Worldwide reef surveys highlight different adaptive responses to heat between coral taxa

Oliver Selmoni[1], Gaël Lecellier[2,3], Véronique Berteaux-Lecellier[2], Stéphane Joost[1]

1- Laboratory of Geographic Information Systems (LASIG), School of Architecture, Civil and Environmental Engineering (ENAC), Ecole Polytechnique Fédérale de Lausanne (EPFL), Lausanne, Switzerland

2- UMR250/9220 ENTROPIE IRD-CNRS-Ifremer-UNC-UR, Labex CORAIL, Nouméa, New Caledonia

3- Université Paris-Saclay, UVSQ, Versailles, France

Contact information: Dr Stéphane Joost, stephane.joost@epfl.ch

Abstract

Coral reefs around the world are under threat due to widespread decline of hard corals caused by anomalous heat waves. Coral taxa of different morphologies are known to have different sensitivities to heat stress. However, little is known about how long-term effects of heat exposure differ between coral taxa, nor in particular how such effects might drive adaptive processes.

Here, we combined worldwide reef survey data with remotely sensed thermal anomalies to evaluate how local rates of taxa-specific coral cover were associated with heat stress. We found a negative association between coral cover and heat stress, where associations were weaker for corals with boulder-like morphology (massive corals), intermediate for corals with arborescent morphology (branching corals) and stronger for corals with encrusting or laminar morphology (plating corals). Additionally, we found that the negative association between branching coral cover and recent exposure to heat stress (measured as the year before a survey) was mitigated by the effect of long-term heat stress (measured since 1985), suggesting that adaptive processes occurred. In contrast, this "mitigating effect" of past heat-stress was not observed for either massive or plating corals.

We hypothesize that these different responses to recent and past heat stress mirror different life history traits of coral taxa. For instance, branching corals are known to show higher sensitivities to heat stress and faster growth rates, two characteristics that might boost adaptive rates via evolutionary processes, when compared with other taxa.

The results of this work suggest that all coral taxa, regardless of their morphology, will be "losers" of coral bleaching, and that conservation strategies should be adjusted to match taxa-specific responses to heat stress.

Keywords

Coral reef – coral bleaching – global warming – heat stress – adaptation – remote sensing – life history traits

Introduction

Over the past 30 years, coral reefs around the world have been suffering from a widespread decline of hard corals (Ateweberhan, McClanahan, Graham, & Sheppard, 2011; Cramer et al., 2020; De'ath, Fabricius, Sweatman, & Puotinen, 2012). This decline threatens the persistence of the entire coral reef ecosystem, as hard corals constitute the physical architecture of these habitats (Pratchett, Thompson, Hoey, Cowman, & Wilson, 2018). A leading cause of this decline is coral bleaching, a stress response driven by heat stress that causes corals to separate from the symbiotic algae living in their tissues (van Oppen & Lough, 2009). When persisting over several weeks, a bleaching state will eventually lead to starvation of coral (Diaz-Pulido & McCook, 2002). By now, extensive reef deterioration following anomalous heat waves have been observed at a global extent, with reports of local loss of coral cover (i.e. the percentage of the reef surface covered by live stony coral) up to 50% (Hughes, Anderson, et al., 2018). By 2050, it is expected that coral bleaching conditions will become persistent worldwide (Van Hooidonk, Maynard, & Planes, 2013).

The sensitivity to bleaching varies between coral species (Loya et al., 2001). Indeed, corals with an arborescent morphology (hereafter referred to as branching corals) are considered to be more sensitive to heat stress than corals with a laminar or an encrusting morphology (hereafter referred to as plating corals) and corals with a boulder-like morphology (hereafter referred to as massive corals; van Woesik, Sakai, Ganase, & Loya, 2011). Part of these differences in thermal susceptibility mirror differences in morphological features that modulate resistance to bleaching and thermal stress, such as the thickness of the tissues and the size of the corallites (the skeletal cups containing individual polyps; Conti-Jerpe et al., 2020; Mydlarz, McGinty, & Harvell, 2010; Robert van Woesik et al., 2012). In contrast, the long-term effects of heat stress exposure are more difficult to assess based on coral morphology alone (van Woesik et al., 2011). This is because differences in life history traits between coral species (such as growth rates and fecundity) are likely to drive different rates of recovery of coral cover after a heat stress event (Darling, Alvarez-Filip, Oliver, McClanahan, & Côté, 2012; Osborne et al., 2017).

Substantial differences in heat tolerance can also be observed between corals from the same species (Bay & Palumbi, 2014; Schoepf, Stat, Falter, & McCulloch, 2015). Such tolerance can be the result of adaptive processes driven by previous exposure to thermal stress (Hughes et al., 2019). These adaptive processes can occur at two levels: (1) at the physiological level (acclimatization), when a colony temporarily adjusts its metabolism to cope with the stressful condition; and (2) at the genetic level (evolutionary adaptation), when the repeated exposure to stress selects the individuals of a population that carry the genetic traits conferring increased tolerance (Palumbi, Barshis, Traylor-Knowles, & Bay, 2014). Understanding how these adaptive processes contribute to increased heat tolerance in different coral species is of paramount importance in order to organize effective conservation efforts (Matz, Treml, & Haller, 2020; Schoepf et al., 2019).

Over the last decade, the combination of field survey records with remote sensed data for sea surface temperature has become one of the main tools used to measure coral decline driven by heat stress. Multiple studies have shown associations between heat stress events and coral cover decline both at local (Babcock et al., 2020; Head et al., 2019; Romero-Torres et al., 2020; Selmoni, Lecellier, Vigliola, Berteaux-Lecellier, & Joost, 2020; Soto, Muller Karger, Hallock, & Hu, 2011) and global scales (Selig, Casey, & Bruno, 2012). In other studies, the metric of bleaching intensity was found to be positively associated with heat stress on the

Australian Great Barrier Reef (Hughes et al., 2017, 2019; Hughes, Kerry, et al., 2018), as well as across larger spatial scales (for instance, the Indo-Pacific region; Hughes, Anderson, et al., 2018; McClanahan, Darling, et al., 2020; McClanahan et al., 2019; McClanahan, Maina, et al., 2020; Sully, Burkepile, Donovan, Hodgson, & van Woesik, 2019). Notably, some of these studies investigated how past and recent thermal stress interact to drive coral cover decline/bleaching intensity, suggesting the existence of coral adaptation but without being able to distinguish acclimatization from evolutionary adaptation (Head et al., 2019; Hughes et al., 2019; McClanahan, Maina, et al., 2020; Selmoni, Lecellier, et al., 2020; Sully et al., 2019). Very few of these works focus on the differences in heat stress responses between coral species (Hughes, Kerry, et al., 2018; McClanahan, Darling, et al., 2020), and thus very little information was collected to assess differences in heat stress adaptive potential between coral species.

In this study, we combine global coral cover data obtained from the Catlin Seaview Survey project (González-Rivero et al., 2016, 2014) with time series of sea surface temperature anomalies computed from remote sensing data by the Coral Reef Watch (Skirving et al., 2020). The goal here is to investigate worldwide how coral decline and adaptation may be driven by heat stress in coral taxa with different types of morphologies. We first evaluate how the degree of heat stress experienced by reefs over the past 20 years is associated with local differences in coral cover. These differences concern (1) overall coral cover rates, (2) a diversity index derived from taxa-specific coral cover rates and (3) coral cover rates of three groups of coral taxa based on morphology: branching, plating and massive. Next, we assess how such rates of coral cover and diversity driven by recent heat stress (measured across the year before the survey) are modulated (i.e. accentuated or mitigated) either by short-term heat stress (measured across the two previous years) or long-term heat stress exposure (measured across more than 20 previous years). We hypothesize taxa-specific responses to heat stress mirror the differences in heat tolerance and the potential for evolutionary adaptation determined by distinct life history traits.

