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REPORT

Symbiont shuffling linked to differential photochemical dynamics of *Symbiodinium* in three Caribbean reef corals

Ross Cunning[1] · **Rachel N. Silverstein**[1,2] · **Andrew C. Baker**[1]

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Abstract Dynamic symbioses with functionally diverse dinoflagellate algae in the genus *Symbiodinium* may allow some reef corals to alter their phenotypes through 'symbiont shuffling', or changes in symbiont community composition. In particular, corals may become more bleaching resistant by increasing the relative abundance of thermally tolerant *Symbiodinium* in clade D after bleaching. Despite the immediate relevance of this phenomenon to corals living in warming oceans—and to interventions aimed at boosting coral resilience—the mechanisms governing how, why, and when symbiont shuffling occurs are still poorly understood. Here, we performed controlled thermal bleaching and recovery experiments on three species of Caribbean corals hosting mixtures of D1a (*S. trenchii*) and other symbionts in clades B or C. We show that the degree of symbiont shuffling is related to (1) the duration of stress exposure and (2) the difference in photochemical efficiency (F_v/F_m) of co-occurring symbionts under stress (i.e., the 'photochemical advantage' of one symbiont over the other). The advantage of D1a under stress was greatest in *Montastraea cavernosa*, intermediate in *Siderastrea siderea*, and lowest in *Orbicella faveolata* and correlated positively with the magnitude of shuffling toward D1a. In holobionts where D1a had less of an advantage over co-occurring symbionts (i.e., only slightly higher F_v/F_m under stress), a longer stress duration was required to elicit commensurate increases in D1a abundance. In fact, across these three coral species, 92.9% of variation in the degree of symbiont shuffling could be explained by the time-integrated photochemical advantage of D1a under heat stress. Although F_v/F_m is governed by numerous factors that this study is unable to resolve mechanistically, its strong empirical relationship with symbiont shuffling helps elucidate general features that govern this process in reef corals, which will help refine predictions of coral responses to environmental change and inform interventions to manipulate symbiont communities to enhance coral resilience.

Keywords Coral bleaching · Symbiont shuffling · qPCR · Photochemical efficiency · Mutualism · Photophysiology

Introduction

Coral reef ecosystems are declining globally at an alarming rate, primarily due to mass coral bleaching caused by anthropogenic increases in sea surface temperature (Hoegh-Guldberg et al. 2007). Heat-induced bleaching, or the loss of corals' nutritional symbionts (*Symbiodinium* spp.; Jokiel and Coles 1977), often leads to coral mortality, which precipitates reef ecosystem degradation (Glynn 1993). Worst-ever coral bleaching and mortality have recently been recorded on many reefs in the central and western Pacific (Hughes et al. 2017; Couch et al. 2017), and annual recurring bleaching events are projected to become increasingly frequent in the near future (van Hooidonk et al. 2015).

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✉ Ross Cunning
ross.cunning@gmail.com

[1] Department of Marine Biology and Ecology, Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, FL 33149, USA

[2] Miami Waterkeeper, 12568 N. Kendall Dr., Miami, FL 33185, USA

However, depending on the severity of bleaching, some corals may recover their *Symbiodinium* communities within weeks to months (Jokiel and Coles 1977; Jones and Yellowlees 1997; Cunning et al. 2016) and ultimately return to a healthy state. Moreover, the loss and subsequent re-establishment of the symbiotic algal community may provide an opportunity for change in its composition, i.e., the relative abundance of different *Symbiodinium* types (Buddemeier and Fautin 1993; Baker 2001). When such 'symbiont shuffling' (Baker 2003) occurs, the new configuration of the *Symbiodinium* assemblage may be better suited to tolerate future bleaching stressors (Berkelmans and van Oppen 2006; Silverstein et al. 2015), indicating that bleaching may have adaptive value in allowing corals to rapidly acclimatize to changing conditions. Moreover, this phenomenon could be leveraged as a way to increase the resilience of reef corals through directed manipulation of *Symbiodinium* communities (Baker et al. 2008).

