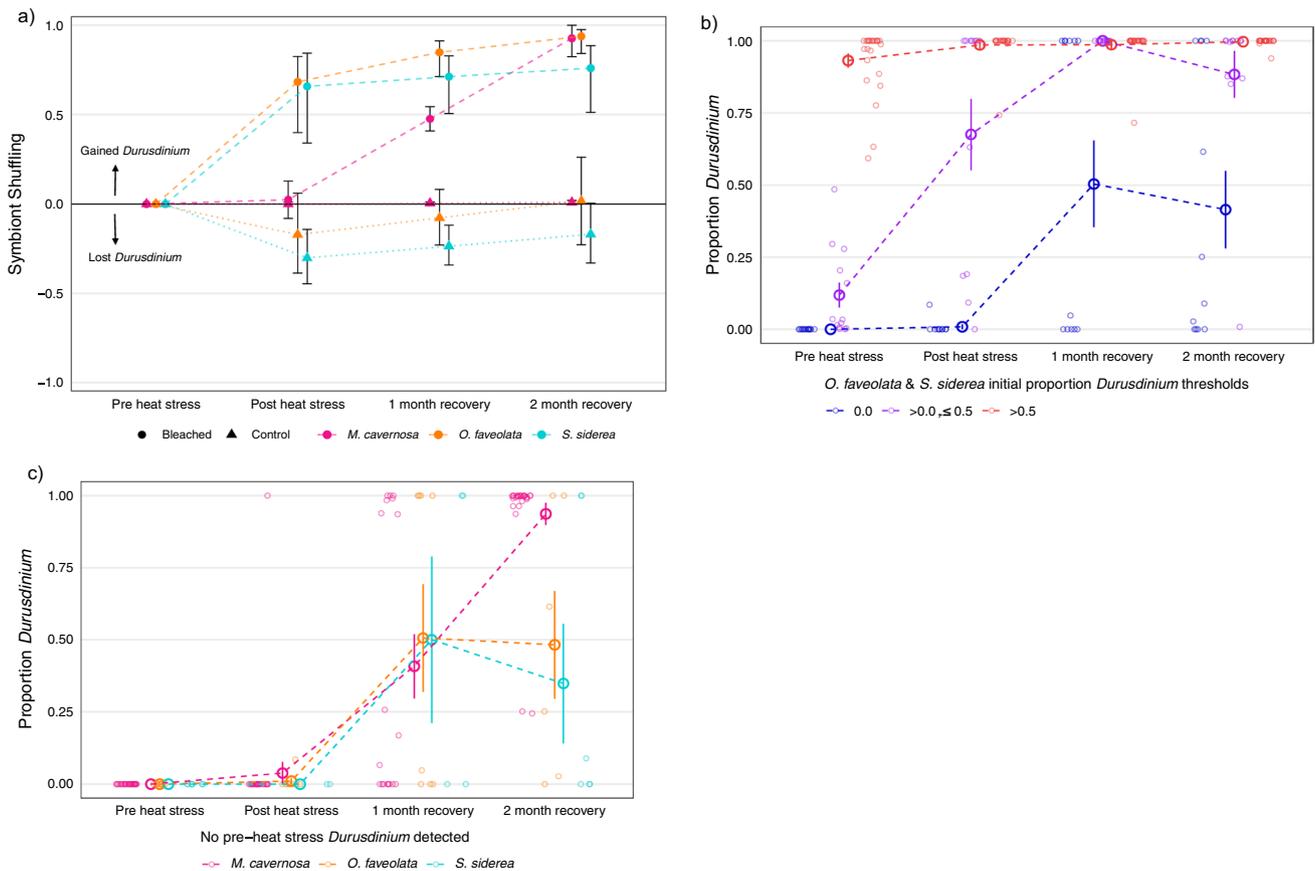
complete (>85%) *Durusdinium* dominance. Fitting a broken-stick mixed effects linear model (van Buuren 2022) to combined *O. faveolata* and *S. siderea* data revealed a significant change in the slope of the regression between initial proportion *Durusdinium* and final proportion *Durusdinium* at 0.27% initial *Durusdinium*, above which the model predicted recovery with 100% *Durusdinium*, implicating 0.27% *Durusdinium* as a minimum threshold for predicting *Durusdinium* dominance upon recovery in these species.

In contrast, *M. cavernosa* corals that initially hosted no *Durusdinium* were not limited by the absence of pre-heat stress background *Durusdinium* in their recovery with high proportions of *Durusdinium*: after two months of recovery, the proportion of *Durusdinium* was significantly higher in *M. cavernosa* than in *O. faveolata* or *S. siderea* corals, comparing only corals hosting no detectable *Durusdinium* before heat stress ( $z=2.324$ ,  $p=0.020$ ) (Fig. 3c). Indeed, 25 out of 27 *M. cavernosa* colonies recovered after two months to host >90% *Durusdinium* (Fig. 3c).

