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Increased dominance of heat-tolerant symbionts creates resilient coral reefs in near-term ocean warming

Ana M. Palacio-Castro[a,b,c,1], Tyler B. Smith[d], Viktor Brandtneris[d], Grace A. Snyder[a], Ruben van Hooidonk[b,c], Juan L. Maté[e], Derek Manzello[f], Peter W. Glynn[a], Peggy Fong[g], and Andrew C. Baker[a]

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Climate change is radically altering coral reef ecosystems, mainly through increasingly frequent and severe bleaching events. Yet, some reefs have exhibited higher thermal tolerance after bleaching severely the first time. To understand changes in thermal tolerance in the eastern tropical Pacific (ETP), we compiled four decades of temperature, coral cover, coral bleaching, and mortality data, including three mass bleaching events during the 1982 to 1983, 1997 to 1998 and 2015 to 2016 El Niño heatwaves. Higher heat resistance in later bleaching events was detected in the dominant framework-building genus, *Pocillopora,* while other coral taxa exhibited similar susceptibility across events. Genetic analyses of *Pocillopora* spp. colonies and their algal symbionts (2014 to 2016) revealed that one of two *Pocillopora* lineages present in the region (*Pocillopora* "type 1") increased its association with thermotolerant algal symbionts (*Durusdinium glynnii*) during the 2015 to 2016 heat stress event. This lineage experienced lower bleaching and mortality compared with *Pocillopora* "type 3", which did not acquire *D. glynnii*. Under projected thermal stress, ETP reefs may be able to preserve high coral cover through the 2060s or later, mainly composed of *Pocillopora* colonies that associate with *D. glynnii*. However, although the low-diversity, high-cover reefs of the ETP could illustrate a potential functional state for some future reefs, this state may only be temporary unless global greenhouse gas emissions and resultant global warming are curtailed.

coral bleaching | *Durusdinium glynnii* | El Niño | *Pocillopora* | thermal stress

Significance

Global warming is causing the loss of coral reefs worldwide, as a result of heat-induced coral bleaching and mortality. Here, we examined the potential mechanisms that have increased the heat resistance of dominant framework-building coral taxa (*Pocillopora* spp.) on reefs in the eastern tropical Pacific. We propose that increasing abundance of a thermotolerant symbiotic alga (*Durusdinium glynnii*) hosted by these corals has facilitated the maintenance of high coral cover after three mass coral bleaching events. This study reveals a mechanism by which some reefs may be more resilient than previously thought and illustrates how future reefs might still maintain high cover for several decades, albeit with low diversity, provided other stressors are minimized.

Coral reefs are increasingly threatened by global climate change. In particular, mass bleaching and mortality events caused by elevated sea surface temperatures (SSTs) have resulted in coral loss worldwide (1–5). However, our capacity to predict reef responses and forecast coral species' survival trajectories under projected climate conditions is limited. For example, reefs previously exposed to bleaching have exhibited less coral bleaching and mortality in subsequent events (6–12), indicating that the outcome of a heat stress event not only depends on its duration or intensity, but could vary based on its "ecological memory"—the thermal history of the reef community and its past responses (12, 13). Increases in coral reef thermotolerance following heat stress can result from multiple mechanisms that operate at different timescales, such as differential mortality of susceptible coral species (14, 15) and/or genotypes (16), selection of hosts that associate with stress-resistant symbionts (10, 17), epigenetic changes in surviving colonies (18), individual coral colony acclimatization through changes in gene expression (19, 20) or shifts in the composition of algal symbiont communities (10, 21). While all these mechanisms warrant further research, here we assess how some of these mechanisms could be key for the future of coral reefs in the eastern tropical Pacific (ETP) region.

Coral reefs in the ETP offer a unique opportunity to study the relative roles of these mechanisms in increasing thermal resistance using one of the world's longest running datasets on disturbance events and associated changes in coral cover. Benthic cover data have been collected in some ETP locations since the early 1970s using consistent methods across five decades. During this period, ETP reefs experienced three major bleaching events triggered by the warm phase of the El Niño-Southern Oscillation cycle, or "El Niño". Although these three El Niño events were classified as "very strong" (Oceanic Niño Index [ONI] ≥ 2.0), local and region-wide studies have shown less severe coral responses over subsequent events (9, 22–25).

Early molecular studies in *Pocillopora*, the main reef-building genus in most ETP reefs, identified that colonies hosting an algal symbiont in the genus *Durusdinium* (*Durusdinium glynnii,* formerly *Symbiodinium* D1 (26)) were more resistant to temperature and light stress than colonies hosting other symbionts in the genus *Cladocopium* (formerly clade C) (10, 17, 23, 27). These studies also showed higher frequencies of colonies harboring *D. glynnii* following bleaching events (10, 17), and some of them proposed that selective mortality of colonies harboring *Cladocopium* was the dominant mechanism driving these

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[1]To whom correspondence may be addressed. Email: apalacio@rsmas.miami.edu.

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frequency changes (17, 28). However, the alternative mechanism (of changes in the algal community composition of surviving colonies in favor of *D. glynnii*) has not been tested in *Pocillopora* under high heat stress.

The purpose of this study was to test (1) if the less severe impacts that followed later El Niño events in the ETP can be explained by differences in the magnitude of heat stress during each event, or whether there is evidence for increased stress tolerance during the later events. To understand the potential mechanisms that could increase heat tolerance in this region, we (2) compared the susceptibility of different coral species across El Niño events, and (3) assessed the dynamics of the algal symbiont communities in tagged *Pocillopora* colonies during the last event. We propose that the increasing abundance of *D. glynnii* in *Pocillopora* after heat disturbances has increased ETP reefs thermotolerance, and discuss the potential limits of the *Pocillopora* + *D. glynnii* association for the future of ETP reefs.

Results

Heat Stress and Coral Cover. The most complete coral cover and coral bleaching datasets for the ETP region were available for Uva Island Reef, Panama (7.815°N, 81.759°W). We estimated heat stress using Degree Heating Weeks (DHW; a time-integrated index of accumulated heat stress) (29) during the 1982 to 1983, 1997 to 1998, and 2015 to 2016 marine heatwaves associated with El Niño, and assessed whether the loss of coral cover could be solely explained by differences in heat stress during each heatwave. Between 1980 and 2018, coral cover at Uva Island was mainly composed of a single coral genus (*Pocillopora*), with other scleractinians accounting for <3.2% of the benthic cover across years (*SI Appendix*, Fig. S1). However, *Pocillopora* cover at Uva Island experienced significant change over time (Generalized linear mixed model $P < 0.001$). As a result of the heat stress experienced during the 1982 to 1983 El Niño (maximum DHW during the event = 7.6; Fig. 1*A*), pre-1982-83 *Pocillopora* cover (1980 = 44.1% ± 46.5 SD) was reduced by 85 to 99% (1983 = 6.1% ± 4.6 SD; 1984 = 0.3% ± 0.1 SD; z-test $P < 0.001$ for both comparisons; Fig. 1*B*). Despite the similar or higher maximum level of heat stress during the 1997 to 1998 and 2015 to 1016 heatwaves (maximum DHW = 10.3 and 8.0, respectively; Fig. 1*A*), *Pocillopora* cover showed a steady recovery after 1984, with only moderate coral cover losses in 1998 and 2016 (16.2% reduction in both events, z-test $P > 0.05$ for the 1997 vs. 1998 and 2014 vs. 2016 comparisons; Fig. 1*B*). Indeed, *Pocillopora* cover at Uva Island recovered to pre-1982-83 levels by 2002 (cover values from 2002 to 2018 were not different from initial cover in 1980; z-test $P > 0.05$ for all pairwise comparisons; Fig. 1*B* and *SI Appendix*, Tables S1 and S2). While a second reef confirmed this pattern of increasing *Pocillopora* resistance to heat stress (Canal de Afuera; 7.69595°N, 81.63296°W; *Pocillopora* cover in 2015 = 57.4% ± 9.5 SD, 2016 = 57.0% ± 12.1 SD; z-test $P > 0.05$), a third reef with high cover of non-*Pocillopora* corals pre-1982-83 El Niño (Secas Island reef, 7.951183°N, 82.01098°W; non-*Pocillopora* cover in 1980 = 18.2% ± 25.5 SD) showed no recovery for these species (mean nonpocilloporid cover <1.5% between 1983 and 2018; *SI Appendix*, Fig. S1 and Table S3).