Material and methods

Coral cover data

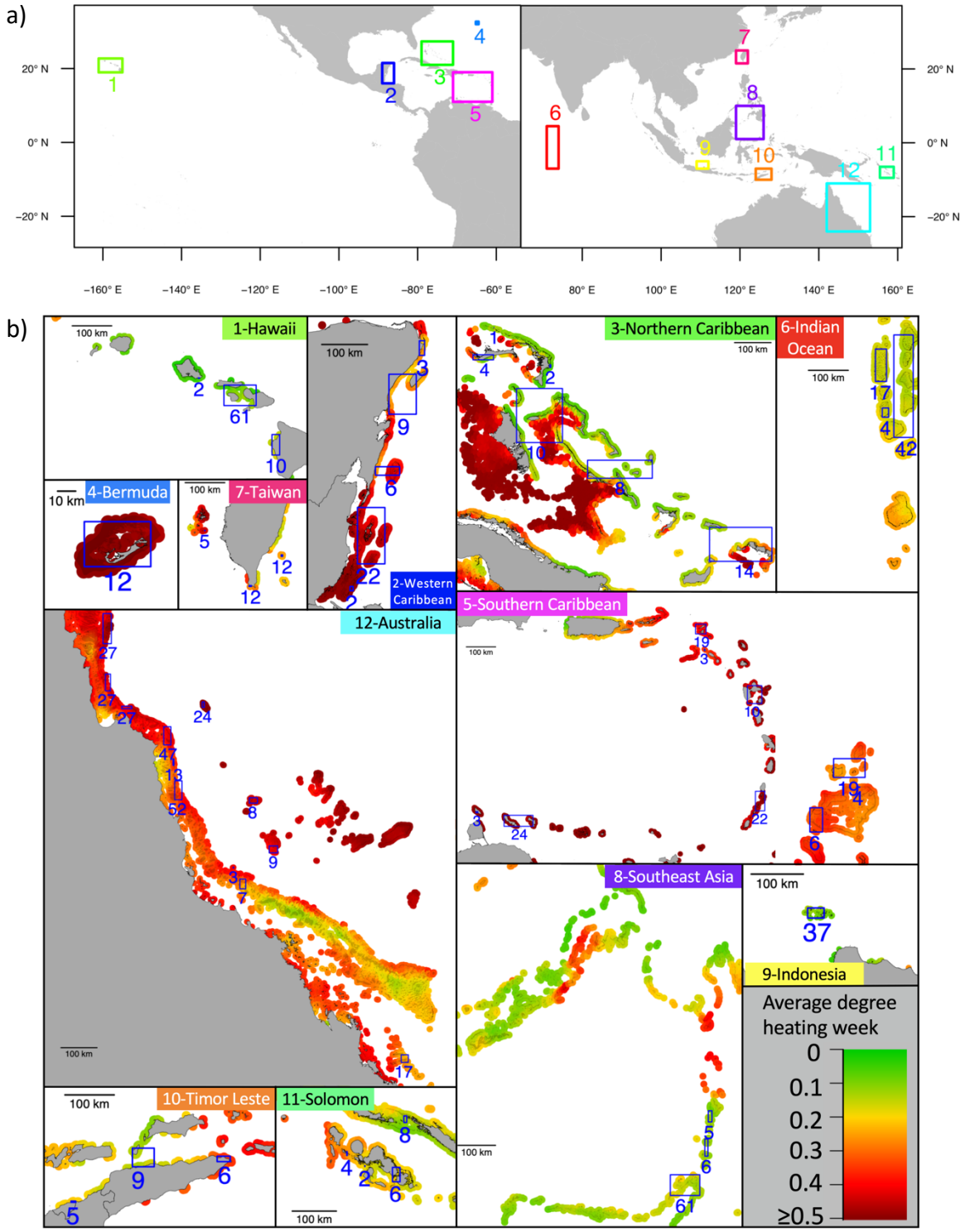
The coral cover data were obtained from the Catlin Seaview Survey (CSS) project (González-Rivero et al., 2016, 2014). When we accessed the data in January 2021, there were a total of 860 surveys performed along 579 transects (380 transects visited one time, 140 two times, 36 three times, and 23 four times) across twelve study areas around the world between 2012 and 2018 (Fig. 1a). The CSS project applied the same standardized framework to each survey when recording and analyzing field data. First, field surveys were performed using an underwater 360° camera that took a picture every three seconds along a 1.6-2 km transect, maintaining a constant depth of 10 meters. Next, field pictures were processed using automated image recognition based on machine learning algorithms. Such algorithms were trained using labels that were manually annotated by coral taxonomists (Beijbom, Edmunds, Kline, Mitchell, & Kriegman, 2012).

For each reef survey, the CSS data provided (1) the overall measure of hard coral cover rates and (2) the coral cover rates for 78 groups of corals labelled using visual characteristics (for instance "*Acropora* corymbose/tabular/plate", "*Porites*" or "*Pocilloporidae*"). Since coral species differ between regions, only part of these 78 labels were observed in each of the different study areas. We therefore manually created broader groups of corals based on morphology to facilitate comparability between study areas. This was done in three steps. First, we retrieved the CSS metadata showing the list of species for each of the 78 coral labels. Second, we consulted the Coral Trait Database (Madin et al., 2016) to determine morphology (according to Veron, 2000) of the species in each label group. Third, we established three broader groups of corals based on morphology: branching (including coral morphologies "branching", "digitate", "corymbose" and "tabular"), plating ("encrusting" and "laminar") and massive ("massive" and "sub-massive"). For each of these broad groups of coral morphologies (hereafter referred to as coral taxa), we computed the average hard coral cover for each survey using a custom script (see "Data and code availability" section) in the R environment (v. 3.5.1; R Core Team, 2021).

Diversity index

The CSS coral cover data of the 78 coral labels were used to compute the Simpson's diversity index (Simpson, 1949) of each survey. For each study area, we first excluded the coral labels that were not observed in any of the surveys (*i.e.,* average coral cover equal to 0). Next, the coral cover of the retained labels were used to compute the Simpson diversity index for each survey using the "diversity" function of the VEGAN R package (v. 2.5; Oksanen et al., 2019). Note that VEGAN returns the diversity index as 1-(Simpson's diversity), so that higher values (i.e. towards 1) correspond to higher diversity.

Figure 1. The study regions. a) Distribution of the twelve study regions. b) For each study region, the map shows the average Degree Heating Week (DHW) values for the 1985-2020 period. The blue squares indicate areas were coral cover surveys from the Catlin Seaview Surveys project were performed, with the numbers corresponding to the number of surveys per area. The reef surfaces were derived from the "Global Distribution of Coral Reefs" dataset of the UNEP (UNEP-WCMC, WorldFish-Center, WRI, & TNC, 2021)



Heat stress data

The heat stress data were retrieved from the Coral Reef Watch database, as part of the 5km-resolution sea surface temperature products (Skirving et al., 2020). The variable we used to describe heat stress was the Degree Heating Week (DHW, Fig. 1b), as it has been shown to be directly correlated with coral bleaching occurrence and severity (Kayanne, 2017; G. Liu et al., 2014; McClanahan et al., 2019). For a given day, DHW is calculated as the sum of the temperature hotspots (that is, temperatures that exceeded by 1°C the maximal monthly average) from the preceding 12-weeks period. We used the CSS metadata to retrieve the coordinates of every survey location (at the mid-point of the transects), and extracted the daily DHW from 1985 to 2020 for each coordinate using the RASTER R package (v. 3.0; Hijmans, 2016). We discarded 82 surveys for which DHW values could not be extracted due to coordinates located on pixels adjacent to the coastline. In total, we extracted daily DHW values for 778 surveys.

For each reef survey, we computed five different metrics of average DHW (Fig. 2). The first metric represents recent heat stress ($\overline{DHW}_{1yr}$) and is calculated as the average DHW during the year that preceded the survey date (Fig. 2a). Similarly, we computed an estimation of past heat stress as the average DHW across the 10 years ($\overline{DHW}_{10yrs}$; Fig. 2b) and the 20 years ($\overline{DHW}_{20yrs}$; Fig. 2c) that preceded the survey. Additionally, we computed two metrics of past heat stress which excluded the first year before the sampling date. The first of these metrics covers the previous two years ($\overline{DHW}_{1-3yrs}$; Fig. 2d), while the second covers all of the previous years ($\overline{DHW}_{>1yr}$; Fig. 2e). These two variables were developed as estimators of past heat stress that do not overlap with recent heat stress ($\overline{DHW}_{1yr}$), so that they could be used in bi-variate model construction (see the "Statistical analysis" section).

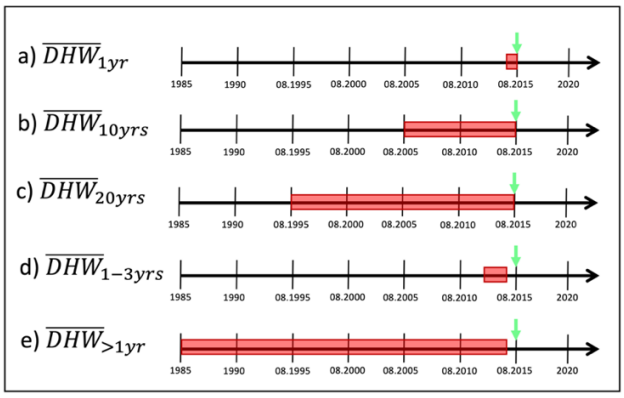


Figure 2. Degree heating week (DHW) time series averages. The figure displays the differences in the calculation of the five DHW averages used in this study. The green arrows indicate a hypothetical date for the coral cover survey, and the red boxes show the periods of interest for the calculation of average DHW with the different methods.

