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 (ENSO) 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 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.

these two algal symbionts (n = 2; Fig. S5). More sensitive quantification of the relative abundance of each symbiont genus (i.e., *Cladocopium* and *Durusdinium*) using real-time 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. 3a), 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. 3b). After the second peak of heat stress in April 2016 (Fig. 3a) 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. 3b). 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 3c). Conversely, none of the *Pocillopora* type 3 acquired *D. glynnii* during 2015 or 2016 (Fig. 3b). By April 2016 four type 3 colonies had experienced almost complete mortality (> 95% tissue loss) and one experienced partial mortality (< 95% tissue loss; Fig. 3c and 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 2 showed almost complete mortality), contributed to increase the frequency of *Pocillopora* colonies that hosted *D. glynnii* after the 2015-16 heatwave (Fig. 3b-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. 3c). 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* (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

these non-pocilloporid 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 = 3-10), 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 non-pocilloporid 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 to 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 to 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 of cold and nutrient-rich water, high turbidity, or depressed aragonite saturation states (50).

During the 2015-16 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 versus heat bleaching (17, 28, 51), variations in the severity of the bleaching stress (27), or warmer recovering temperatures during the 2015-16 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 2015-16 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 2014-16, we also estimated that selective mortality alone is unlikely to fully explain the changes in *Pocillopora* algal communities recorded during the 1997-98 heatwave (10). Indeed, our results from 2014-16 and estimations of the symbiont dynamics during 1997-98 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 1982-83 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 1982-83 event points to a naive coral assemblage dominated by *Cladocopium,* especially since the magnitude of the 1982-83 event was similar or less than the subsequent two events (7.6 DHW compared to 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 1982-83 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., MMM + 2.5°C and MMM + 2.25°C compared to 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 1997-98 heatwave in reefs from Ecuador, Costa Rica, and Colombia, which had previously experienced widespread bleaching and mortality in 1982-83 (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 (1981-2018)

The DHW index (29, 61) was used to compare cumulative heat stress at Uva Island reef during the 1982-83, 1997-98, and 2015-16 El Niño events. The raster package (62) for R was used to extract daily sea surface temperature (SST) data for the 1981-2016 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 1985-2012, and from this, the maximum monthly mean (MMM) temperature for that time period was extracted (29.16 ºC). Daily HotSpot values were obtained for each El Niño period (1982-83, 1997-98, and 2015-16) 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 ºC over the previous 84 days, 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 1982-83 event, and because the DHW calculated using OI-SST correlated well with DHW calculated using available *in-situ* temperature from 2014-2016 (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 Figs. S6-S7 for comparison with other temperature sources).

Changes in coral cover (1980-2018)

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 4m x 5m plot. The chain-transect dataset consists of 10m 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 4m x 5m 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 1982-83 El Niño thermal stress event (Glynn 1976). *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 (Tables S1-S3). Coral cover by other scleractinian species at Uva Island was minimal (< 3.2% of the benthos across all years and datasets; 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 2015-16 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 supplementary information.

Coral bleaching and mortality assessments (1982-83, 1997-98, and 2015-16 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. 1a). The data corresponding to the 1982-83 and 1997-98 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 (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 1982-83 and 1997-98 analyses (23, 69). Only surveys from < 10m depth were included to reduce the confounding effects of depth on coral bleaching (30). August 2014 data, taken just prior to the 2015-16 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 2015-16 were responding to heat stress (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 (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 versus healthy) general linear model that included Year (sampling time), Species, and its interaction (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 (Tables S6-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. 1a, 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 supplementary information.

Individual Pocillopora *colony responses to the latest El Niño event (2014-2016)*

Tissue sampling (2014-2016): Prior to the 2015-16 El Niño (August 2014), *Pocillopora* colonies (n = 29) at shallow depths (3 - 9 m) that were ≥ 5m 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 supplementary material). 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. 2a). The samples were collected by clipping ~1 cm from a branch tip, and preserved by incubating for 90 min at 65°C in 400-800 µL of a solution of 1% SDS and 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 PCR and real-time PCR (qPCR) assays.

Symbiodiniaceae community dynamics (2014-2016): 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) real-time PCR (qPCR) assays. The symbiont-to-host 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 versus 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). Symbiont-to-host 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 open reading frame (ORF) region (48, 79). Similarly, because the qPCR assays (previous section) only identify algal symbionts to the genus level, the ribosomal internal transcribed spacer 2 (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 2014-16 (Table S9) were used to estimate the potential role of symbiont shuffling during the 1997-98 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 2014-16 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 7 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 reflects 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 3 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 2014-16.