Comparative Species Response to Repeated Heat Stress. To assess coral species' heat susceptibility across heatwaves, we conducted individual colony assessments at Uva Island reef (<10 m) and compared the proportion of colonies of each species affected each year (colonies exhibiting ≥ 50% tissue loss and/or ≥10% of tissue bleaching). The maximum heat stress experienced over the 6-mo period preceding the colony assessments differed by survey and did not always represent the maximum stress that occurred during a heatwave (see red crosses in Fig. 1*A*). Data from 1997 to 1998 were collected under the lowest heat stress (October 1997 and March 1998; max DHWs over the 6-mo period preceding the survey = 5.58), followed by 1983 (March 1983; max DHWs = 6.09), and 2015 to 2016 (August 2015 and April 2016; max DHWs = 6.8 and 8.2, respectively; Fig. 1*A*).

The proportion of colonies affected by heat stress varied per year, species, and their interaction (generalized linear model $P < 0.001$). The hydrozoan *Millepora intricata* and the scleractinians *Pavona varians* and *Pavona clavus* were the most heat-sensitive species overall. These taxa exhibited the highest proportion of colonies affected during all bleaching events and no evidence of reduced susceptibility over successive heatwaves (Fig. 2). In *M. intricata*, virtually all (97 to 100%) colonies were affected by heat stress across all heatwaves (Fig. 2), but no data were collected for this species in 1998 since it was temporarily extirpated from shallow habitats in the region after 1997 (30). In *P. varians* and *P. clavus* > 77% of colonies were affected each year, with the exception of 1997 when only ~14% of the colonies exhibited bleaching or mortality (Fig. 2). The lower response in 1997 was common across all scleractinians (Fig. 2), likely because observations were taken during the ramp-up phase of the first incidence of heat stress, before the full response of corals developed in this El Niño event (Fig. 1*A*). Scleractinian heat stress responses were higher during the 1998 survey, although these data were also collected before the heat stress peak of the 1997 to 1998 heatwave (Fig. 1*A*).

While *Pocillopora elegans* and *Pocillopora damicornis* were among the most heat-sensitive species in 1983, they showed higher resistance during the following bleaching events (Fig. 2 and *SI Appendix*, Fig. S2). During the 1983 surveys, 70 to 88% of the *Pocillopora* spp. colonies were affected by heat stress. This contrasts with only 7 to 18% of colonies during the 1997 to 1998 surveys, and is particularly striking compared with 21 to 38% of colonies during the 2015 to 2016 surveys, which was recorded during the highest levels of heat stress (Fig. 2 and *SI Appendix*, Fig. S3).

Gardineroseris planulata and *Porites lobata* were the least susceptible species during the 1983 surveys, with ~45%, and ~14% affected colonies, respectively (Fig. 2, *SI Appendix*, Fig. S2). In *G. planulata*, the proportion of colonies affected was significantly higher during the 2015 to 2016 surveys (81 to 85%, Fig. 2) suggesting that the higher stress in 2015 to 2016 increased the probability of this coral experiencing bleaching or mortality. Similarly, *P. lobata* had a higher proportion of colonies affected in 1998, 2015, and 2016 (35 to 52%), compared with 1983, but these differences were not significant (Tukey HSD $P > 0.5$).

Additional individual colony assessments performed at two other locations in the Gulf of Chiriquí (Canal de Afuera and Secas Islands) during the 2015 to 2016 marine heatwave supported the generality of individual species responses across the wider Gulf of Chiriquí (*SI Appendix*, Fig. S4). These responses included low heat stress susceptibility in *Pocillopora*, compared with high susceptibility in *M. intricata*, *P. varians* and *P. clavus*, and intermediate susceptibility in *P. lobata*.

Algal Symbiont Dynamics, Bleaching, and Mortality. To understand the mechanisms of increasing heat resistance in ETP *Pocillopora*, we assessed the Symbiodiniaceae community dynamics and tissue mortality in 29 individually tagged colonies prior to (August 2014) and during the 2015 to 2016 El Niño heatwave (August 2015 and April 2016; Fig. 3*A*). Based on the mitochondrial open reading frame (ORF) region, ~79% of the tagged colonies (23 of 29) were *Pocillopora* type 1, although they

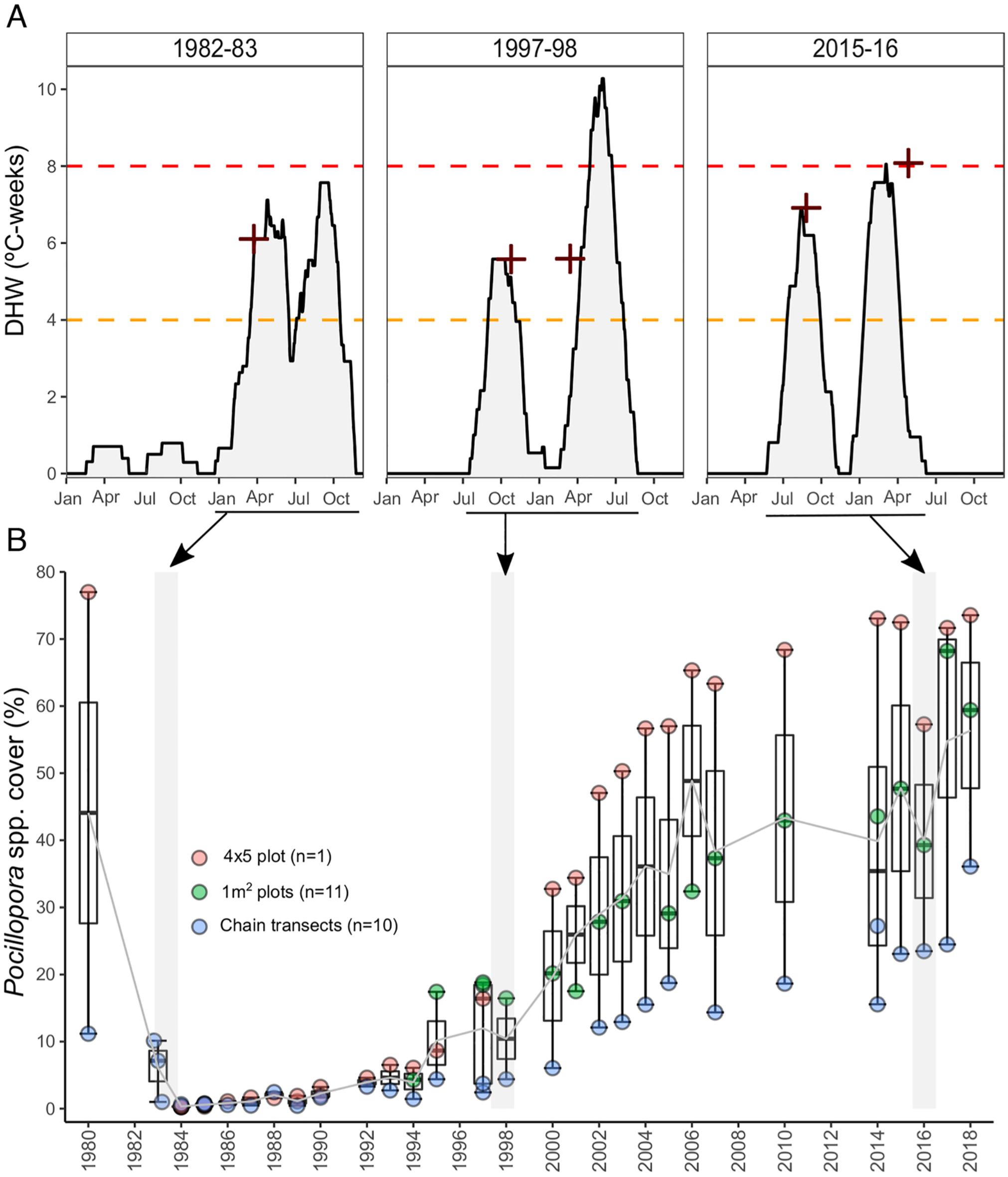

Fig. 1. Heat stress and *Pocillopora* cover dynamics at Uva Island during three major El Niño events. (*A*) DHW during the 1982 to 1983, 1997 to 1998, and 2015 to 2016 El Niño. The yellow dashed line marks the 4 DHW threshold for likelihood of bleaching, and the red dashed line marks eight DHW threshold for likelihood of mortality. Red crosses denote the dates when colony assessments of bleaching and mortality were performed, and the corresponding maximum heat stress levels experienced in the 6-mo prior to the time of the survey (Fig. 2). (*B*) *Pocillopora* spp. cover estimated using aggregated data from three datasets. The circles represent the mean values from a dataset for each month-year. The gray line represents the mean *Pocillopora* cover from all three datasets. The boxplots show the median (second quartile), first and third quartiles, with the bars extending from the minimum to the maximum mean coral cover recorded per dataset. Gray vertical bars demarcate the periods of very strong El Niño events (ONI > 2 °C).

were visually identified as multiple morphospecies (*P. capitata*, *P. damicornis* and *P. verrucosa*). Prior to the El Niño (August 2014), internal transcribed spacer 2 (ITS2) symbiont profiles showed that type 1 colonies predominantly hosted *Cladocopium latusorum* (n = 9), *D. glynnii* (n = 12), or a combination of these two algal symbionts (n = 2; *SI Appendix*, Fig. S5). More sensitive quantification of the relative abundance of each symbiont genus (i.e., *Cladocopium* and *Durusdinium*) using quantitative PCR (qPCR) showed that although type 1 *Pocillopora* commonly hosted a dominant symbiont, a second algal type was sometimes detected at low abundances (*D. glynnii* was detected in 6 of 9 colonies dominated by *C. latusorum*, and *C. latusorum* was detected in 4 of 12 colonies dominated by *D. glynnii*). The remaining ~21% of the colonies (6 of 29) were identified as *Pocillopora* type 3 and only exhibited macromorphology corresponding to *P. damicornis.* Based on their ITS2 profiles, type 3 colonies hosted *Cladocopium pacificum*, and *D. glynnii* was not detected in the ITS2 profiles or by qPCR.