Statistical analysis

Previous studies have employed repeated measures of coral cover over time to determine the trends of coral growth or decline, and then used statistical analyses to match these trends with sea surface temperature data (Babcock et al., 2020; Head et al., 2019; Selig et al., 2012; Soto et al., 2011). This approach is not transposable to the CSS dataset, as most of the transects were surveyed only once. For this reason, we employed a different method to investigate how local differences in coral cover rates were associated with historical patterns of heat stress measured at the survey sites.

In practice, we investigated the association between coral cover rates and heat stress using generalized linear mixed-models (GLMMs), where the random factors controlled for spatial autocorrelation between survey sites (Dormann et al., 2007). We employed four levels of random factors representing spatial autocorrelation at different spatial scales and progressively nested into each other (*i.e.* the factors covering smaller spatial scales were nested into those covering larger spatial scales). The first two random factors were:

1) the oceanic regions as defined by the CSS metadata (five levels: Australia, Southeast Asia, Pacific, Atlantic and Indian Ocean);
2) the study areas (twelve levels, Fig. 1a);

We designed additional random factors to control for spatial autocorrelation at a local scale (within each study area). This was done by applying the following clustering approach in the R environment. First, we computed the Euclidean distances between surveys sites, and applied a hierarchical clustering using the Ward distance method. The result was a tree of distances between survey sites that was used to compute the two additional random factors (3 and 4):

3) survey sites located up to 100 km from each other;
4) survey sites located up to 7 km from each other.

The two threshold values (100 km and 7 km) used in the clustering procedure were chosen as they corresponded to the average value and the minimal value, respectively, of the mean Euclidean distances measured between survey sites within each study area.

GLMMs were built using the GLMMTMB R package (v. 1.0; Brooks et al., 2017). We investigated five response variables recorded at each survey site: overall coral cover (Fig. 3a), Simpson's Diversity (Fig. 3b), coral cover of branching corals (Fig. 3c), coral cover of plating corals (Fig. 3d) and coral cover of massive corals (Fig. 3e). As the values of these variables are rates

between 0 and 1, we used the beta regression method to model their response (Ferrari & Cribari-Neto, 2004). The five explanatory variables were the DHW averages (Fig. 2) described in the "Heat stress data" section: $\overline{DHW}_{1yr}$ (Fig. 3f), $\overline{DHW}_{10yrs}$ (Fig. 3g), $\overline{DHW}_{20yrs}$ (Fig. 3h), $\overline{DHW}_{1-3yrs}$ (Fig. 3i), and $\overline{DHW}_{>1yr}$ (Fig. 3l).

We ran the analysis for two types of GLMMs: univariate and bi-variate (Table 1). In univariate GLMMs, we investigated the association of each of the five response variables with either $\overline{DHW}_{1yr}$, $\overline{DHW}_{10yrs}$ or $\overline{DHW}_{20yrs}$. The goal was to evaluate how local patterns of coral cover and diversity can be explained by recent and past heat stress.

For each of the five response variables, two bi-variate GLMMs were computed. The first investigated the association of the response variable with (1) $\overline{DHW}_{1yr}$ and (2) the interaction between $\overline{DHW}_{1yr}$ and $\overline{DHW}_{1-3yrs}$, while the second model employed (1) $\overline{DHW}_{1yr}$ and (2) the interaction between $\overline{DHW}_{1yr}$ and $\overline{DHW}_{>1yr}$ as explanatory variables. The goal of these bi-variate models was to evaluate how past heat stress (measured on the short-term for the first model, and on the long-term for the second) modulates (i.e. accentuates or mitigates) the effect of recent heat stress on coral cover and diversity.

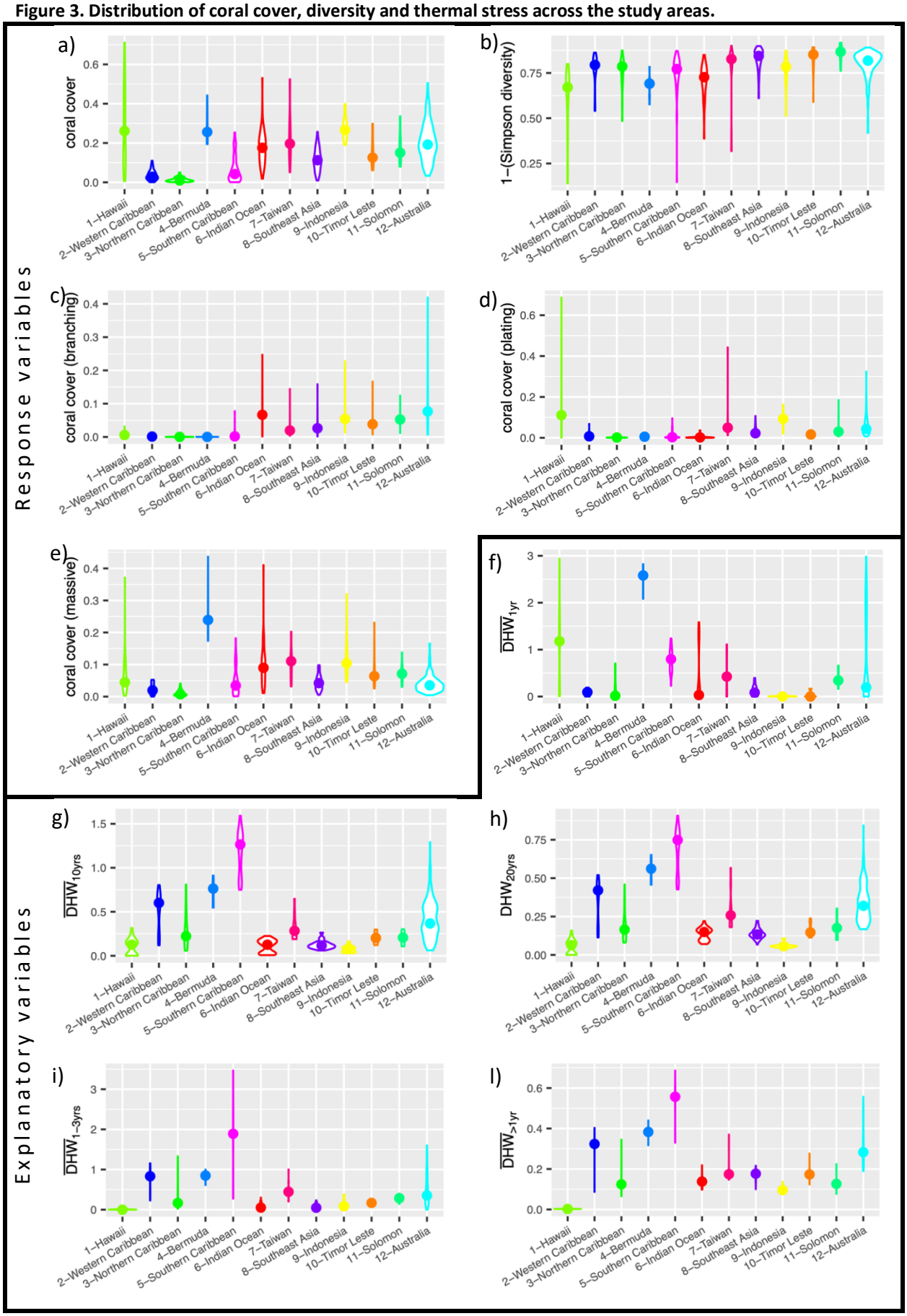
Table 1. List of the models computed. The table displays the formulae of the univariate and bi-variate models computed for every response variable (overall coral cover: $CC_{overall}$, Simpson's diversity: SD, branching coral cover: $CC_{branching}$, plating coral cover: $CC_{plating}$, massive coral cover: $CC_{massive}$). The explanatory variables used in univariate models are the averages of degree heating weak ($\overline{DHW}$) measured during the year ($\overline{DHW}_{1yr}$), the ten years ($\overline{DHW}_{10yrs}$) and the twenty years ($\overline{DHW}_{20yrs}$) before the survey. In bi-variate models, the explanatory variables are (1) $\overline{DHW}_{1yr}$ and (2) the interaction between $\overline{DHW}_{1yr}$ and $\overline{DHW}$ measured during either the two previous years ($\overline{DHW}_{1-3yrs}$) or all the previous years ($\overline{DHW}_{>1yr}$). α indicates the intercept, β the effects of the explanatory variables.