Symbiodinium is a highly diverse genus comprised of nine clades (Pochon et al. 2014), which are further subdivided into numerous types (with species descriptions underway; LaJeunesse et al. 2014; Wham et al. 2017) with varying functional biology (Suggett et al. 2015; Goyen et al. 2017). *Symbiodinium* D1a, also referred to as *S. trenchii*, is a heat-tolerant symbiont that confers a bleaching threshold ~ 1–2 °C higher than other *Symbiodinium* types (Silverstein et al. 2017). Increases in the abundance of clade D symbionts have been observed during and after bleaching in several coral species (Baker et al. 2004; Jones et al. 2008; LaJeunesse et al. 2009), and increases in clade A have been observed in others (Grottoli et al. 2014). Moreover, the majority of coral species surveyed have been observed in association with *Symbiodinium* from multiple clades (Silverstein et al. 2012), suggesting that the potential for symbiont shuffling is widespread among corals.

Nevertheless, the mechanisms governing the process of symbiont shuffling, and why it readily occurs in some corals but not others, are still poorly understood. In *Orbicella faveolata*, symbiont shuffling was shown to depend on the severity of bleaching (i.e., the magnitude of disturbance to the existing community), as well as the environmental conditions during recovery (Cunning et al. 2015a), suggesting that the relative performance of different symbionts influences the trajectory of symbiont community re-establishment. These dynamics may also be influenced by the changing internal environment and/or metabolic requirements of the host (Suggett et al. 2017). However, general rules that link symbiont performance to variability in symbiont shuffling among coral species with different *Symbiodinium* types have never been identified. Ultimately, a deeper understanding of symbiont community dynamics in corals is a critical foundation for predicting corals' responses to environmental change (Logan et al. 2014) and manipulating symbiont communities as a way to increase resilience in coral reef restoration (van Oppen et al. 2015).

Here, we investigated symbiont shuffling through controlled bleaching experiments with three Caribbean coral species hosting mixed *Symbiodinium* assemblages: *O. faveolata* (with clades B and D), *Siderastrea siderea* (with clades C and D), and *Montastraea cavernosa* (with clades C and D). Symbiont photophysiological performance was measured as photochemical efficiency (F_v/F_m), an emergent phenotype reflecting numerous underlying processes including photoacclimation and photodamage (Suggett et al. 2009, 2015). While differences in F_v/F_m cannot be attributed to a specific mechanism, we interpret higher values as an advantage reflecting greater capacity for PSII photochemistry. We used this metric to test links between the photophysiological performance of co-occurring symbionts and the magnitude of symbiont shuffling after bleaching.

Materials and methods

Experimental manipulations

Two separate bleaching and recovery experiments were conducted. The first experiment included both *O. faveolata* (3 colonies, 22–37 cores per colony, $n = 87$ cores total) and *S. siderea* (12 colonies, 5–15 cores per colony, $n = 138$ cores total), with bleaching treatments of exposure to 32 °C for 7, 10, and 14 d (Cunning et al. 2015a) and recovery for 3 months at 24 or 29 °C. The second experiment was conducted on *M. cavernosa* (9 colonies, 6–9 cores per colony, $n = 69$ cores total), with a bleaching treatment of 32 °C for 10 d (Silverstein et al. 2015) and recovery for 3 months at 24 or 29 °C. Prior to experimentation, the *O. faveolata* cores contained varying mixtures of *Symbiodinium* in clades B and D (Cunning et al. 2015a), while *S. siderea* colonies contained mixtures of clades C and D (Cunning 2013). *Montastraea cavernosa* contained only clade C *Symbiodinium* upon collection, but an initial bleaching and recovery experiment involving some of these cores produced a range of mixtures of clades C and D (Silverstein et al. 2015). Both experiments were conducted in the same indoor, semi-recirculating coral culture facility at the University of Miami. For additional details on coral collection and experimental setup, see Silverstein et al. (2015) and Cunning et al. (2015a).