Despite the accumulation of considerable thermal stress during the first peak of temperature in August 2015 (Fig. 3*A*), only three of the *Pocillopora* type 1 colonies that already hosted high abundances of *D. glynnii* in 2014 (>45% of the algal communities) showed increases in the proportion of this symbiont (Fig. 3*B*). After the second peak of heat stress in April 2016 (Fig. 3*A*) the proportion of *D. glynnii* increased in all but one *Pocillopora* type 1 that were not already dominated by this algal symbiont in 2015 (n = 8, Fig. 3*B*). By the end of the El Niño, three type 1 colonies exhibited almost complete mortality (>95% tissue loss), while five additional colonies exhibited partial mortality (<95% tissue loss; Fig. 3*C*). Conversely, none of the *Pocillopora* type 3 acquired *D. glynnii* during 2015 or 2016 (Fig. 3*B*). By April 2016 four type 3 colonies had experienced almost complete mortality (>95%

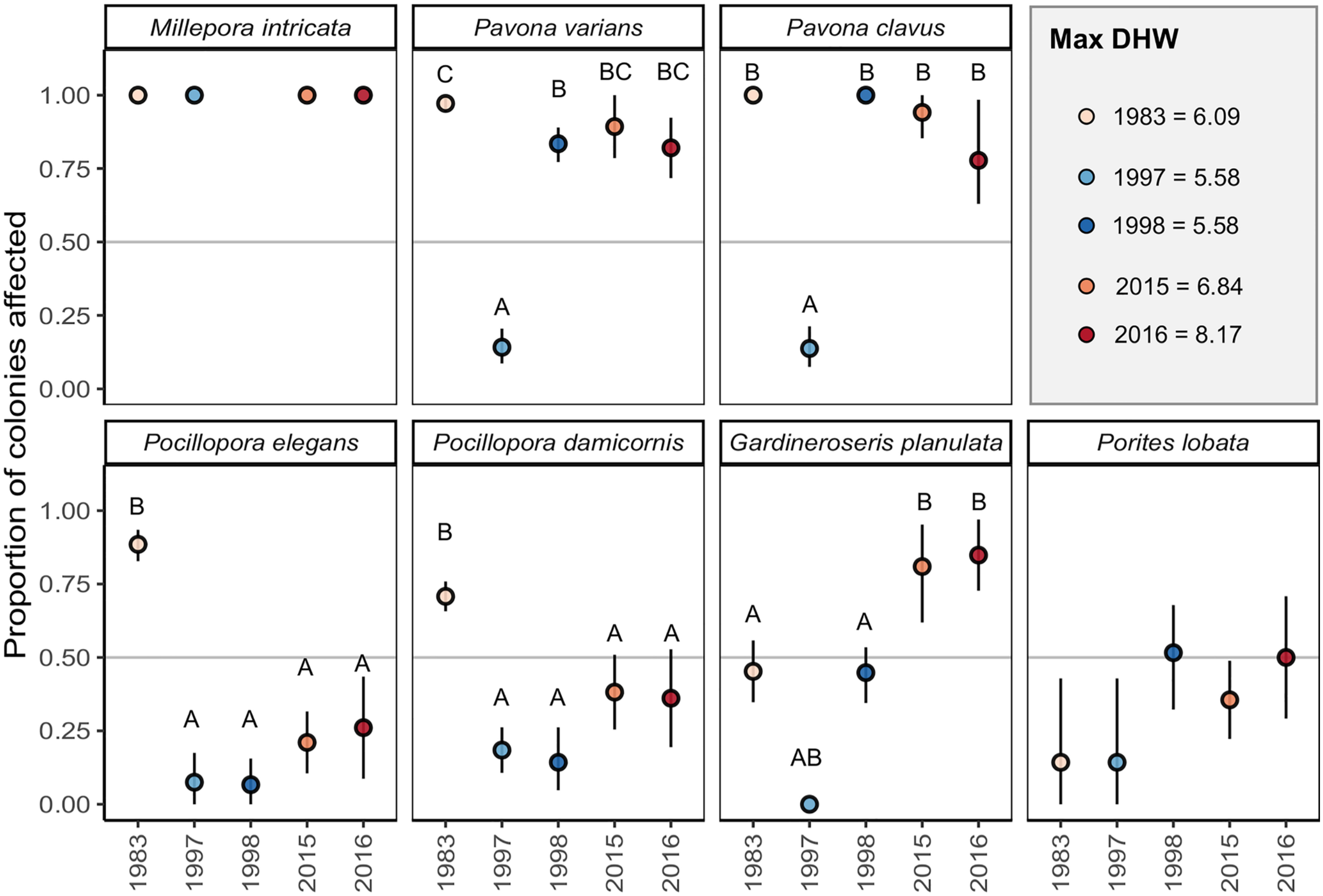

Fig. 2. Proportion of colonies affected (±95% CIs) by heat stress in March 1983, October 1997, March 1998, August 2015, and April 2016. Letters in the panels represent non-overlapping Tukey Honestly Significant Difference (HSD) groups ($P < 0.05$) for comparisons among years inside each species. Colonies affected included those exhibiting bleaching in >10% of the tissue and/or mortality in >50% of the tissue. No *Millepora* colonies were found in the studied area by the 1998 sampling. Specific sampling dates and the preceding DHW conditions at Uva Island at the time of the sampling are shown in Fig. 1*A*. Comparisons among species inside each year are shown in *SI Appendix*, Fig. S2.

tissue loss) and one experienced partial mortality (<95% tissue loss; Fig. 3*C* and *SI Appendix*, Table S9).

Based on the mortality (colonies with >95% tissue loss) and the symbiont community dynamics observed in the tagged colonies initially dominated by *Cladocopium*, both selective mortality (7 of 15 *Cladocopium* colonies, of which 3 also acquired *D. glynnii*), as well as increases in *D. glynnii* abundance (8 of 15 *Cladocopium* colonies, of which two showed almost complete mortality), contributed to increase the frequency of *Pocillopora* colonies that hosted *D. glynnii* after the 2015 to 2016 heatwave (Fig. 3 *B* and *C*). However, symbiont shuffling was only observed in *Pocillopora* type 1. In this taxon, the combined effects of symbiont dynamics and differential colony mortality resulted in an increase of tagged colonies dominated by *D. glynnii,* from 61% in 2014 to 91% in 2016 (Fisher's exact test, $P < 0.05$; Fig. 3*C*). Overall, ~46.7% of the initial type 1 *Cladocopium*-dominated colonies had experienced almost total mortality by 2016 (7 of 15) and ~40% (6 of 15) had shuffled (without mortality) to communities dominated by *D. glynnii* (*SI Appendix*, Table S9). Conversely, none of the colonies with algal communities dominated by *D. glynnii* in 2014 changed their dominant symbiont or experienced total mortality.

Coral bleaching, quantified by a reduction in the symbiont-to-host (S/H) cell ratio (31), was also dependent on the *Pocillopora* lineages and their capacity to increase *D. glynnii* abundance during heat stress. Prior to heat stress (August 2014), the algal symbiont abundance (S/H = *Cladocopium* + *Durusdinium* cells present per coral host cell) was similar between *Pocillopora* type 1 and type 3, as well as between colonies predominantly hosting *Cladocopium* or *Durusdinium* (S/H = 0.031 ± 0.014 SE; Fig. 4; Tukey HSD $P > 0.05$ for all pairwise comparisons). During heat stress, significant reductions in S/H cell ratio were recorded in *Pocillopora* type 3, which only hosted *Cladocopium.* In this coral, symbiont relative abundance was 73% lower in August 2015 with respect to 2014 (S/H = 0.008 ± 0.031 SE; Tukey HSD $P > 0.05$), and 83% lower by April 2016 with respect to 2014 (S/H = 0.004 ± 0.031; Tukey HSD $P < 0.05$; Fig. 4). Conversely, *Pocillopora* type 1 colonies, which increased *D. glynnii,* maintained similar total symbiont abundance during 2015 and 2016 to those recorded in 2014 (S/H > 0.03; Tukey HSD $P > 0.05$ for both pairwise comparisons; Fig. 4).