Response variable	Univariate models	Bi-variate models
Overall coral cover	1) $CC_{overall} \sim \alpha + \beta(\overline{DHW}_{1yr})$ 2) $CC_{overall} \sim \alpha + \beta(\overline{DHW}_{10yrs})$ 3) $CC_{overall} \sim \alpha + \beta(\overline{DHW}_{20yrs})$	4) $CC_{overall} \sim \alpha + \beta_1(\overline{DHW}_{1yr}) + \beta_2(\overline{DHW}_{1yr}:\overline{DHW}_{1-3yrs})$ 5) $CC_{overall} \sim \alpha + \beta_1(\overline{DHW}_{1yr}) + \beta_2(\overline{DHW}_{1yr}:\overline{DHW}_{>1yr})$
Simpson's diversity	6) $SD \sim \alpha + \beta(\overline{DHW}_{1yr})$ 7) $SD \sim \alpha + \beta(\overline{DHW}_{10yrs})$ 8) $SD \sim \alpha + \beta(\overline{DHW}_{20yrs})$	9) $SD \sim \alpha + \beta_1(\overline{DHW}_{1yr}) + \beta_2(\overline{DHW}_{1yr}:\overline{DHW}_{1-3yrs})$ 10) $SD \sim \alpha + \beta_1(\overline{DHW}_{1yr}) + \beta_2(\overline{DHW}_{1yr}:\overline{DHW}_{>1yr})$
Branching coral cover	11) $CC_{branching} \sim \alpha + \beta(\overline{DHW}_{1yr})$ 12) $CC_{branching} \sim \alpha + \beta(\overline{DHW}_{10yrs})$ 13) $CC_{branching} \sim \alpha + \beta(\overline{DHW}_{20yrs})$	14) $CC_{branching} \sim \alpha + \beta_1(\overline{DHW}_{1yr}) + \beta_2(\overline{DHW}_{1yr}:\overline{DHW}_{1-3yrs})$ 15) $CC_{branching} \sim \alpha + \beta_1(\overline{DHW}_{1yr}) + \beta_2(\overline{DHW}_{1yr}:\overline{DHW}_{>1yr})$
Plating coral cover	16) $CC_{plating} \sim \alpha + \beta(\overline{DHW}_{1yr})$ 17) $CC_{plating} \sim \alpha + \beta(\overline{DHW}_{10yrs})$ 18) $CC_{plating} \sim \alpha + \beta(\overline{DHW}_{20yrs})$	19) $CC_{plating} \sim \alpha + \beta_1(\overline{DHW}_{1yr}) + \beta_2(\overline{DHW}_{1yr}:\overline{DHW}_{1-3yrs})$ 20) $CC_{plating} \sim \alpha + \beta_1(\overline{DHW}_{1yr}) + \beta_2(\overline{DHW}_{1yr}:\overline{DHW}_{>1yr})$
Massive coral cover	21) $CC_{massive} \sim \alpha + \beta(\overline{DHW}_{1yr})$ 22) $CC_{massive} \sim \alpha + \beta(\overline{DHW}_{10yrs})$ 23) $CC_{massive} \sim \alpha + \beta(\overline{DHW}_{20yrs})$	24) $CC_{massive} \sim \alpha + \beta_1(\overline{DHW}_{1yr}) + \beta_2(\overline{DHW}_{1yr}:\overline{DHW}_{1-3yrs})$ 25) $CC_{massive} \sim \alpha + \beta_1(\overline{DHW}_{1yr}) + \beta_2(\overline{DHW}_{1yr}:\overline{DHW}_{>1yr})$

For each GLMM, we reported the estimate (β, with its standard deviation) and the p-value from the Wald test for the fixed effects (Brooks et al., 2017). The visualization of the regression lines was performed using the VISREG package (v. 2.7; Breheny & Burchett, 2017) and custom R functions.

In addition, we evaluated the goodness-of-fit of each of the GLMMs by measuring the difference between the model's Akaike Information Criterion (AIC; Bozdogan, 1987) and the AIC of a null model. For univariate models, the corresponding null model was a GLMM using a constant value as explanatory variable. For bi-variate models, the null model was the univariate GLMMs using $\overline{DHW}_{1yr}$ as explanatory variable. This approach allowed us to evaluate how accounting for the effect of past heat stress on recent heat stress (i.e. the interaction term of bi-variate models) improves the goodness-of-fit, compared to a model including recent heat stress only ($\overline{DHW}_{1yr}$). According to the rules of thumb for model selection (Burnham & Anderson, 2004), a model with $dAIC < -2$ (where $dAIC = AIC_{null\,model} - AIC_{model}$) has an improved goodness-of-fit, compared to the null model.

Figure 3. Distribution of coral cover, diversity and thermal stress across the study areas.



250

Results

Univariate models

We first built univariate models to evaluate how coral cover and diversity from field surveys were associated with average heat stress ($\overline{DHW}$) calculated over different time periods (1 year, 10 years and 20 years) before the survey dates.

<u>*Overall coral cover and Simpson's diversity*</u>

All univariate association models between coral cover rates and heat stress showed a higher goodness-of-fit than the null model ($dAIC(\overline{DHW}_{1yr}) = -77.9$, $dAIC(\overline{DHW}_{10yrs}) = -45.1$, $dAIC(\overline{DHW}_{20yrs}) = -32.9$; Fig. 4a). All of these models showed significant negative associations ($\mathrm{p} < 0.00001$), where a stronger effect was observed for DHW averages computed over longer periods ($\beta(\overline{DHW}_{1yr}) = -0.03 \pm 0.01$, $\beta(\overline{DHW}_{10yrs}) = -0.12 \pm 0.02$, $\beta(\overline{DHW}_{20yrs}) = -0.23 \pm 0.04$).

The same negative associations were observed between heat stress and Simpson's Diversity (Fig. 4b), though only the association with $\overline{DHW}_{1yr}$ was significant ($\mathrm{p} = 0.01$, $\beta = -0.01 \pm 0.003$) and with a higher goodness-of-fit than the null model ($dAIC = -4.13$).

<u>*Taxa-specific coral cover*</u>

We then focused on taxa-specific rates of coral cover, and observed negative associations with heat stress for all the taxa (Fig. 5a-c). However, the magnitude of such negative effects differed between taxa. Overall, the largest magnitude of effects was observed for plating corals ($\beta(\overline{DHW}_{1yr}) = -0.01 \pm 0.001$, $\beta(\overline{DHW}_{10yrs}) = -0.04 \pm 0.01$, $\beta(\overline{DHW}_{20yrs}) = -0.09 \pm 0.1$; Fig. 5b), followed by branching corals $\beta(\overline{DHW}_{1yr}) = -0.01 \pm 0.002$, $\beta(\overline{DHW}_{10yrs}) = -0.03 \pm 0.01$, $\beta(\overline{DHW}_{20yrs}) = -0.05 \pm 0.1$; Fig. 5a), and finally by massive corals $\beta(\overline{DHW}_{1yr}) = -0.01 \pm 0.001$, $\beta(\overline{DHW}_{10yrs}) = -0.02 \pm 0.01$, $\beta(\overline{DHW}_{20yrs}) = -0.03 \pm 0.14$; Fig. 5c). All of the taxa-specific models were significant ($\mathrm{p} < 0.02$), with a higher goodness-of-fit than the null models ($dAIC < -2$), with the exception of the association between $\overline{DHW}_{20yrs}$ and branching coral cover ($dAIC = -1.62$).

Bi-variate models

We employed bi-variate models to evaluate how the negative associations of both coral cover and diversity with recent heat stress ($\overline{DHW}_{1yr}$) were modulated by heat stress averages calculated either over the short-term (the previous 2 years, $\overline{DHW}_{1-3yrs}$) or the long-term (all of the previous years since 1985, $\overline{DHW}_{>1yr}$; Fig. 4a-b, Fig. 5a-c).

<u>*Overall coral cover and Simpson's diversity*</u>

For coral cover (Fig. 4c, Fig. 4e) and Simpson's diversity (Fig. 4d, Fig. 4f), none of the bi-variate models showed a higher goodness-of-fit ($dAIC > -2$) when compared with the null model (i.e. the univariate model with $\overline{DHW}_{1yr}$).