Sampling and data collection

In both experiments, maximum F_v/F_m of *Symbiodinium* within each coral core was measured prior to heat stress

and at the end of heat stress using an imaging PAM fluorometer (Walz, Effeltrich, Germany) to deliver a saturating pulse at 2800 µmol photons m^{-2} s^{-1} at 460 nm for 800 ms. At the same time points, small tissue biopsies were taken from each core for genomic DNA extraction, and quantitative qPCR assays were used to compute the relative abundance of *Symbiodinium* clades, including the proportion of clade D (represented exclusively by D1a/*S. trenchii*; Pettay et al. 2015) within the community. Tissue samples were collected again after 3 months of recovery from bleaching to analyze changes in *Symbiodinium* community structure (i.e., symbiont shuffling). For additional details on sampling and data collection, see Silverstein et al. (2015) and Cunning et al. (2015a).

Data analysis

F_v/F_m was analyzed by a linear mixed model (*lmer*; Bates et al. 2015) with fixed effects of time (pre- or post-heat stress), proportion D1a (measured at the same time point), and coral species, with random intercepts for each colony. Backward elimination of nonsignificant effects from a fully crossed model was performed using partial F tests in *lmerTest* (Kuznetsova et al. 2015). By relating the photochemical efficiency of *Symbiodinium* communities to their taxonomic composition (sensu Suggett et al. 2009), we can tease apart the relative photochemical performance of the two different symbionts in each coral. Specifically, regression coefficients for the proportion of D1a were interpreted as the photochemical advantage of D1a for each coral species under ambient (pre-heat stress; A^D_{Amb}) and heated (post-heat stress; A^D_{Heat}) conditions and tested for statistical differences by pairwise comparisons using *lsmeans* (Lenth 2016). Stress duration (i.e., 7, 10, or 14 d) was not included as a predictor since it had no impact on the photochemical advantage of D1a in the first experiment (i.e., no significant interaction between stress duration and proportion of D1a).

Symbiont shuffling was analyzed by modeling the final proportion of D1a (after 3 months of recovery) as a function of the initial proportion D1a (before bleaching), using a quasi-binomial generalized linear model (GLM) with species, stress duration, and recovery temperature as co-predictors. Fitted values for the final proportion of D1a for each species at each stress duration (averaged across recovery temperatures and predicted for *M. cavernosa* at 7- and 14-d durations using the *effects* package; Fox 2003), were plotted against initial proportion of D1a with 90% confidence intervals. From these fitted values, an integrated metric of symbiont shuffling was generated across the full range of initial D1a proportions by calculating the area between the fitted curve for each group and the diagonal line of identity. (The line of identity indicates no change in symbiont proportions.) This metric was scaled to a range of − 1 (complete loss of D1a) to + 1 (complete dominance by D1a), with zero indicating no symbiont shuffling.

Finally, we used a quasi-binomial GLM to model the integrated symbiont shuffling response as a function of the photochemical advantage of D1a under heat stress (A^D_{Heat}) for each species and days of exposure to heat stress. All data analysis was conducted using R v3.3.1 (R Core Team 2016). Data and R code to reproduce all analyses and figures presented here are available at github.com/jrcunning/symshuff-3c, and archived at Zenodo (Cunning 2017).

Results

Photochemistry of symbiont assemblages

Measured values of F_v/F_m were significantly affected by the proportion of D1a in symbiont assemblages (Fig. 1), but this effect varied among coral species and between ambient and heat stress conditions (three-way interaction, $F = 4.06$, $p = 0.018$). In all three coral species, a higher relative abundance of D1a led to lower F_v/F_m under ambient conditions, but higher F_v/F_m under heat stress. Within each species and treatment, we operationally define the photochemical advantage of D1a (Fig. 2) as the difference in F_v/F_m when proportion D1a = 1 and when proportion D1a = 0 (i.e., the slope of each line in Fig. 1). The advantage of D1a under ambient conditions (A^D_{Amb}) was significantly more negative (i.e., a greater disadvantage) in *O. faveolata* (− 0.09) compared to *M. cavernosa* (− 0.034, $p = 0.011$) and intermediate (− 0.051, but not significantly different, $p > 0.1$) in *S. siderea*. Under heat