The mortality and symbiont shuffling probabilities obtained from the 2014 to 2016 tagged colonies were used to assess the potential effect of these two mechanisms on previously described increments in the prevalence of *Durusdinium*-colonies during the 1997 to 1998 bleaching event (10). We combined the 2014 to 2016 probabilities with the loss of *Pocillopora* cover experienced after the 1997 to 1998 El Niño (~16.2%, Fig. 1*B*) to test whether changes in *Durusdinium* prevalence from 42.6% before the heatwave (July 1995) to 78.57% during heat stress (September 1997) (10) could be better explained by the mortality of *Cladocopium* colonies alone or by the combination of selective mortality and symbiont shuffling. We estimated that the loss of 16.2% *Pocillopora* cover during the 1997 to 1998 heatwave (assumed to be

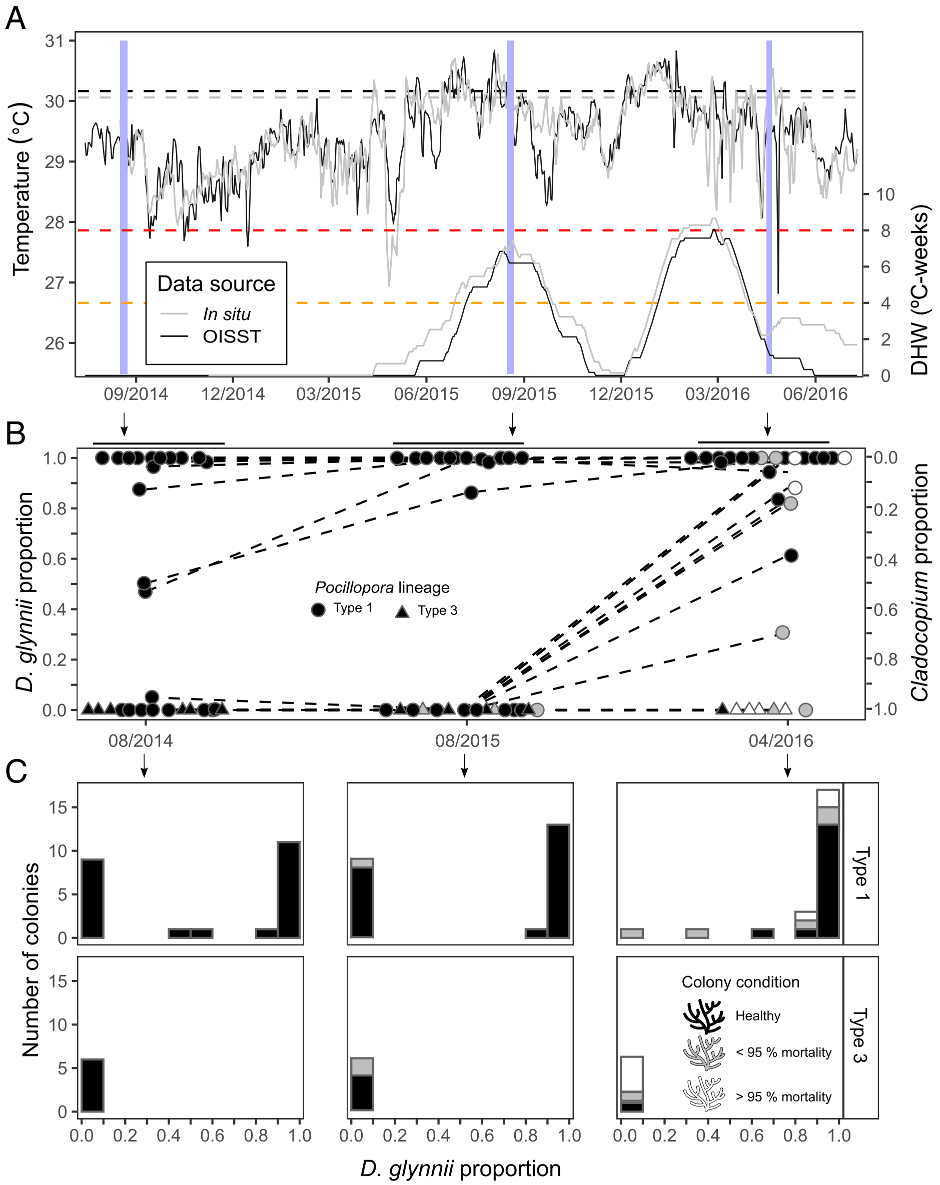

Fig. 3. *Pocillopora* symbiont community composition and colony condition before and during the 2015 to 2016 El Niño. (*A*) Temperature and DHW conditions during the sampling periods. The upper plot and left-hand axis show the mean daily temperature (solid lines) and bleaching threshold (dashed lines) for each dataset. Lower plot and right-hand axis show DHW calculated from each data source. The blue vertical lines represent the periods when the coral samples were collected. (*B*) Symbiont community trajectory (proportion of *D. glynnii*) in tagged colonies of *Pocillopora* type 1 (circles) and type 3 (triangles). Color of samples indicates colony health condition as in panel c. Points have been horizontally jittered to allow visualization of all colonies in each time point. *Cladocopium* quantification is performed at the genus level, but each *Pocillopora* lineage hosts different *Cladocopium* types. (*C*) Distribution of type 1 and type 3 colonies hosting different *D. glynnii* proportions before the El Niño (August 2014, left-hand panel), during the peak of heat stress (August 2015, center), and after El Niño (April 2016, right-hand panel). Filling colors represent the colony condition.

Cladocopium cover loss) would only increase the initial *Durusdinium* prevalence from 42.6 to ~58.8%, thus additional shuffling in ~27.7% of the colonies toward *D. glynnii* needs to occur to match the observed *D. glynnii* prevalence in 1997 (Fig. 5*A*). This estimated symbiont shuffling corresponds to ~48.3% of the 1995 *Cladocopium* colonies, and it is not far from the 40% calculated shuffling percentage from the 2014 to 2016 data (Fig. 5*A*).

Projected Heat Stress and Coral Cover Response. To contextualize the higher heat resistance observed at Uva Island (e.g., low cover loss under up to ~10 DHW) with future climate scenarios, we used the coupled model intercomparison projects climate models' (CMIP6) projections and estimated the DHW that Uva Island reef would experience during the coming decades up to the end of the century. Under the shared socioeconomic pathways (SSP) 8.5, which represents current rates of emissions and emissions growth, Uva Island is expected to experience significant levels of heat stress (>4 DHW) on an annual basis as soon as 2030, with severe levels (>10 DHW) starting by 2050 (Fig. 5*B*). Under these conditions, our symbiont data (Fig. 5*A*) suggest that *Cladocopium*-dominated *Pocillopora* would become increasingly rare throughout the 2020s and 2030s, and virtual dominance of *D. glynnii* in these hosts might be achieved by the 2040s. However, because the thermal tolerance of *Pocillopora* spp. hosting *D. glynnii* is likely to be ~1.25 to 1.5 °C higher than in colonies hosting *Cladocopium* (32, 33), heat stress will not accumulate on these holobionts to the same extent.

Adjusted heat stress projections, that account for hypothetical 1.25 and 1.5 °C higher bleaching thresholds in *Durusdinium*-dominated pocilloporid reefs, show that high *D. glynnii* prevalence

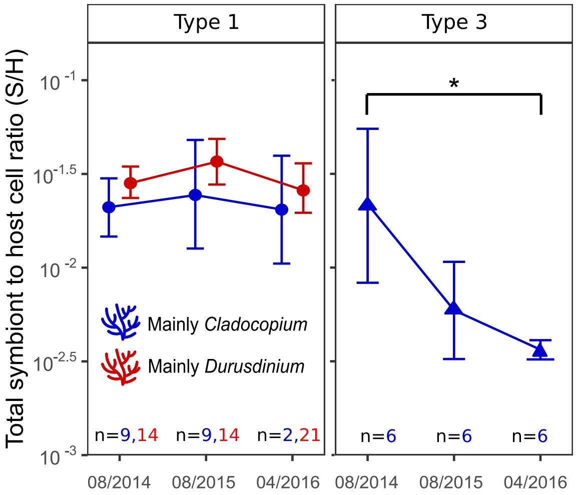

Fig. 4. Algal symbiont abundance (mean S/H ± 95% confidence intervals) in *Pocillopora* colonies sampled before and during the 2015 to 2016 El Niño. Only *Pocillopora* type 3 had significant reductions in total S/H cell ratio with respect to its values in 2014 ($P < 0.05$). Colors in each panel represent the dominant symbiont genus (>50% of the community) at each sampling point. Numbers (n) in the panels represent the number of colonies used in the cell ratio estimations.

might delay the occurrence of annual DHW >4 in these reefs until ∼2055 and ∼2070, respectively, and the occurrence of annual DHW >8 until 2070 and 2080 (Fig. 5*B*). Under the most optimistic scenario of *D. glynnii* thermotolerance (1.5 °C increase in bleaching the threshold), and given the absence of other disturbances, pocilloporid reefs that host *D. glynnii* might be able to maintain high coral cover through warming trends that continue up to the 2070s, but after that time unsustainable levels of annual severe bleaching become likely.