<u>*Taxa-specific coral cover*</u>

As we focused on taxa-specific coral cover rates, we observed that the types of associations differed between taxa. In branching corals, the bi-variate model with $\overline{DHW}_{1-3yrs}$ resulted in a higher goodness-of-fit than the null model ($dAIC = -4.5$) and the effect of the interaction term ($\overline{DHW}_{1yr}$:$\overline{DHW}_{1-3yrs}$) was significant ($\mathrm{p} = 0.01$) and of positive sign (Fig. 5d). Indeed, the negative effect of $\overline{DHW}_{1yr}$ on branching coral cover appeared to decrease in magnitude with higher levels of $\overline{DHW}_{1-3yrs}$.

The same effect on branching coral cover was observed for the interaction term that included $\overline{DHW}_{>1yr}$ (Fig. 5g). In this case, we observed a higher goodness-of-fit of the model ($dAIC = -28.6$) and a larger magnitude of the effect of the interaction term ($\mathrm{p} < 0.00001$). For instance, the effect of $\overline{DHW}_{1yr}$ on branching coral cover was $\beta = -0.024 \pm 0.003$ for $\overline{DHW}_{>1yr}$ between 0 and 0.1, decreased to $\beta = -0.016 \pm 0.002$ for $\overline{DHW}_{>1yr}$ between 0.2 and 0.3, and was close to zero ($\beta = +0.001 \pm 0$) for $\overline{DHW}_{>1yr}$ above 0.4.

For the plating coral taxon, we found that the bi-variate model with $\overline{DHW}_{>1yr}$ had a higher goodness-of-fit than the null model ($dAIC = -8.8$, Fig. 5h). Remarkably, here the effect of the interaction term was negative ($\mathrm{p} = 0.001$), resulting in the negative association between $\overline{DHW}_{1yr}$ and plating coral cover to increase its magnitude for higher levels of $\overline{DHW}_{>1yr}$.

In contrast, neither bi-variate models for massive coral cover resulted in increased goodness-of-fit ($dAIC > -2$) when compared to the null model.

311 All the coefficients and statistics describing both the univariate and bi-variate association
312 models are displayed in the Supplementary Table 1.

Figure 4. Association between coral cover and diversity with heat stress. The plots display the association of two variables measured from reef surveys (a, c and e: overall coral cover; b, d, f: Simpson's index of coral taxa diversity) with different variables describing past heat stress. In a and b, the plots display the association of coral cover and diversity with the average degree heating week ($\overline{DHW}$) calculated during the year ($\overline{DHW}_{1yr}$, magenta), the 10 years ($\overline{DHW}_{10yrs}$, blue) and the 20 years ($\overline{DHW}_{20yrs}$, dark blue) that preceded the survey dates. In c and d, the plots show the association of coral cover and diversity with $\overline{DHW}_{1yr}$ across different ranges of average DHW during the two previous years ($\overline{DHW}_{1-3yrs}$). In e and f, the plots show the association of coral cover and diversity with $\overline{DHW}_{1yr}$ across different ranges of average DHW during all the previous years (i.e. since 1985; $\overline{DHW}_{>1yrs}$). For each association model, the plots display the goodness-of-fit compared to a null model ($dAIC$) and the p-values (p) of the fixed effects.

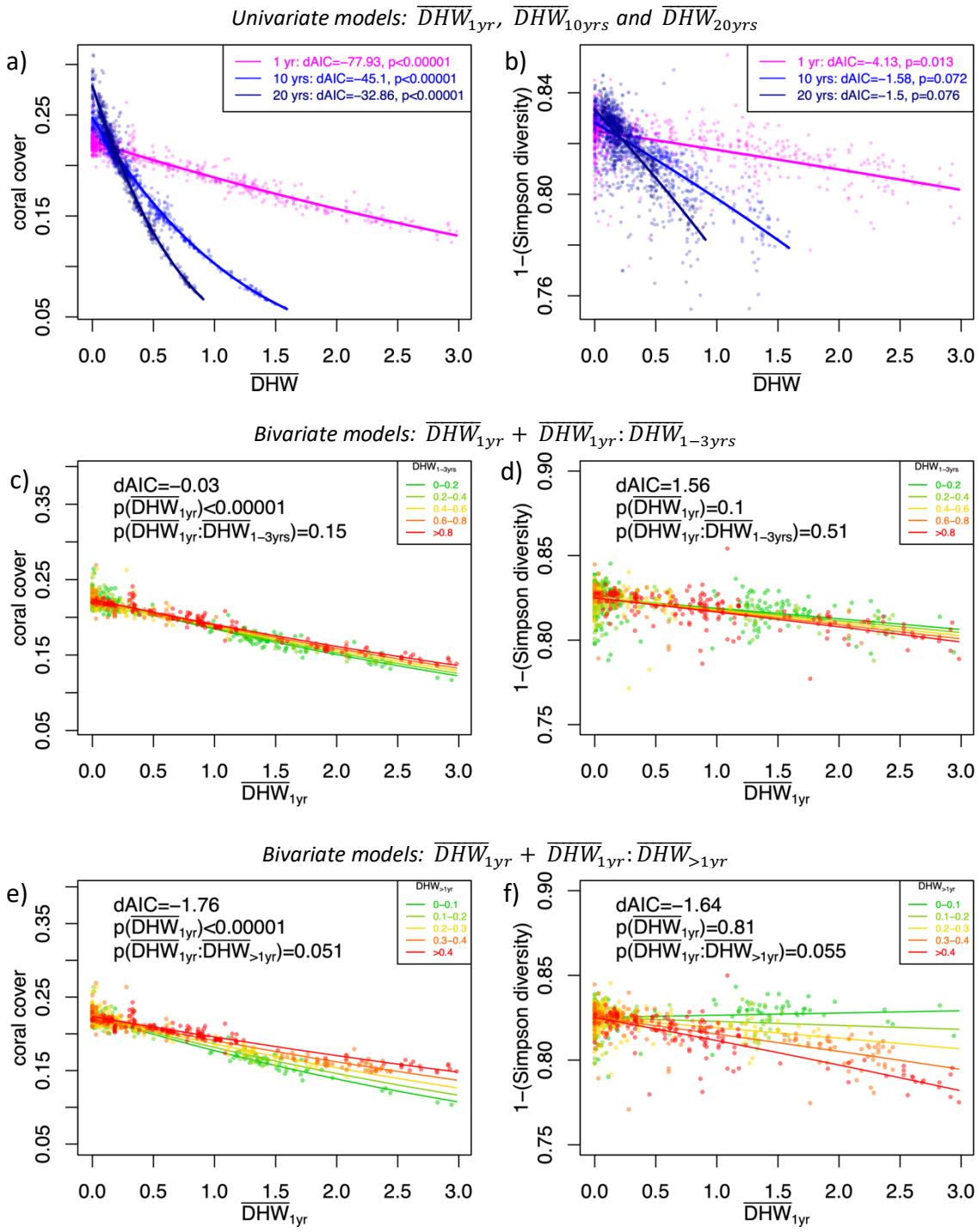
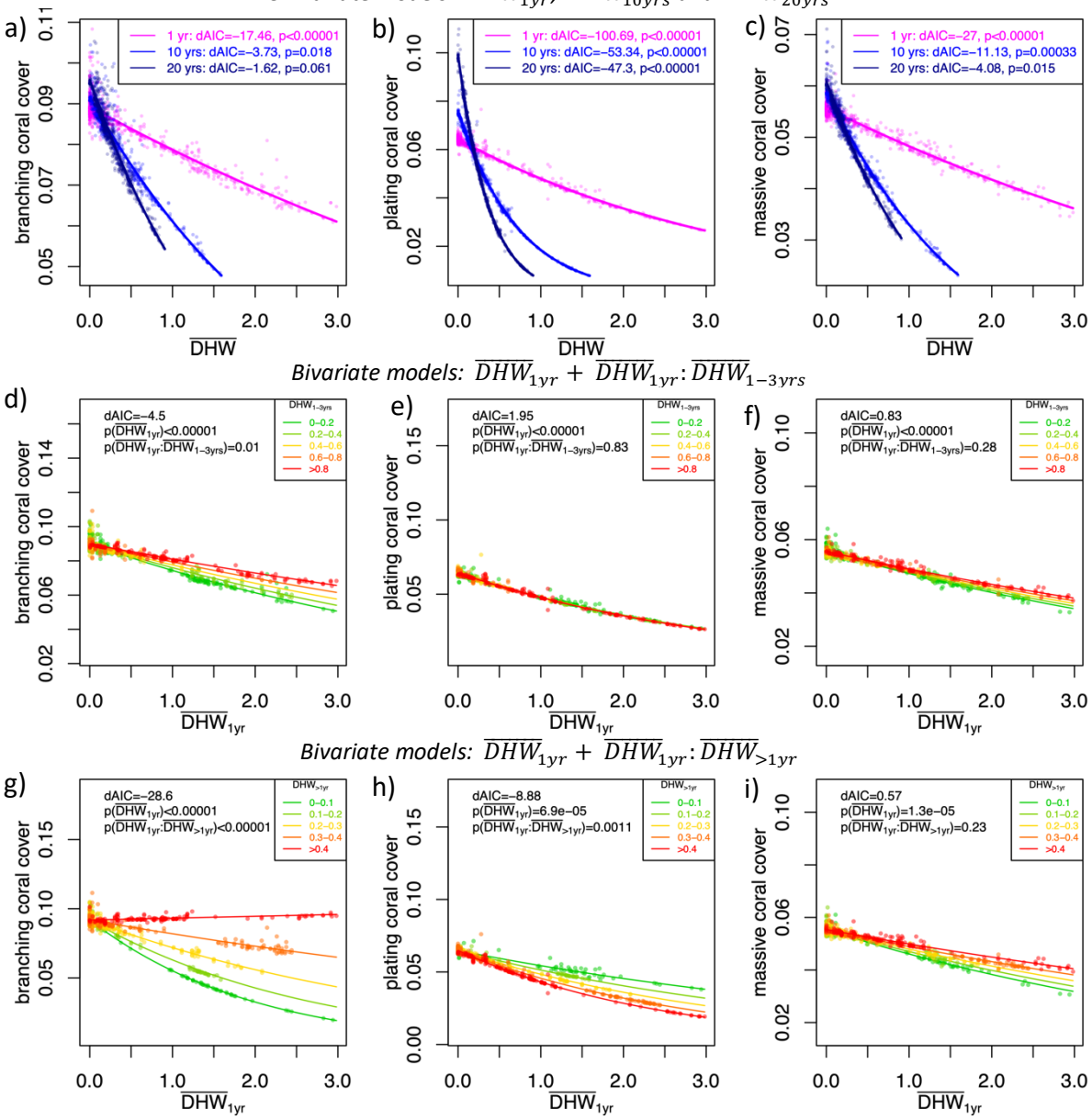