## Discussion

### Effect of background *Durusdinium* on symbiont shifts following recovery from bleaching

*Durusdinium* became dominant in most *O. faveolata* and *S. siderea* colonies by the end of heat stress, even before symbiont:host cell ratios had begun to recover, indicating these were likely residual *Durusdinium* that were present



**Fig. 3** Symbiont shuffling magnitude and timing. **a** Shuffling metrics (for April and October corals combined) were calculated at each of three sampling time points after heat stress, with error bars representing 95% confidence intervals of predicted values. **b**, **c** Proportion *Durusdinium* detected at each of the four sampling time points (bleached corals only, April and October corals combined), with

small points representing individual cores. Larger points and error bars represent the mean  $\pm$  SE for each group. **b** *Orbicella faveolata* and *Siderastrea siderea* corals are grouped together and then categorised by pre-heat stress proportion *Durusdinium*. **c** only corals hosting no detectable *Durusdinium* before the start of heat stress are included

before heat stress (Glynn 1996; but see Claar et al. 2020 for symbiont recovery during heat stress). Indeed, the mere existence of an effect of initial proportions on recovered proportions of *Durusdinium* in these coral species implicates shuffling as the predominant mechanism for the observed assemblage shifts. But regardless of the origins of these recovered *Durusdinium*, the initial presence of this symbiont increased the average percentage *Durusdinium* recovered in *O. faveolata* and *S. siderea* from  $< 50\%$  to  $> 85\%$  *Durusdinium*. Low abundance ‘background’ *Durusdinium* in *O. faveolata* and *S. siderea* played a disproportionately large role in shaping post-recovery symbiont communities, suggesting residual *Durusdinium* are competitively superior over residual *Cladocopium* in bleached tissue and/or that residual *Durusdinium* hinder the acquisition of exogenous *Cladocopium*. The mechanism for these priority effects (Palmer et al. 2002; McIlroy et al. 2019) may play out via niche pre-emption (commonly seen in microbiome assembly (Debray et al. 2022)), whereby residual *Durusdinium*

exclude *Cladocopium* by resource competition only when given this ‘head-start’; without priority effects, *D. trenchii* grown in mixed cultures with *Cladocopium* is competitively inferior in assimilating the nitrogen necessary for niche exploitation (McIlroy et al. 2020).

Field surveys of *Acropora millepora* on the Great Barrier Reef during a natural bleaching event found that a minimum background threshold of 0.3% *Durusdinium* predicted mild, as opposed to severe, bleaching, and subsequent recovery with mainly *Durusdinium* (Bay et al. 2016). Here, using an experimental approach, we report a remarkably similar minimum threshold of 0.27% pre-bleaching *Durusdinium* in two Caribbean species, which predicts recovery from bleaching with symbiont communities reliably dominated (often exclusively) by *Durusdinium*, in contrast to the variable mixed communities following recovery shown by corals with initial *Durusdinium* proportions below this threshold. However, we report markedly different *Durusdinium* recovery dynamics in *M. cavernosa*, which recovered with

often complete *Durusdinium* dominance even when these symbionts were not present at detectable levels prior to heat stress. The competitive success of *Durusdinium* over *Cladocopium* without niche pre-emption in *M. cavernosa* may suggest either lower niche overlap between competing symbionts, or relatively superior resource assimilation by *Durusdinium*, which could be due to genetic differences in the *Cladocopium* of *M. cavernosa*, *O. faveolata*, and *S. siderea*, and/or host differences such as skeletal light scattering, or control of symbiosome nitrogen availability (Wangpraseurt et al. 2012; Krueger et al. 2020). This result supports earlier findings that *M. cavernosa* showed a higher propensity to recover from bleaching with *Durusdinium* compared to *O. faveolata* and *S. siderea* (Cunning et al. 2018, 2018, 2018).

Our results support the potentially critical role of low abundance symbionts in driving resilience following disturbance, with a corresponding interaction between symbiont and host species. However, background symbionts may also pose an indirect energetic cost to the host if symbionts divert some of their resources to competitive antagonism. Indeed, the proportion of photosynthate transferred to the host coral has been shown to decrease under heat stress when diverse symbiont communities are present (Kenkel and Bay 2018), and coral life histories with generally lower environmental sensitivity have been found to show relatively higher partner specificity (Putnam et al. 2012). In contrast, it has long been argued that access to functionally diverse symbionts broadens the ecological niche of the host, facilitating recovery from different stressors (Buddemeier and Fautin 1993; Baker 2003), and robustness analyses from Red Sea corals has shown rare, low-abundance symbionts may increase holobiont resilience under disturbance, if corals are able to recover with these previously low-abundance symbionts (Ziegler et al. 2018). Although the functional role of background symbionts in coral holobionts remains broadly unresolved (Lee et al. 2016), our findings contribute to the growing body of evidence supporting the ecological significance of background symbionts in shaping coral climate resilience.