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 2014-16) 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

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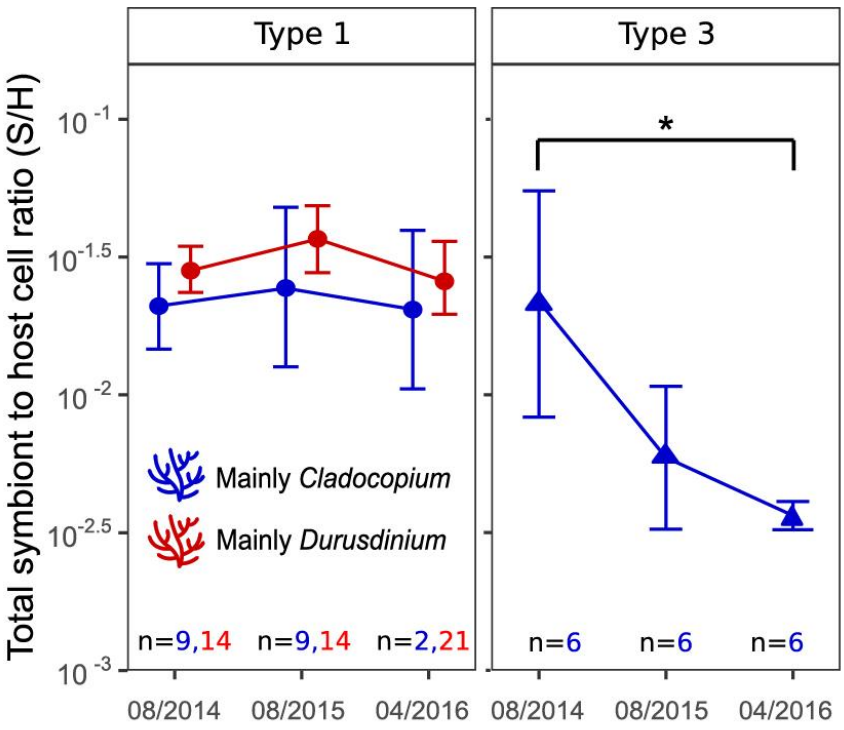

Figure 4. Algal symbiont abundance (mean S/H ± 95% confidence intervals) in *Pocillopora* colonies sampled before and during the 2015-16 El Niño. Only *Pocillopora* type 3 had significant reductions in total S/H cell ratio with respect to its values in 2014 ($p < 0.05$). Colors in each panel represent 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.

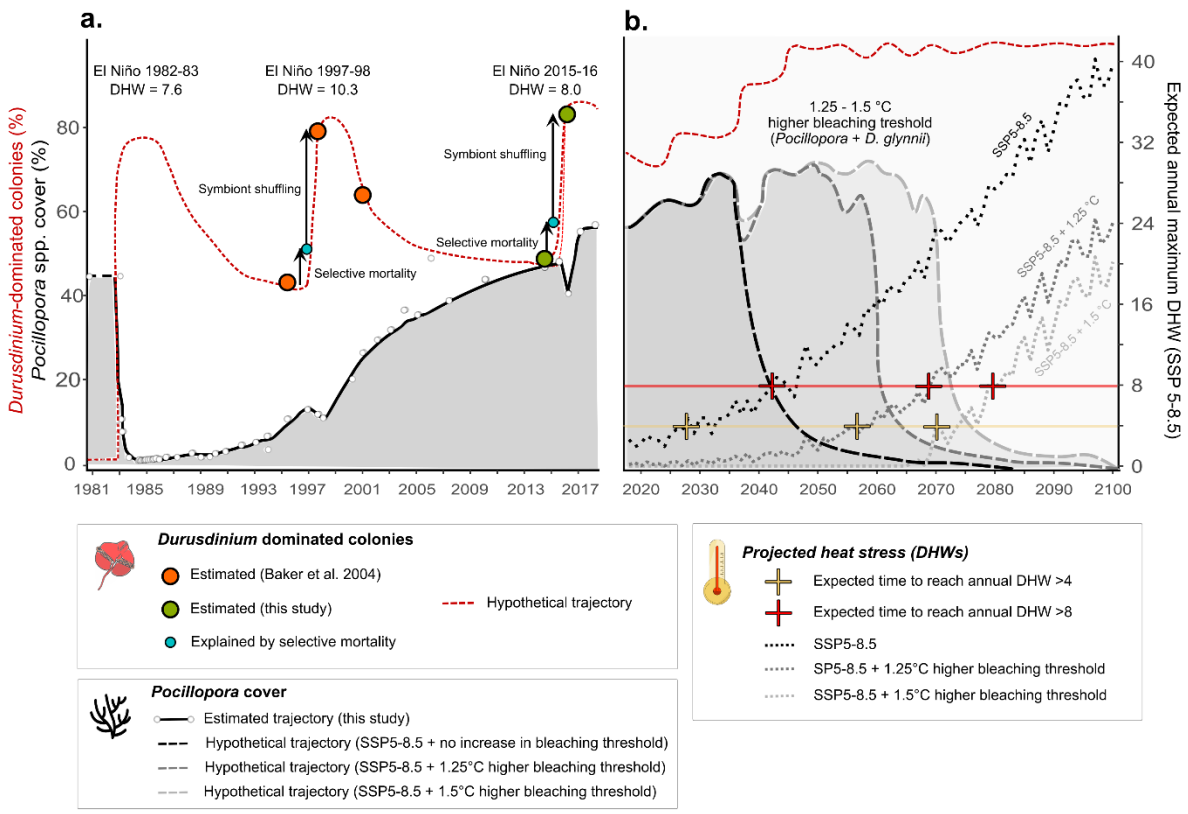

Figure 5. Conceptual model of *Pocillopora* spp. cover and *D. glynnii* prevalence under repeated heat stress (DHW). **a.** Observed and hypothesized changes in *Pocillopora* spp. cover and *D. glynnii* prevalence during the 1982-83, 1997-98 and 2015-16 El Niño heatwaves at Uva Island reef. The orange 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 1997-98 and 2016-16 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 4 and 8 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.