Figure 5. Taxa-specific association between coral cover and heat stress. The plots display the association of coral cover rates from reef surveys for three coral taxa (a, d, g: branching corals; b, e, h: plating corals; c, f, i: massive corals) with different variables describing past heat stress. In a, b and c, the plots display the association of coral cover with the average degree heating week ($\overline{DHW}$) calculated during the year ($\overline{DHW}_{1yr}$, magenta), the 10 years ($\overline{DHW}_{10yrs}$, blue) and the 20 years ($\overline{DHW}_{20yrs}$, dark blue) that preceded the survey dates. In d, e and f, the plots show the association of coral cover with $\overline{DHW}_{1yr}$ across different ranges of average DHW during the two previous years ($\overline{DHW}_{1-3yrs}$). In g, h and i, the plots show the association of coral cover with $\overline{DHW}_{1yr}$ across different ranges of average DHW during all the previous years (i.e. since 1985; $\overline{DHW}_{>1yrs}$). For each association model, the plots display the goodness-of-fit compared to a null model ($dAIC$) along with the p-values (p) of the fixed effects.

Univariate models: $\overline{DHW}_{1yr}$, $\overline{DHW}_{10yrs}$ *and* $\overline{DHW}_{20yrs}$



Discussion

The global decline of coral cover and diversity driven by heat stress

We observed that local rates of coral cover were negatively associated with past heat stress exposure (Fig. 4a). We hypothesize that such negative association describes a causal link, as these observations are consistent with previous studies in the field (Babcock et al., 2020; Head et al., 2019; Hughes, Kerry, et al., 2018; Selig et al., 2012; Soto et al., 2011).

Recent exposure (*i.e.* within one year) to intense heat stress is known to drive a significant decline of coral cover. This was previously shown during the mass coral bleaching event in 2016, which caused a 50% relative decline of coral cover (*i.e.* the ratio of coral cover after and before the event) in the north of the Australian Great Barrier Reef (Hughes, Kerry, et al., 2018) and a 29% decline in the Chagos Archipelago (Indian Ocean; Head et al., 2019). Average DHW values for these two regions in 2016 were ~2.3 and ~3.5°C-week, respectively, and represent heat waves of extreme magnitude. In the present study, recent heat stress was generally below 1°C-week (Fig. 3f), yet even this lower heat stress was significantly associated with coral decline. For instance, one year at an average DHW of 1°C-week was estimated to result in an absolute coral cover decline of ~3% (Fig. 4a).

The recurrence of heat stress events across larger temporal frames (10-20 years) can drive even more severe declines in coral cover. For example, a previous study surveying reefs from north-western Australia for over 20 years indicated that recurrent heat stress was associated with a relative decline of coral cover by 38-92% (Babcock et al., 2020). Our results corroborate this finding, and we estimate that a 20-year period with an average DHW of 0.5°C-week corresponds to an absolute coral cover decline of ~11% (Fig. 4a). To put this number in context, an average 0.5°C-week corresponds to the long-term heat observed for most of the reefs in the southern Caribbean and in some reefs in the northern Great Barrier Reef since 1985 (Fig. 1).

The diversity of coral taxa was found to be negatively associated with heat stress exposure, where such association was particularly noticeable for recent heat stress (Fig. 4b). We hypothesize that this decline in diversity is due to an asymmetrical sensitivity to heat stress between different coral taxa, as suggested by previous studies (Hughes, Kerry, et al., 2018;

Loya et al., 2001; McClanahan, Darling, et al., 2020). Indeed, all taxa-specific coral cover was found to be negatively associated with heat stress, but the magnitude of these associations varied between taxa (Fig. 5a-c). For instance, after one year at an average DHW of 1°C-week we estimated a coral cover decline of 0.7% for massive corals, 0.9% for branching corals and 1.3% for plating corals. Similar differences were observed for long-term heat stress, where a 20-year period at an average DHW of 0.5°C-week was estimated to drive a decline of coral cover by 1.7% for massive corals, 2.3% for branching corals and 4.7% for plating corals.

Life history traits mirror heat responses

Coral cover of massive corals showed the lowest rates of decline in association with heat stress (Fig. 5c). This was not surprising, as the majority of massive corals are considered to constitute "stress-tolerant" taxa (Darling et al., 2012; Hughes, Kerry, et al., 2018; Loya et al., 2001). Several life history traits are suggested to drive heat tolerance in massive corals, such as (1) thicker tissues that provide protection against heat stress (Mydlarz et al., 2010); (2) larger corallites, which are indicators of a trophic strategy that can compensate for the absence of the symbiotic input during a bleaching event (Conti-Jerpe et al., 2020); and (3) slower growth rates and longer generation times, promoting energy storage (Darling et al., 2012; van Woesik et al., 2012). Of note, the negative association between massive coral cover and recent heat stress did not appear to be significantly modulated by the levels of past heat stress (Fig. 5f, Fig. 5i). This might suggest that adaptive processes to heat stress rarely occurred in massive corals over the past decades.