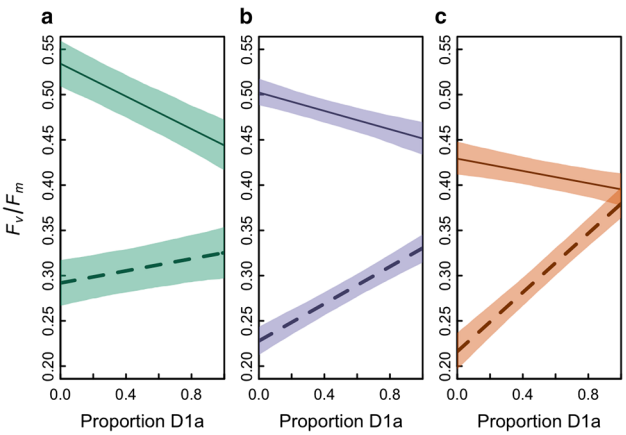


Fig. 1 Photochemical efficiency (F_v/F_m) as a function of the proportion of D1a *Symbiodinium* in **a** *Orbicella faveolata*, **b** *Siderastrea siderea*, **c** *Montastraea cavernosa*. Solid lines represent ambient conditions, and dotted lines represent the relationship under heat stress (32 °C). Shaded regions represent 90% confidence intervals around fitted values

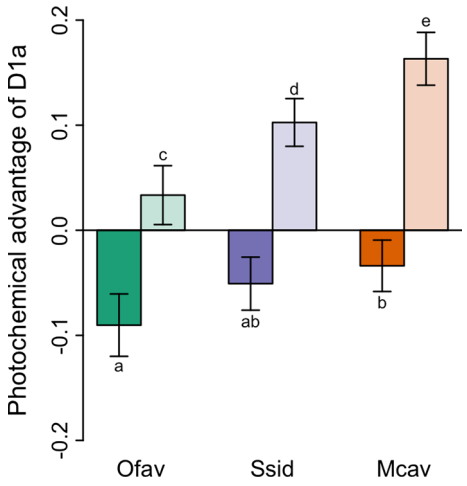


Fig. 2 Photochemical advantage of D1a symbionts in each coral species (Mcav = *Montastraea cavernosa*, Ssid = *Siderastrea siderea*, Ofav = *Orbicella faveolata)* under ambient conditions (darker bars) and under heat stress (lighter bars). Values indicate the difference in F_v/F_m of corals with all and no D1a symbionts (i.e., slopes of the lines in Fig. 1); error bars indicate 95% confidence intervals

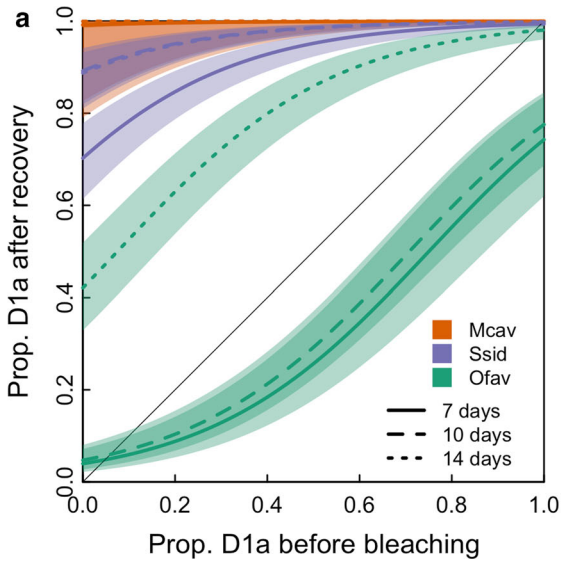
stress, the advantage of D1a (A^D_{Heat}) was greatest in *M. cavernosa* (0.163), intermediate in *S. siderea* (0.103), and lowest in *O. faveolata* (0.033, all pairwise comparisons, $p < 0.002$; Fig. 2).