Discussion

Global climate models predict that most reefs in the world will experience annual heat stress levels >8 DHW before 2070 (34). Despite growing evidence of increased heat tolerance in some coral species, much about coral's adaptive capacities and the underlying mechanisms remains unknown. ETP reefs, in general, have been resilient to three mass bleaching events and have either recovered from or tolerated high heat stress levels associated with El Niño (9). Although the 1982 to 1983 El Niño caused devastating coral mortality across the ETP (>85% cover loss), with the exception of the central and southern Galápagos (35), most reefs recovered 10 to 15 y following massive mortality and experienced less bleaching and mortality in subsequent heatwaves (9, 11, 23, 25, 36, 37). Understanding the mechanisms by which these reefs have acclimatized or adapted to warmer temperatures will help elucidate the potential limits of increased thermal resistance, as well as the physiological and ecological trade-offs that may result from it (e.g., loss of biodiversity, slower coral growth, or higher susceptibility to other stressors).

Based on the comparative responses of different coral taxa to repeated warming, and on the dynamic changes in the algal symbiont communities described during the last heat event, we propose that ETP reefs have increased their heat resistance through mechanisms that include 1) the selection of *Pocillopora* over other coral genera that do not associate with thermotolerant symbionts in the region; 2) the selection of *Pocillopora* type 1 over type 3 [since the former associates with *D. glynnii* more frequently than other *Pocillopora* types in the region (38, 39)], and 3) the potential acquisition of *D. glynnii* during or after heat stress in *Pocillopora* colonies initially hosting *Cladocopium* (10). It is likely that these resistant corals repopulated ETP reefs after mass coral bleaching and mortality through a combination of tissue resheeting (40), asexual proliferation of surviving clones (41), and the recruitment of local, sexually produced larvae from these surviving corals (42, 43), which would result in a gradual increase in the heat-resistance of the overall coral community, but could reduce coral diversity and potential resilience to other stressors.

The ETP harbors one of the least diverse coral faunas in the tropics, with reefs commonly dominated by a few species in the genera *Pocillopora* and *Porites*, complemented in lower abundance by *Pavona*, *Gardineroseris* and *Psammocora* (44). After multiple mass bleaching events in the ETP, *Pocillopora* has exhibited higher recovery capacity compared to other scleractinians, likely related to its higher growth rate and capacity for asexual reproduction through fragmentation, as well as increased heat resistance, related to its capacity to host thermotolerant *D. glynnii*. Contrastingly, nonpocilloporid corals in the ETP either continued to be highly susceptible to heat (e.g., *P. varians* and *P. clavus*) or showed moderate heat susceptibility under medium levels of stress that increased as bleaching conditions became more extreme (e.g., *G. planulata* and *P. lobata*). The algal symbiont communities in these nonpocilloporid species in the ETP are dominated by *Cladocopium* (23, 45) with the occasional detection of other symbiont genera, including *Durusdinium,* at only background densities (46). Under the ocean temperatures anticipated to occur in the next two decades in the region (expected annual maximum DHW = 3 to 10), ETP reefs are likely to maintain high coral cover composed of dense *Pocillopora* frameworks and positive reef accretion (47). However, these anticipated heat levels could be enough to further reduce coral diversity, with nonpocilloporid species becoming progressively less abundant. The loss of the ecological functions of massive, plating, and nodular species could lead to the loss of ecological redundancy and resilience to other stressors.

More frequent heatwave events in the next decades could also alter the relative abundance of *Pocillopora* types in the ETP and might lead to a further loss of diversity. However, these changes would be difficult to quantify given the overlapping morphologies of the *Pocillopora* lineages (39, 48). Differential responses to heat stress have been detected among cryptic *Pocillopora* lineages at Moorean reefs (French Polynesia), and resulted in lower relative abundances of a sensitive type in locations that experienced more severe heat stress (15). In our study, the response of the *Pocillopora* lineages suggested that type 3 colonies were less likely to host and acquire thermotolerant *D. glynnii* compared with type 1, and that the type 3 lineage was more susceptible to bleach and die under heat stress. This hypothesis requires further testing given that the number of type 3 colonies sampled was low and none of them hosted *D. glynnii,* thus the effects of the host and symbiont identity cannot be separated. Although other studies have found that *D. glynnii* association with type 3 colonies is less common compared to type 1 (39), this symbiont–host combination has been reported in the ETP (38). Controlled experiments that compare the performance and physiological response to environmental stressors among the different *Pocillopora* lineages, in combination with their multiple algal symbionts, are necessary to anticipate future changes in these host–symbiont distributions. The wider distribution of *Pocillopora* type 1 in the ETP compared with type 2 (only reported for Clipperton Island) and type 3 (reported in the southern locations such as Panama and The Galapagos), suggests a higher competitive capacity of type 1 in the region (49). Although the higher success of type 1 could be associated with higher heat resistance, it is also possible that this lineage responds better to other common ETP disturbances such as the upwelling