### Seasonal coral-symbiont associations

Coral colonies from April 2019 were collected at cool temperatures (25 °C) during the spring warming phase, whilst colonies from October 2019 were collected at a warmer temperature (29 °C) but during an autumnal cooling phase. Seasonal temperature changes in south Florida are also accompanied by summer increases in photosynthetically active radiation (PAR), with associated increased net and gross primary productivity in reef-building corals (Owen et al. 2021). Similarly, dissolved inorganic nitrogen (DIN) is commonly linked to algal symbiont density increases and is typically higher in January-June on Floridian reefs compared to July-December (Muscatine et al. 1989; Dubinsky

et al. 1990; Muller-Parker et al. 1994; Marubini and Davies 1996; Lapointe et al. 2004). Consequently, the differences detected in *M. cavernosa* and *S. siderea* symbiont communities in April and October are unlikely to be attributable solely to temperature, but rather a combination of co-varying environmental factors. The temperatures at Emerald reef in 2019 (which was not considered a bleaching year in Florida) were perhaps not sufficiently high to confer the photochemical advantage necessary for *Durusdinium* to proliferate and exclude co-occurring symbionts between April and October in these three coral species, in light of evidence that more severe heat stress can induce larger shifts in favour of *Durusdinium* (LaJeunesse et al. 2009; Cunning et al. 2015).

In alignment with prior knowledge of Floridian seasonality in host and symbiont biomass (Fitt et al. 2000; Warner et al. 2002), the April-to-October increase in *M. cavernosa* symbiont:host cell ratio likely reflects a host biomass decrease that outweighed *Cladocopium* decrease. In contrast, the April-to-October decrease in *S. siderea* S:H likely reflects *Cladocopium* decreases that outweighed any host biomass decreases. This contrasting result may indicate a larger summer decrease in *M. cavernosa* biomass, in response to the energetic demands of higher summer rates of respiration and following photosynthate transfer minima from low-density symbiont populations (Fitt et al. 2000; Thornhill et al. 2011). Similarly, the type(s) of *Cladocopium* hosted by *S. siderea* may be more prone to seasonal population density acclimatisation, supposedly decreasing during warming summer temperatures and longer daylight hours (Stimson 1997; Fitt et al. 2000; Warner et al. 2002; Thornhill et al. 2011). The three coral species in this study have similar mounding/massive morphologies, but finer scale morphological differences, such as corallite arrangement and host tissue thickness, may shape the photic microenvironment within colonies, influencing symbiont dynamics (Loya et al. 2001; Wangpraseurt et al. 2012). An increase in the per-cell number of symbionts could theoretically result in a faster accumulation of reactive oxygen species (ROS) during heat stress (Cunning and Baker 2013), but further studies to directly measure intracellular ROS production or oxidative damage are needed to substantiate the role of S:H in exacerbating oxidative stress and triggering bleaching (Gardner et al. 2017; Baird et al. 2018).

Many coral bleaching predictive models are based on events that occur during the summer (Grottoli et al. 2014; van Hooidonk et al. 2020), yet recent marine heatwaves often extend beyond the summer (Sen Gupta et al. 2020), as observed during the most recent global mass bleaching event (2014–17) (Hughes et al. 2018; van Hooidonk et al. 2020). Indeed, seasonal variability in coral thermal tolerance has been highlighted as a priority research theme, on the basis of predicted winter warming and extended warm summer temperatures (Ziegler et al. 2021). Seasonal

variation in thermotolerant symbionts and their role in shaping the bleaching resistance and resilience of their host may be critical for informing this research question.

In conclusion, our results shed light on two specific factors which should be incorporated into bleaching models and predictions, namely seasonal variation in the symbiont to host cell ratio and the effect of background thermotolerant symbionts in driving symbiont shuffling following bleaching. The prospect of increased symbiont loads in corals outside of typical summer bleaching periods may further elevate bleaching risk if bleaching threshold temperatures are exceeded outside of the usual summertime window (van Hooijdonk et al. 2020; Cooley et al. 2022). Results reported here contribute to understanding of the role of background symbionts in coral species' propensity to shift symbiont assemblages under disturbance and support the importance of background Symbiodiniaceae in shaping patterns of coral species-specific symbiont flexibility. *Durusdinium* symbionts, in particular, may facilitate coral recovery from the increasing threat of extended heatwaves (Claar et al. 2020), in addition to increasing bleaching resistance. Regardless of the putative benefits or costs of hosting *Durusdinium*, continued study of this symbiont genus remains crucial for predicting and managing coral resilience, given its increasing abundance on warming, urbanised reefs (Baker et al. 2004; Poquita-Du et al. 2020; Rubin et al. 2021; Palacio-Castro et al. 2023), which typify the pressures facing many of the world's tropical corals.

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#### Declarations

**Conflict of interest** On behalf of all authors, the corresponding author states that there is no conflict of interest.

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