Symbiont shuffling

The proportion of D1a after recovery from bleaching (Fig. 3a) depended on the initial proportion of D1a ($F = 224.742$, $p < 1e{-}04$) and an interaction among coral species, heat stress duration, and recovery temperature ($F = 5.527$, $p = 0.005$). Fitted values were averaged across recovery temperatures to focus on differences among species and heat stress durations. Across the full range of initial D1a proportions, the integrated symbiont shuffling response, *S* (Fig. 3b), showed a loss of D1a in *O. faveolata* after recovery from 7 and 10 d of heat stress ($S = -0.378$ and -0.318, respectively), but a gain of D1a after recovery from 14 d of heat stress ($S = 0.6$). In contrast, *S. siderea* underwent greater shuffling toward D1a after 7 d ($S = 0.835$), 10 d ($S = 0.946$), and 14 d ($S = 0.944$) of heat stress. *Montastraea cavernosa* shuffled almost completely to D1a assemblages following 10 d of stress ($S = 0.996$), and thus, the statistical model also predicted near complete shuffling to clade D symbionts after 7 d ($S = 0.996$) and 14 d ($S = 1$) of heat stress.

Relationship between photochemistry and symbiont shuffling

The magnitude of symbiont shuffling showed a statistically significant relationship (Fig. 4a) with both the photochemical advantage of D1a under heat stress (A^D_{Heat}, $F = 414.9$, $p < 1e{-}04$) and the duration of heat stress



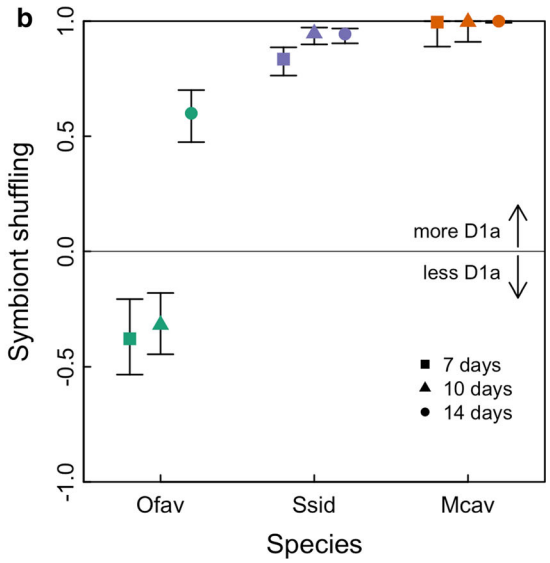


Fig. 3 Symbiont shuffling in three coral species. **a** Proportion of D1a *Symbiodinium* before bleaching and after recovery; diagonal line of identity represents no change in symbiont proportions. Fitted values for each species (indicated by color; Mcav = *Montastraea cavernosa*, Ssid = *Siderastrea siderea*, Ofav = *Orbicella faveolata*) and heat stress duration (indicated by line type) are plotted with shaded areas representing 95% confidence intervals. **b** Integrated symbiont shuffling response (from before bleaching to after recovery) for each species and bleaching treatment, calculated as the area above or below the diagonal line of identity, normalized to a range of − 1 (i.e., a complete loss of D1a symbionts) to + 1 (i.e., complete dominance by D1a symbionts)