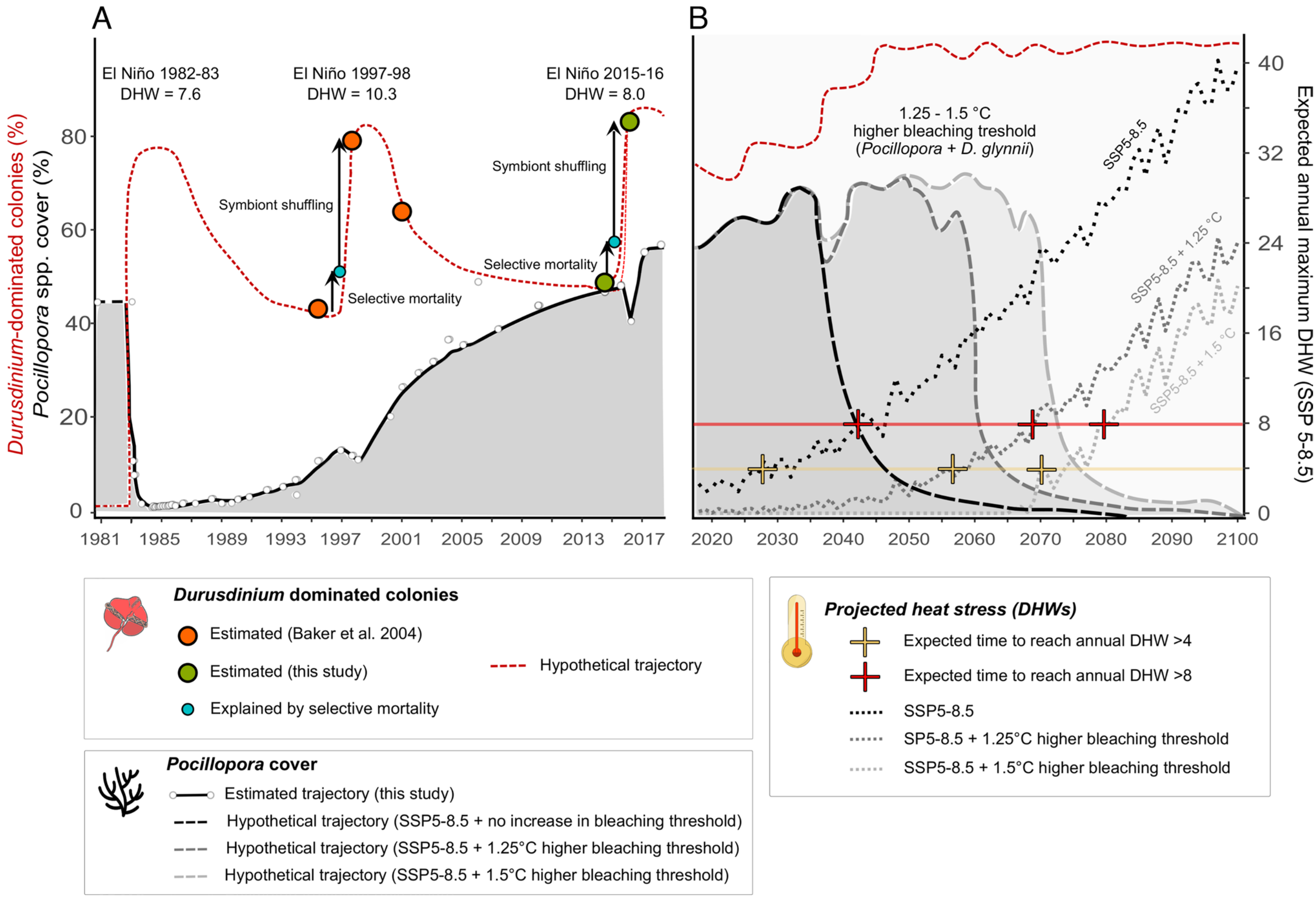

Fig. 5. Conceptual model of *Pocillopora* spp. cover and *D. glynnii* prevalence under repeated heat stress (DHW). (*A*) Observed and hypothesized changes in *Pocillopora* spp. cover and *D. glynnii* prevalence during the 1982 to 1983, 1997 to 1998, and 2015 to 2016 El Niño heatwaves at Uva Island reef. The orange and green dots represent the proportion of *Pocillopora* colonies hosting *D. glynnii* at Uva Island based on colony sampling. The blue dots represent the increases in *D. glynnii* that could be attributed to differential mortality of *Cladocopium*-dominated colonies based on the *Pocillopora* cover loss recorded after the 1997 to 1998 and 2016 to 2016 heatwaves. The remaining *D. glynnii* increases not explained by mortality are attributed to symbiont shuffling. (*B*) Hypothetical coral cover trajectories under the SSP 5-8.5 scenario (black), as well as the SSP 5-8.5 scenario + an increment in bleaching threshold in reefs composed of *Durusdinium*-dominated *Pocillopora* by 1.25 °C (dark gray) and 1.5 °C (light gray). The yellow and red crosses demarcate the approximate year when Uva Island reef would start experiencing four and eight DHW, respectively, under the three different scenarios. Warming trends from 2020 to 2050 are likely to be punctuated by climatological anomalies, such as El Niño events, that could lead to additional bleaching/mortality and further increases in *D. glynnii* dominance.

of cold and nutrient-rich water, high turbidity, or depressed aragonite saturation states (50).

During the 2015 to 2016 El Niño, two different processes resulted in increasing frequency of *Pocillopora* colonies dominated by *D. glynnii:* higher mortality of colonies that predominantly hosted *Cladocopium* in 2014 (in *Pocillopora* type 1 and 3) and increasing abundance of *D. glynnii* in colonies initially dominated by *Cladocopium* (in *Pocillopora* type 1). Increases in the proportion of *Pocillopora* hosting *D. glynnii* have been also reported for the Gulf of California after a low-temperature bleaching event (17). However, during this event, the proportion of *Pocillopora* type 1 hosting *D. glynnii* mainly increased through the mortality of *Cladocopium*-colonies (17), while changes in the composition of the symbiont communities of the surviving colonies (symbiont shuffling) were minimal (28). These differences between *Pocillopora* type 1 symbiont dynamics in these studies could reflect the differential effect of cold bleaching vs. heat bleaching (17, 28, 51), variations in the severity of the bleaching stress (27), or warmer recovering temperatures during the 2015 to 2016 event, which could favor the proliferation of thermotolerant symbionts in the surviving colonies over more heat-sensitive symbionts (52). Contrasting with *Pocillopora* type 1, we did not observe symbiont changes in type 3 colonies during the 2015 to 2016 heatwave. Since *Pocillopora* type 3 is known to associate with both *Cladocopium* and *D. glynnii* in the ETP (38), it is possible that the acquisition of novel algal types in this coral is limited to early-life stages (53), or that different disturbances or recovery conditions are required to induce changes in the composition of *Pocillopora* type 3 symbiont communities (52).

Based on the algal symbiont dynamics observed in tagged colonies during 2014 to 2016, we also estimated that selective mortality alone is unlikely to fully explain the changes in *Pocillopora* algal communities recorded during the 1997 to 1998 heatwave (10). Indeed, our results from 2014 to 2016 and estimations of the symbiont dynamics during 1997 to 1998 support that acquisition of *D. glynnii* by the surviving colonies is an important driver of the increased thermotolerance of these reefs. However, our ability to extend these projections further back to 1982 to 1983 is constrained by a lack of data on algal symbiont community structure before or after this event. Nevertheless, the loss of >90% of pocilloporid cover on these reefs following the 1982 to 1983 event points to a naive coral assemblage dominated by *Cladocopium,* especially since the magnitude of the 1982 to 1983 event was similar or less than the subsequent two events (7.6 DHW compared with 10.3 and 8.0 DHW) and the fact that *D. glynnii* imparted high thermotolerance to pocilloporids during the latter two events. The balance of evidence suggests that the relative abundance of *D. glynnii* on these reefs prior to 1982 to 1983 was extremely low, likely accompanied (and perhaps driven by) a relatively high abundance of type 3 *Pocillopora*, which together rendered these reefs vulnerable to high-temperature stress.

Given the increasing prevalence of *D. glynnii* colonies after bleaching, we anticipate that this symbiont would become predominant in pocilloporid reefs as heat stress events grow in frequency and intensity. These symbiont changes would likely increase the bleaching threshold of the reef and could delay the time at which unsustainable heat stress levels will be reached (32, 33, 54). To explore this scenario, we incorporated two additional thresholds for DHW accumulation based on the higher thermotolerance expected for *D. glynnii* [e.g., maximum monthly mean (MMM) + 2.5 °C and MMM + 2.25 °C compared with MMM + 1 °C], rather than defining different DHW thresholds at which resistant vs. sensitive taxa are affected (e.g., >15 DHW vs. >5 DHW). Indeed, because reef communities comprise diverse taxa with varied thermal tolerance, characterizing the magnitude of thermal stress at a particular site in terms of a single DHW value can be problematic for rapidly changing reefs because it assumes a single bleaching threshold. We therefore avoided treating our site of interest as being characterized by a certain DHW and instead used the DHW metric to refer to the amount of thermal stress experienced by the organism(s) of interest (in this case holobiont combinations). Such considerations may improve our ability to detect or model adaptive or compensatory responses into future conditions. It is important to note, however, that exact present and future bleaching thresholds for the *Pocillopora* + *D. glynnii* holobionts remain uncertain, and caution should be taken when projecting trajectories of future coral cover.

Because of the high dominance of *Pocillopora* spp. in the ETP, the mechanisms for increased heat tolerance described here likely apply to other coral reefs throughout this region. The milder bleaching responses after the 1997 to 1998 heatwave in reefs from Ecuador, Costa Rica, and Colombia, which had previously experienced widespread bleaching and mortality in 1982 to 1983 (23–25), support the generality of increased heat tolerance in the ETP. However, different hydrographic conditions are likely to lead to differential persistence of acquired heat tolerance following a bleaching event. For example, ETP locations with colder water temperatures (e.g., Baja California and The Galapagos Islands) or that experience seasonal upwelling (e.g., Gulf of Panama and Bahia Salinas) (50) might be more likely to reverse to algal communities that are dominated by *Cladocopium* (52, 55), and have sometimes escaped exposure to previous heatwaves (56). Although the resulting differences in the current prevalence of *D. glynnii* among pocilloporid ETP reefs could lead to differences in the present-day heat tolerance in different locations, under future warmer ocean temperatures an increasing number of reefs are likely to experience conditions favorable for *D. glynnii* proliferation.

Concluding Remarks. The future of coral reefs in the ETP largely depends on the capacity of *Pocillopora* populations to persist and sustain reef accretion under rapid climate change. Until now, most ETP reefs have been resilient to strong El Niño disturbances, exhibiting recovery of coral cover after massive mortality, as well as higher resistance to heat stress during the last warming events (9, 11). This pattern contrasts with regional declining trends in coral cover in the Caribbean (57), the Indo-Pacific (58), and the Great Barrier Reef (59). Although multiple mechanisms likely contribute to resilience in ETP reefs (e.g., healthy herbivore populations, dominance of fast-growing coral species, isolation from other anthropogenic disturbances, selection of resistant host genotypes) (11, 41), our results suggest that the acquisition of thermotolerant algal symbionts by *Pocillopora* type 1, as well as the selection of colonies hosting this symbiont, have likely played a dominant role in increasing tolerance to temperature disturbances and allowing these framework-builders to maintain reef structures that have retained stable coral cover over the latest El Niño-related marine heatwaves. Moreover, based on relatively modest bleaching and mortality following the last two heatwaves, these changes appear to have primed these reefs to be more thermotolerant to future heat disturbance. Even under worst-case emissions scenarios (SSP5-8.5), pocilloporid ETP reefs hosting thermotolerant *D. glynnii* may be able to persist with high levels of coral cover well into the second half of the current century, indicating that some reef systems may be more resilient to warming than previously thought, and suggesting that the winnowing of reef communities to a few resilient species might be a common fate for some reefs. However, although the low-diversity, high-cover reefs of the ETP may illustrate a potential ecological state for some future reefs, this state may only be temporary unless global greenhouse gas emissions and resultant global warming are curtailed.