In contrast, branching corals displayed higher levels of coral cover decline in association with recent heat stress (Fig. 5a). This is consistent with previous studies (Hughes, Kerry, et al., 2018; Loya et al., 2001). Indeed, branching corals have thinner tissues, which underpins a higher sensitivity to heat exposure, as well as smaller corallites, which are indicators of a Symbiodinium-dependent feeding strategy (Conti-Jerpe et al., 2020; Darling et al., 2012; Mydlarz et al., 2010). We also found that the decline of branching coral cover appeared to be mitigated by past thermal stress (Fig. 5d, Fig. 5g), and that such mitigation was stronger for long-term heat stress (measured for more than 20 years before surveys), than for short-term heat stress (measured during the two years before surveys). Of note, previous works

378 estimated that the time frame used for computing short-term heat stress (*i.e.* two years)
379 corresponds to the time required for acclimatization processes that boost heat tolerance in
380 corals (Palumbi et al., 2014). Our results therefore suggest that branching corals might be
381 adapting to heat stress, and that such adaptation might occur predominantly through
382 evolutionary processes, rather than through acclimatization. To support these hypotheses,
383 recent genotype-environment association studies detected signals of heat adaptation in the
384 branching species of *Acropora millepora* in the south-western Pacific (Fuller et al., 2020;
385 Selmoni et al., 2021) and *Acropora digitifera* in Japan (Selmoni, Rochat, Lecellier, Berteaux-
386 Lecellier, & Joost, 2020).
387 The rates of evolutionary adaptation to a rapidly changing environment are expected to be
388 enhanced by (1) the intensity of natural selection and (2) the shortness of generation time
389 (Catullo, Llewelyn, Phillips, & Moritz, 2019; Kawecki & Ebert, 2004; Quigley, Bay, & van Oppen,
390 2019). These two elements support the view of branching corals adapting faster than massive
391 corals through evolutionary processes. Indeed, the selection imposed by heat stress is likely
392 to be more intense for branching corals, as their morphological characteristics provide
393 reduced protection against this kind of stress, compared to massive corals. Furthermore, the
394 majority of branching corals are classified as having "competitive" life history traits, defined
395 by higher growth rates and larger colony sizes than "stress-tolerant" massive corals (Darling
396 et al., 2012). As the fecundity of a coral colony is known to strongly correlate with colony size
397 (Álvarez-Noriega et al., 2016), the fast growth of branching corals is likely to result in shorter
398 reproductive cycles, leading to a faster evolutionary adaptation to environmental conditions
399 (Catullo et al., 2019). Of note, coral bleaching experiments in north-western Australia
400 reported increased heat resistance for branching corals living in thermally variable
401 environments, whereas massive corals from the same reefs showed lower increases in heat
402 resistance (Schoepf et al., 2015). This work corroborates the hypothesis of a differential
403 potential for heat adaptation between branching and massive corals.
404 Remarkably, plating corals were the taxon that showed the highest rates of coral cover
405 decline in association with heat stress (Fig. 5b). Plating corals are predominantly found in taxa
406 with a "generalist" or with a "weedy" life history trait (Darling et al., 2012). Life history traits
407 of these taxa reflect intermediate traits when compared with "stress-tolerant" massive corals
408 and "competitive" branching corals. On the one hand, corallite size is smaller than that of
409 "stress-tolerant" corals, which might indicate a higher sensitivity to heat stress (Conti-Jerpe

et al., 2020; Darling et al., 2012). On the other hand, growth rates are slower than "competitive" taxa, which might cause longer generation times (Álvarez-Noriega et al., 2016; Darling et al., 2012). We therefore hypothesize that higher rates of coral cover decline associated with heat stress in plating corals might be due to the fact that (1) plating corals are more sensitive to heat stress than massive corals and (2) plating coral rates of evolutionary adaptation are slower than for branching corals. In this regard, it is interesting to observe that the negative association between plating coral cover and recent heat stress was accentuated by the effect of long-term heat stress (Fig. 5h). This observation might indicate that the slow generation time of plating corals hampers coral cover recovery between heat waves.

Limitations

In this work, we assumed that local rates of coral cover were driven by the effect of degree heating weeks as measured via remote sensed data. However, coral cover is a general indicator of the state of health of the reef and can be affected by other environmental stressors, many of which are not necessarily related to heat stress (De'ath et al., 2012). Two complementary approaches could be used to mitigate this limitation. First, the association analysis could include a wider range of environmental variables that describe other potential stressors for corals survival (such as water pH, turbidity or human pollution; Bessell-Browne et al., 2017; P. J. Liu, Meng, Liu, Wang, & Leu, 2012; Mollica et al., 2018). Such analyses could also include additional metrics describing heat stress, in order to determine how the magnitude versus the frequency of thermal anomalies contribute to coral cover decline (McClanahan et al., 2019; Sully et al., 2019). Second, the analysis of coral cover data can be complemented with bleaching records, as these represent an incontrovertible signal of heat stress in corals. While this has already been done in previous studies (Hughes, Kerry, et al., 2018; McClanahan, Darling, et al., 2020), one main limitation is that worldwide bleaching records are scattered across space and time (Donner, Rickbeil, & Heron, 2017). This issue could be tackled with future advances in bleaching detection via remote sensing, which could provide a standardized view of bleaching events at a worldwide scale (Hedley et al., 2016).

The three broad categories of coral taxa that we used in this work (branching, plating and massive) are a simplification of the morphological characteristics of corals. Indeed, corals

441 display a continuum of morphologies, with substantial variation observed even between
442 corals from the same taxa (Darling et al., 2012; Pratchett et al., 2015). We could therefore
443 replace these categorical classifiers of coral morphs with a set of continuous variables
444 describing colony shape (such as size, branch extension, radial extension, vertical extension,
445 horizontal extension and corallite size). This would allow future research to investigate how
446 the association between coral cover and heat stress is expressed along a continuum of
447 morphological characteristics, so that the resulting predictions on heat tolerance could be
448 projected to any coral species.
449
450 *Perspectives*
451
452 Coral taxa with different morphological traits and distinct life history traits are all suffering
453 significant declines in coral cover due to heat stress. If confirmed by future studies, this would
454 imply that there are no coral bleaching winners (Loya et al., 2001; van Woesik et al., 2011),
455 but only losers of different types.
456 For massive corals, the decline appears to be less severe, but the presumptive low rates of
457 evolutionary adaptation raise an alarm: how much additional heat can massive corals tolerate
458 without resorting to evolutionary processes? For branching corals, however, evolutionary
459 adaptation might promote coral cover recovery. However, such recoveries will likely depend
460 on how widespread the distribution of adapted colonies are presently, and at what rate the
461 adaptive traits would spread across reef systems in the years to come. For plating corals, the
462 situation appears more concerning, as neither heat sensitivity nor adaptive processes seem
463 to have the potential for opposing coral cover decline.
464 The hypotheses formulated in this work should now be tested using field experiments.
465 Genotype-environment association studies have already demonstrated their power for
466 characterizing the potential of evolutionary adaptation in coral populations at local scales (for
467 instance in the central Great Barrier Reef, Fuller et al., 2020; or in New Caledonia, Selmoni et
468 al., 2021). This approach should now be extended to wider spatial scales (for instance the
469 entire south-western Pacific) and consider multiple species with different life history traits, in
470 order to obtain a more comprehensive view of coral adaptation across reef systems and coral
471 taxa. In addition, such analyses should be systematically complemented with physiological

assays testing heat tolerance of corals in aquarium experiments (see e.g. Savary et al., 2021), so that the limits of thermal resistance can be estimated for colonies from different taxa, as well as for adapted/non-adapted colonies from the same taxon.

Recent studies on coral evolutionary adaptive potential suggest that reef conservation efforts should be oriented toward reefs exposed to recurrent stress, as these might be the sources for adapted corals in the years to come (Matz et al., 2020; Selmoni, Lecellier, et al., 2020). As coral taxa might have different potentials for adaptation, the effectiveness of such conservation strategies will also depend on the community structure of the reefs. Verification of the hypothesis raised in this study would thus have major implications for coral reef conservation strategies.

Conclusions

We analyzed the association between local rates of coral cover and heat stress at a global scale and found that both recent and past heat stresses are associated with a decline of coral cover and of coral taxonomic diversity. The magnitude of the negative effect of heat stress on coral cover differed between coral taxa, with lower magnitude in massive, intermediate magnitude in branching and higher magnitude in plating corals. Furthermore, we found that the negative association between branching coral cover and recent heat stress appeared to be mitigated by long-term past heat stress, which might suggest the existence of adaptive processes of evolutionary origin. We hypothesize that the observed differences in the effects of heat stress responses mirror distinct life history traits of coral taxa. If confirmed by future studies, such taxa-specific differences would have major implications for coral reef conservation strategies.

Acknowledgements

We thank the Catlin Seaview Survey project for collecting and sharing the field survey data. We thank Annie Guillaume for proofreading the manuscript. The authors declare no conflict of interests.