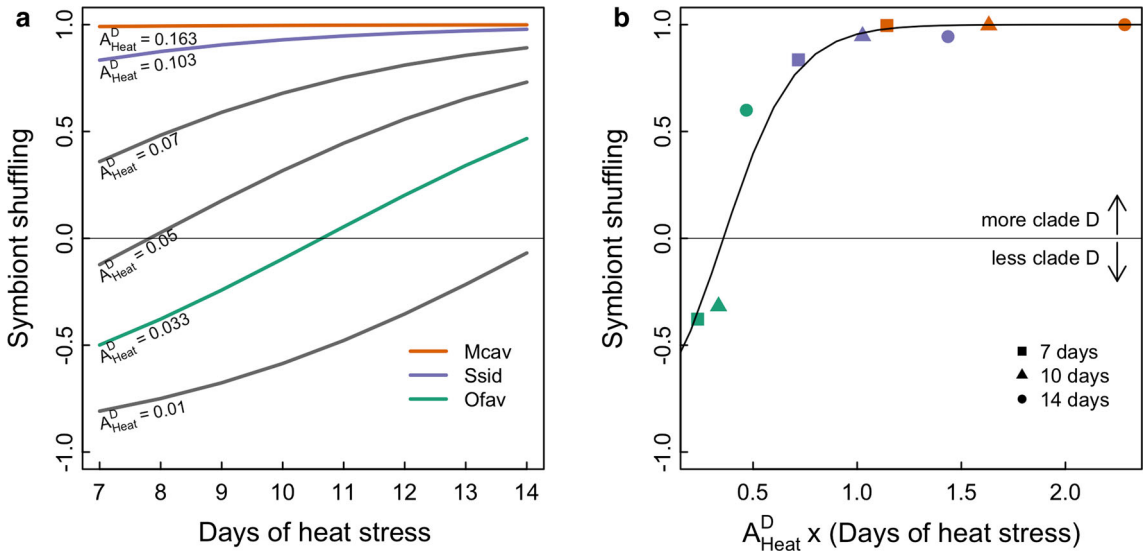


Fig. 4 **a** Symbiont shuffling response (as in Fig. 3b) as a function of heat stress duration (days) and the photochemical advantage of D1a under heat stress (A^D_{Heat}); lines correspond to the A^D_{Heat} values for the three coral species studied (indicated by colored lines; Mcav = *Montastraea cavernosa*, Ssid = *Siderastrea siderea*, Ofav = *Orbicella faveolata*), and other (unobserved) values (gray lines). **b** Symbiont shuffling responses observed across all three species are predicted well (pseudo-$R^2 = 0.93$) by the time-integrated photochemical advantage of D1a under heat stress

($F = 69.7$, $p < 1e{-}04$). Specifically, increases in the amount of D1a were greater for higher values of A^D_{Heat} and longer durations of heat stress. The model predicts the duration of heat stress required to cause symbiont shuffling toward D1a for different values of A^D_{Heat} (Fig. 4a) and shows that 7 d of heat stress resulted in shuffling toward D1a for $A^D_{Heat} > \sim 0.06$. Lower values of A^D_{Heat} caused a decrease in the proportion of D1a after recovery, and when $A^D_{Heat} < \sim 0.01$, D1a decreased even after 14 d of heat stress.

Across these three coral species, the interaction of A^D_{Heat} and the duration of heat stress explained almost all (92.9%) of the variability in the symbiont shuffling response (Fig. 4b).

Discussion

These experiments revealed differences in the degree of symbiont shuffling in three coral species that were strongly related to differences in the photochemical efficiencies of co-occurring symbionts. At ambient temperatures, D1a (*S. trenchii*) symbionts had significantly lower F_v/F_m than the other co-occurring symbionts within each coral host. Since ambient temperatures are not expected to cause photodamage, the reduced photochemical efficiency of D1a may be due to reduced nutrient sufficiency (Parkhill et al. 2001), greater pigment antenna size or association with PSI (Suggett et al. 2009), greater excitation 'spillover' from PSII to PSI (Slavov et al. 2016), or other mechanisms of non-photochemical quenching (Osmond 1994). Indeed, inherent differences in photobiological traits produce taxonomic variation in F_v/F_m among broad microalgal classes (Suggett et al. 2009) as well as different types of *Symbiodinium* (Suggett et al. 2008, 2015). Regardless of the underlying mechanisms, the reduced photochemical efficiency of D1a relative to other *Symbiodinium* in hospite suggests D1a has a reduced potential for PSII photochemistry under ambient conditions. This disadvantage may explain why D-dominated corals tend to grow more slowly under these conditions (Little et al. 2004; Jones and Berkelmans 2010; Cunning et al. 2015b), and why D1a may be displaced by other symbionts in the absence of stress (Thornhill et al. 2006; LaJeunesse et al. 2009).

However, under heat stress, the relative performance of symbionts was reversed, with D1a maintaining a higher photochemical efficiency than each co-occurring symbiont. These reductions in F_v/F_m can be attributed to accumulation of damage impacting photosystem II, which is known to vary among *Symbiodinium* types (Warner et al. 1996). Indeed, clade D *Symbiodinium* have been shown to maintain higher F_v/F_m under heat stress (Rowan 2004; Silverstein et al. 2015), indicative of greater thermal tolerance. However, the magnitude of D1a's advantage under heat stress differed among the three coral species, being greatest in *M. cavernosa*, intermediate in *S. siderea*, and lowest in *O. faveolata*.