Methods

Study Sites. We collected and compiled data from three different sites in the Gulf of Chiriquí, on the Pacific coast of Panama: Uva Island reef (7.815°N, −81.759°W), Secas Island reef (7.95205°N, −82.01118°W), and Canal de Afuera Island reef (7.69595°N, −81.63296°W). However, the most complete dataset was available from Uva Island, with data collection starting in the early 1970s (60).

Temperature Conditions and Accumulated Heat Stress (1981 to 2018). The DHW index (29, 61) was used to compare cumulative heat stress at Uva Island reef during the 1982 to 1983, 1997 to 1998, and 2015 to 2016 El Niño events. The raster package (62) for R was used to extract daily SST data for the 1981 to 2016 period from the NOAA high-resolution Optimal Interpolated SST v2 (OI-SST) product (NOAA/OAR/ESRL PSD, Boulder, Colorado, USA; https://www.esrl.noaa.gov/psd). The climatology for the closest pixel to the reef (7.875°N, 81.875°W) was calculated using OISST data from 1985 to 2012, and from this, the MMM temperature for that time period was extracted (29.16 °C). Daily HotSpot values were obtained for each El Niño period (1982 to 1983, 1997 to 1998, and 2015 to 2016) by subtracting the MMM from the daily SST (HotSpots = SST−MMM, when SST > MMM). Finally, the DHW index was calculated as the rolling sum of all the HotSpots > 1 °C over the previous 84 d, divided by 7 (to convert degree heating days to DHW) (63). The OI-SST data set was chosen over other temperature sources because it covers all the very strong El Niño events, including the 1982 to 1983 event, and because the DHW calculated using OI-SST correlated well with DHW calculated using available in-situ temperature from 2014 to 2016 ($R^2 = 0.9$), suggesting that OISST can be used to accurately describe the relative level of heat stress at our specific locations during the three El Niño (See ESM and *SI Appendix*, Figs. S6 and S7 for comparison with other temperature sources).

Changes in Coral Cover (1980 to 2018). Live coral cover data were obtained from three areas at Uva Island reef that have been repeatedly sampled over time. Permanent plots were established in the 1970s and 1980s prior to, and after, the 1982–83 El Niño thermal bleaching and mass mortality event by one of us (PWG) and R.H. Richmond, and have been repeatedly surveyed by PWG or those directly trained by him (11, 22, 23, 60, 64, 65). Three data types exist: chain-transects, 1 m^2 quadrats, and a 4 m × 5 m plot. The chain-transect dataset consists of 10 m long transects (n = 10) monitored from 1980 to 2018 by recording the benthic composition under each chain link. The 1 m^2 quadrat dataset consists of 1 m^2 quadrats (n = 11) monitored from 1994 to 2018 by drawing and digitalizing the composition of the benthos. The 4 m × 5 m plot is a 20 m^2 area (n = 1) monitored from 1984 to 2018 by drawing and digitalizing the composition of the benthos in individual 1 m^2 quadrats. Coral cover in this plot was estimated (as 77% *Pocillopora*) in 1974, prior to the 1982 to 1983 El Niño thermal stress event [Glynn, 1976 (60)]. *Pocillopora* spp. cover in each dataset was aggregated by calculating the mean cover values per year. These data were then used to test for significant changes in *Pocillopora* cover over time using generalized linear mixed models that included Year as a fixed effect and Data Type as a random effect. Models were run with the nlme 3.1 package (66) for R 3.6.3 (67), and pairwise Tukey-like comparisons between significant effects were performed using the glht function from multcomp v1.4 (68) with multiple comparisons obtained from z-tests (*SI Appendix*, Tables S1–S3). Coral cover by other scleractinian species at Uva Island was minimal (<3.2% of the benthos across all years and datasets; *SI Appendix*, Fig. S1) and therefore it was not included in further data analysis.

In addition to the Uva Island datasets, coral cover data from chain transects established in 2015 on Canal de Afuera reef (n = 6) were used to assess uniformity in the response of another dense *Pocillopora* framework to the 2015 to 2016 El Niño. Data from Secas Island reef (n = 10 chain transects, established in 1980) were also used to test mortality and recovery of non-*Pocillopora* species during all three El Niño events. These datasets were analyzed using the same methods that were used for Uva Island, and are presented in the *SI Appendix*.

Coral Bleaching and Mortality Assessments (1982 to 1983, 1997 to 1998, and 2015 to 2016 El Niño). Coral bleaching and mortality data for Uva Island was collected in March 1983, October 1997, March 1998, August 2014, August 2015 and April 2016 (Fig. 1*A*). The data corresponding to the 1982 to 1983 and 1997 to 1998 heatwaves were compiled from (23, 69, 70) and from PWG's notebooks for these years. Data from 2014, 2015, and 2016 were derived from health assessments of haphazardly chosen individual coral colonies (*SI Appendix*, Table S4). In the health assessments, the percentage of each colony exhibiting stark white bleaching or mortality was recorded. Colonies were classified as affected by thermal stress and bleaching if they exhibited 50% or greater partial mortality or greater than 10% of the surface stark white bleached, following the criteria used for the 1982 to 1983 and 1997 to 1998 analyses (23, 69). Only surveys from <10 m depth were included to reduce the confounding effects of depth on coral bleaching (30). August 2014 data, taken just prior to the 2015 to 2016 marine heatwave, were used to show that partial mortality and bleaching were very low in all coral species before heat stress and, therefore, colonies that exhibited mortality in 2015 to 2016 were responding to heat stress (*SI Appendix*, Fig. S3).

The proportion of affected colonies at each sampling point was calculated using the number of colonies bleached or with partial mortality, divided by the total of colonies surveyed (*SI Appendix*, Table S4). The effects of species and sampling time on the probability of a colony being affected by heat stress were analyzed with a binomial (affected vs. healthy) general linear model that included Year (sampling time), Species, and its interaction (*SI Appendix*, Table S5). This model included data from seven species at Uva Island that had observations across the three El Niño events: *M. intricata*, *P. varians*, *P. clavus*, *P. damicornis*, *P. elegans*, *G. planulata*, and *P. lobata*. Tukey's comparisons among species and years were performed using emmeans and multcomp v1.4 (*SI Appendix*, Tables S6 and S7). Although these tests reflect the comparative response of the different taxa to different heatwaves, the response of a given species across different years should be interpreted considering the specific levels of heat stress which differed among the surveys (Fig. 1*A* and *SI Appendix*, Fig. S3). Additional individual colony assessments from 2015 and 2016 at two other locations in the Gulf of Chiriquí (Canal de Afuera and Secas) were performed using the same methods for Uva surveys and are presented in the *SI Appendix*.

Individual *Pocillopora* Colony Responses to the Latest El Niño Event (2014 to 2016).

Tissue sampling (2014 to 2016). Prior to the 2015 to 2016 El Niño (August 2014), *Pocillopora* colonies (n = 29) at shallow depths (3 to 9 m) that were ≥ 5 m apart were tagged and sampled at Uva Island reef. Colony identification to the species level based on skeletal macromorphology was initially undertaken in the field by a single diver and later verified from pictures by an experienced researcher (PWG; pictures are available in the *SI Appendix*). All the tagged colonies were resampled in August 2015 (middle of the first peak of heat stress), and again in April 2016 (end of the second peak; Fig. 2*A*). The samples were collected by clipping ~1 cm from a branch tip, and preserved by incubating for 90 min at 65 °C in 400 to 800 μL of a solution of 1% sodium dodecyl sulfate (SDS) and deoxyribonucleic acid (DNA) buffer (71). Aliquots (100 μL) from the SDS lysates were used to extract and purify DNA following established procedures (72). Resulting total genomic DNA was used as templates for downstream polymerase chain reaction (PCR) and quantitative PCR (qPCR) assays.

Symbiodiniaceae community dynamics (2014 to 2016). The changes in the composition of the algal symbiont communities (relative abundance of the different Symbiodiniaceae genera) in the tagged *Pocillopora* colonies were assessed with TaqMan-MGB (Life Technologies) quantitative PCR (qPCR) assays. The S/H cell ratio, a metric of algal symbiont cell abundance per coral cell (31), was estimated using qPCRs that targeted the actin gene in *Pocillopora*, *Cladocopium,* and *Durusdinium* (73). The StepOneR repository for R (74) was used to calculate the genus-specific abundance [i.e., *Cladocopium* to host (C/H) cell ratio, and *Durusdinium* to host (D/H) cell ratio] based on the qPCR C_T values of each target. The total S/H cell ratio (Symbiodiniaceae abundance) was then calculated as the sum of all algal genera ratios present in the sample (i.e., total S/H = C/H + D/H), and the proportion of *Durusdinium* in the total community was calculated as [(D/H)/(S/H)]. Changes in the proportion of *Pocillopora* colonies dominated by *Cladocopium* or *Durusdinium* (abundance > 50% of the symbiont community) in 2014 vs. 2016 were assessed with two-tailed Fisher's exact tests of independence.

The changes in symbiont abundance (bleaching) among different sampling times were estimated using mixed linear models with the lmerTest package (75) for R. Total S/H cell ratio, C/H cell ratio, and D/H cell ratio (dependent variables) were compared using models that incorporated the dominant symbiont hosted by each colony (>50% of the algal community) as the explanatory variable (fixed effect), and coral colony as a random effect. Pairwise comparisons for significant models were estimated with emmeans v1.1.3 (76) using the TukeyHSD test (alpha value = 0.05). S/H cell ratios were $\log_{10}$ transformed before statistical testing to reduce the skewness of the data. All calculations and data analyses were performed in R v3.6 (77) and graphs produced with ggplot v3.2.1(78).

Molecular identification of Pocillopora and Cladocopium types (2014). Given the high phenotypic plasticity of *Pocillopora* (48), species identifications using morphology were compared with the mitochondrial lineages of the corals (putative species) obtained by sequencing the ORF region (48, 79). Similarly, because the qPCR assays (previous section) only identify algal symbionts to the genus level, the ribosomal ITS2 was used to determine the specific ITS2 *Cladocopium* types hosted by *Pocillopora* (80). While only one *Durusdinium* species (*D. glynnii*) is reported for *Pocillopora* from the ETP (81), *Pocillopora* colonies in the Gulf of Chiriquí are known to associate with different *Cladocopium* types; *Pocillopora* type 1 with *C. latusorum* (formerly C1b-c), and *Pocillopora* type 3 with *C. pacificum* (formerly C1d) (39, 82). PCR methods followed (79) for ORF and (80) for ITS2, and are described in detail in the ESM.

Mechanisms Involved in *D. Glynnii* Prevalence Changes Following Heat Stress.

The proportion of colonies that experienced mortality (>95% tissue loss) and/or changes in the dominant algal symbiont (shuffling) in the studied corals during 2014 to 2016 (*SI Appendix*, Table S9) were used to estimate the potential role of symbiont shuffling during the 1997 to 1998 heatwave (10). This approach was taken because the samples collected before (1995), during (1997), and after (2001) this heatwave did not follow tagged colonies and therefore the relative changes in the dominant symbionts could respond to selective mortality as well as symbiont shuffling (10).

Based on the 2014 to 2016 data from tagged colonies, ~46.7% (7 of 15) of the *Cladocopium*-colonies in 2014 experienced mortality by 2016 (>95% loss of the coral tissue) and ~40.0% (6 of 15) shuffled to host communities dominated by *D. glynnii*. The remaining 13.3% (2 of 15) survived and maintained *Cladocopium* communities. Three of the seven initially *Cladocopium* colonies that experienced mortality had also increased the proportion of *D. glynnii* by 2016 and became dominated by this algal symbiont. However, since our data only reflect a snapshot of these colonies before and during heat stress, we cannot assess if shuffling or mortality occurred first. To simplify the application of these proportions in colonies that experienced both shuffling and mortality, we first apply the effects of colony mortality (46.7% of the initially *Cladocopium* colonies, regardless if they later acquired or not *D. glynnii*) and then divided the surviving colonies between shuffling and not shuffling. Following these same rules, obtained that there was no mortality (defined as >95% of the tissue loss) in any of the colonies that predominantly hosted *D. glynnii* in 2014 (0 of 14), and therefore mortality probability for *D. glynnii* colonies was defined as zero under ~8 DHW. This implies that the mortality of the three colonies dominated by *D. glynnii* in 2016 (but that originally hosted *Cladocopium*) was included as *Cladocopium* mortality. There was no symbiont shuffling in any of the colonies that predominantly hosted

D. glynnii in 2014 (0 of 14) since none of them became dominated by *Cladocopium* during 2014 to 2016.

We then used the loss of *Pocillopora* cover between 1997 and 1998 (~16.2% cover reduction) and the assumption that this cover loss could be first assigned to mortality of *Cladocopium*-colonies (given the observed 0% mortality in *Durusdinium* colonies in 2014 to 2016) to estimate the changes in *Durusdinium* vs. *Cladocopium* prevalence that can be expected to occur as a consequence of the differential mortality. Following this, the expected *D. glynnii* prevalence after cover loss (16.2%) was estimated as the percentage of *D. glynnii* before bleaching (in 1995) minus expected mortality in *D. glynnii* (0%), over the relative percentage of surviving coral cover (100% before bleaching − % of relative coral cover loss after bleaching). Similarly, expected *Cladocopium* prevalence after selective mortality was estimated as the *Cladocopium* percentage before bleaching, minus the expected mortality in *Cladocopium* (% of relative coral cover loss after bleaching), over the percentage of surviving coral cover (i.e., 100% before bleaching − % of relative coral cover loss after bleaching). Then, we estimated the difference between the expected *D. glynnii* and *Cladocopium* prevalence (derived from the differential mortality) and the observed (measured by colony sampling) *D. glynnii* vs. *Cladocopium* proportions after heat stress (1998). The differences between the expected and observed proportions are then allocated to potential symbiont shuffling. The data and calculations associated with these estimations are included in the Dataset S1.

Projected Heat Stress and *Pocillopora* Cover Response (2018 to 2100). DHW projections for Uva Island were obtained using the new generation of climate models used by the IPCC (CMIP6) forced with emissions from SSPs (83). We used the SST data from the SSP5-8.5 pathway to calculate DHWs for each year between 2018 and 2100. DHWs were estimated as summed anomalies above the bleaching threshold (MMM + 1 °C) from the CoralTemp v3.1 (CRW) climatology for every 3-mo period. This method follows a more conservative approach from van Hooidonk et al. (84), where instead of summing all anomalies above the MMM, we only consider anomalies above the bleaching threshold (MMM + 1 °C). This approach results in lower DHWs values and is more compatible with our estimations of DHW during the El Niño events, which were calculated with anomalies above MMM + 1 °C. Although the SSP5-8.5 represents the worst-case scenario used for climate simulations, this pathway better resembles the historical and anticipated future total CO_2 emissions, at least to 2050 (85, 86). On a global average, the use of the more optimistic SSP2-4.5 pathway only delays the onset of annual severe bleaching conditions (ASB, the annual exceedance of >8 DHW) by ~11 y (84).

In order to account for a potential increase in *Pocillopora* bleaching tolerance when they host *D. glynnii*, adjusted DHWs for this holobiont were recalculated introducing 1.25 and 1.5 °C increments in the bleaching threshold. These estimates were based on the higher bleaching thresholds reported for other coral species when they associate with thermotolerant symbionts (32, 52). General methods for DHW calculations and temperature sources were maintained the same, except for the bleaching thresholds, now adjusted to be 1) MMM + 1 °C + 1.25 °C and 2) MMM + 1 °C + 1.5 °C. These adjusted DHWs intend to forecast when pocilloporid reefs composed by *D. glynnii*-dominated colonies might start experiencing significant levels of heat stress (e.g., >4 to 8 DHWs) even for holobionts with higher thermotolerance.

All links to the repositories, including data and code for the data analyses, are in the supplementary material.

Data, Materials, and Software Availability. Datasets and code are available at Zenodo for the temperature and heat stress analyses (87), coral cover and bleaching analyses (88), and Symbiodiniaceae dynamics during 2014 - 2016 (89). Additional study data are included in the article and/or *SI Appendix*.

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Author affiliations: [a]Department of Marine Biology and Ecology, Rosenstiel School of Marine, Atmospheric, and Earth Science, University of Miami, Miami, FL 33149; [b]Cooperative Institute for Marine and Atmospheric Studies, Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, FL 33149; [c]NOAA Atlantic Oceanographic and Meteorological Laboratory, Ocean Chemistry and Ecosystems Division, Miami, FL 33149; [d]Coral Reefs Research, Reefs Unknown, Saint Thomas, US Virgin Islands 00802; [e]Smithsonian Tropical Research Institute, Balboa, Ancon 0843-03092, Panama; [f]Coral Reef Watch, Center for Satellite Applications and Research, Satellite Oceanography & Climatology Division, U.S. National Oceanic and Atmospheric Administration, MD 20740; and [g]Department of Ecology and Evolutionary Biology, University of California Los Angeles, Los Angeles, CA 90095

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