The variable performance of different symbionts in different coral hosts may be explained by variation in symbiont-specific photobiological traits and/or host-

specific traits that modulate symbiont performance. For example, coral tissue architecture may influence internal light and nutrient microenvironments (Wangpraseurt et al. 2015), and host regulation of nitrogen and/or carbon dioxide supply to symbionts may influence their performance (Tansik et al. 2017). In both *O. faveolata* and *S. siderea*, D1a symbionts showed the same F_v/F_m (Fig. 1a, b), indicating that differences in the relative advantages of D1a were driven by the differential performance of the other co-occurring symbiont. D1a in *M. cavernosa* had slightly lower F_v/F_m under ambient conditions (and higher under heat stress) compared to D1a in the other two corals. However, since this followed repeated bleaching in a separate experiment for *M. cavernosa* (Silverstein et al. 2015), we are unable to attribute these differences to unique host traits, the influence of prior bleaching and recovery, or random experimental effects.

Nevertheless, we could test whether the relative photophysiological performance of the two symbionts within each coral host was predictive of the magnitude of symbiont shuffling within that host following heat stress. Indeed, $\sim$ 93% of the variability in symbiont shuffling was predicted by A^D_{Heat} and the duration of heat stress applied. Specifically, greater increases in D1a occurred when A^D_{Heat} was higher and when heat stress was longer. Symbiont assemblages in which D1a had less of an advantage under stress (e.g., *O. faveolata*) required more stress to induce shuffling to D1a, while assemblages in which D1a had a large advantage (e.g., *M. cavernosa*) required less stress. This finding suggests that both the relative sensitivity to stress and the duration of stress determine symbiont shuffling, similar to the way that both concentration and duration of exposure influence a pharmacological response (Miller et al. 2000).

This statistical result reveals predictors of symbiont shuffling but not necessarily the mechanisms underlying them. However, we hypothesize that if D1a performs better at 32 °C, it may be expelled at lower rates than co-occurring symbionts (Silverstein et al. 2017), or may even continue to proliferate. Furthermore, after heat stress is alleviated (but corals have bleached), amplified internal light environments characteristic of bleached corals (Wangpraseurt et al. 2012) may sustain the photochemical advantage of D1a, allowing it to proliferate at higher rates as the symbiont population regrows. Only once symbionts reach high densities may the internal microenvironment (e.g., darker, more nutrient-scarce conditions) again put D1a at a disadvantage, explaining why clade D may be gradually replaced over time in the absence of stress (Thornhill et al. 2006). Importantly, the rate of compositional change in the scenario outlined here would be proportional to the relative difference in the advantage of one symbiont over another, consistent with our observations across coral species.

Whether these same rules may apply in other *Symbiodinium* communities that shuffle between clade C and D types (e.g., *Acropora millepora* on the Great Barrier Reef; Jones et al. 2008) as well as those without clade D that shuffle between other types (e.g., *Porites* with clades A and C; Grottoli et al. 2014), remains to be investigated. Other populations of *O. faveolata* may shuffle variously among clades A, B, C, and D (Baker 1999; Grottoli et al. 2014). In contrast, symbiont shuffling may be rare in other coral taxa, such as *Pocillopora* in the Mexican Pacific (McGinley et al. 2012) and *Montipora capitata* in Hawaii (Cunning et al. 2016), despite the fact that these corals host members of *Symbiodinium* clades C and D that differ greatly in their sensitivity to stress. While the links identified here may not explain symbiont community dynamics in all cases, this study expands our understanding of symbiont shuffling in a variety of important Caribbean reef-building coral taxa. A better understanding of this phenomenon may help to (1) predict responses of symbiont communities from in situ measurements of F_v/F_m, a metric that is commonly collected but perhaps underexplored with respect to ecological applications, (2) refine predictive models of coral responses to environmental change (Logan et al. 2014), and (3) develop methods to manipulate symbiont communities in corals, which may be an increasingly important tool in coral reef conservation (van Oppen et al. 2015; Aswani et al. 2015).

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