References

Álvarez-Noriega, M., Baird, A. H., Dornelas, M., Madin, J. S., Cumbo, V. R., & Connolly, S. R. (2016). Fecundity and the demographic strategies of coral morphologies. *Ecology*, *97*(12), 3485–3493. https://doi.org/10.1002/ecy.1588

Ateweberhan, M., McClanahan, T. R., Graham, N. A. J., & Sheppard, C. R. C. (2011). Episodic heterogeneous decline and recovery of coral cover in the Indian Ocean. *Coral Reefs*, *30*(3), 739. https://doi.org/10.1007/s00338-011-0775-x

Babcock, R. C., Thomson, D. P., Haywood, M. D. E., Vanderklift, M. A., Pillans, R., Rochester, W. A., … Depczynski, M. (2020). Recurrent coral bleaching in north-western Australia and associated declines in coral cover. *Marine and Freshwater Research*. https://doi.org/10.1071/MF19378

Bay, R. A., & Palumbi, S. R. (2014). Multilocus adaptation associated with heat resistance in reef-building corals. *Current Biology*, *24*(24), 2952–2956. https://doi.org/10.1016/j.cub.2014.10.044

Beijbom, O., Edmunds, P. J., Kline, D. I., Mitchell, B. G., & Kriegman, D. (2012). Automated annotation of coral reef survey images. In *Proceedings of the IEEE Computer Society Conference on Computer Vision and Pattern Recognition* (pp. 1170–1177). https://doi.org/10.1109/CVPR.2012.6247798

Bessell-Browne, P., Negri, A. P., Fisher, R., Clode, P. L., Duckworth, A., & Jones, R. (2017). Impacts of turbidity on corals: The relative importance of light limitation and suspended sediments. *Marine Pollution Bulletin*, *117*(1–2), 161–170. https://doi.org/10.1016/j.marpolbul.2017.01.050

Bozdogan, H. (1987). Model selection and Akaike's Information Criterion (AIC): The general theory and its analytical extensions. *Psychometrika*, *52*(3), 345–370. https://doi.org/10.1007/BF02294361

Breheny, P., & Burchett, W. (2017). Visualization of regression models using visreg. *R Journal*, *9*(2), 56–71. https://doi.org/10.32614/rj-2017-046

Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., … Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R Journal*, *9*(2), 378–400.

https://doi.org/10.32614/rj-2017-066

Burnham, K. P., & Anderson, D. R. (2004, November 30). Multimodel inference: Understanding AIC and BIC in model selection. *Sociological Methods and Research*. Sage PublicationsSage CA: Thousand Oaks, CA. https://doi.org/10.1177/0049124104268644

Catullo, R. A., Llewelyn, J., Phillips, B. L., & Moritz, C. C. (2019, October 7). The Potential for Rapid Evolution under Anthropogenic Climate Change. *Current Biology*. Cell Press. https://doi.org/10.1016/j.cub.2019.08.028

Conti-Jerpe, I. E., Thompson, P. D., Wong, C. W. M., Oliveira, N. L., Duprey, N. N., Moynihan, M. A., & Baker, D. M. (2020). Trophic strategy and bleaching resistance in reef-building corals. *Science Advances*, *6*(15), 5443–5453. https://doi.org/10.1126/sciadv.aaz5443

Cramer, K. L., Jackson, J. B. C., Donovan, M. K., Greenstein, B. J., Korpanty, C. A., Cook, G. M., & Pandolfi, J. M. (2020). Widespread loss of Caribbean acroporid corals was underway before coral bleaching and disease outbreaks. *Science Advances*, *6*(17), eaax9395. https://doi.org/10.1126/sciadv.aax9395

Darling, E. S., Alvarez-Filip, L., Oliver, T. A., McClanahan, T. R., & Côté, I. M. (2012). Evaluating life-history strategies of reef corals from species traits. *Ecology Letters*, *15*(12), 1378–1386. https://doi.org/10.1111/j.1461-0248.2012.01861.x

De'ath, G., Fabricius, K. E., Sweatman, H., & Puotinen, M. (2012). The 27-year decline of coral cover on the Great Barrier Reef and its causes. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(44), 17995–17999. https://doi.org/10.1073/pnas.1208909109

Diaz-Pulido, G., & McCook, L. J. (2002). The fate of bleached corals: Patterns and dynamics of algal recruitment. *Marine Ecology Progress Series*, *232*, 115–128. https://doi.org/10.3354/meps232115

Donner, S. D., Rickbeil, G. J. M., & Heron, S. F. (2017). A new, high-resolution global mass coral bleaching database. *PloS One*, *12*(4), e0175490. https://doi.org/10.1371/journal.pone.0175490

Dormann, C., McPherson, J., Araújo, M., Bivand, R., Bolliger, J., Carl, G., … Wilson, R. (2007, October 1). Methods to account for spatial autocorrelation in the analysis of species distributional data: A review. *Ecography*. John Wiley & Sons, Ltd. https://doi.org/10.1111/j.2007.0906-7590.05171.x

Ferrari, S. L. P., & Cribari-Neto, F. (2004). Beta regression for modelling rates and proportions.

Journal of Applied Statistics, *31*(7), 799–815. https://doi.org/10.1080/0266476042000214501

Fuller, Z. L., Mocellin, V. J. L., Morris, L. A., Cantin, N., Shepherd, J., Sarre, L., … Przeworski, M. (2020). Population genetics of the coroal Acropora millepora: Toward genomic prediction of bleaching. *Science*, *369*(6501). https://doi.org/10.1126/science.aba4674

González-Rivero, M., Beijbom, O., Rodriguez-Ramirez, A., Holtrop, T., González-Marrero, Y., Ganase, A., … Hoegh-Guldberg, O. (2016). Scaling up ecological measurements of coral reefs using semi-automated field image collection and analysis. *Remote Sensing*, *8*(1), 30. https://doi.org/10.3390/rs8010030

González-Rivero, M., Bongaerts, P., Beijbom, O., Pizarro, O., Friedman, A., Rodriguez-Ramirez, A., … Hoegh-Guldberg, O. (2014). The Catlin Seaview Survey - kilometre-scale seascape assessment, and monitoring of coral reef ecosystems. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *24*(S2), 184–198. https://doi.org/10.1002/aqc.2505

Head, C. E. I., Bayley, D. T. I., Rowlands, G., Roche, R. C., Tickler, D. M., Rogers, A. D., … Andradi-Brown, D. A. (2019). Coral bleaching impacts from back-to-back 2015–2016 thermal anomalies in the remote central Indian Ocean. *Coral Reefs*, *38*(4), 605–618. https://doi.org/10.1007/s00338-019-01821-9

Hedley, J. D., Roelfsema, C. M., Chollett, I., Harborne, A. R., Heron, S. F., Weeks, S. J., … Mumby, P. J. (2016, February 6). Remote sensing of coral reefs for monitoring and management: A review. *Remote Sensing*. MDPI AG. https://doi.org/10.3390/rs8020118

Hijmans, R. J. (2016). raster: Geographic Data Analysis and Modeling. Retrieved from https://cran.r-project.org/package=raster

Hughes, T. P., Anderson, K. D., Connolly, S. R., Heron, S. F., Kerry, J. T., Lough, J. M., … Wilson, S. K. (2018). Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. *Science*, *359*(6371), 80–83. https://doi.org/10.1126/science.aan8048

Hughes, T. P., Kerry, J. T., Álvarez-Noriega, M., Álvarez-Romero, J. G., Anderson, K. D., Baird, A. H., … Wilson, S. K. (2017). Global warming and recurrent mass bleaching of corals. *Nature*, *543*(7645), 373–377. https://doi.org/10.1038/nature21707

Hughes, T. P., Kerry, J. T., Baird, A. H., Connolly, S. R., Dietzel, A., Eakin, C. M., … Torda, G. (2018). Global warming transforms coral reef assemblages. *Nature*, *556*(7702), 492–496. https://doi.org/10.1038/s41586-018-0041-2

Hughes, T. P., Kerry, J. T., Connolly, S. R., Baird, A. H., Eakin, C. M., Heron, S. F., … Torda, G.

(2019, January 10). Ecological memory modifies the cumulative impact of recurrent climate extremes. *Nature Climate Change*. Nature Publishing Group. https://doi.org/10.1038/s41558-018-0351-2

Kawecki, T. J., & Ebert, D. (2004). Conceptual issues in local adaptation. *Ecology Letters*, *7*(12), 1225–1241. https://doi.org/10.1111/j.1461-0248.2004.00684.x

Kayanne, H. (2017). Validation of degree heating weeks as a coral bleaching index in the northwestern Pacific. *Coral Reefs*, *36*(1), 63–70. https://doi.org/10.1007/s00338-016-1524-y

Liu, G., Heron, S., Eakin, C., Muller-Karger, F., Vega-Rodriguez, M., Guild, L., … Lynds, S. (2014). Reef-Scale Thermal Stress Monitoring of Coral Ecosystems: New 5-km Global Products from NOAA Coral Reef Watch. *Remote Sensing*, *6*(11), 11579–11606. https://doi.org/10.3390/rs61111579

Liu, P. J., Meng, P. J., Liu, L. L., Wang, J. T., & Leu, M. Y. (2012). Impacts of human activities on coral reef ecosystems of southern Taiwan: A long-term study. *Marine Pollution Bulletin*, *64*(6), 1129–1135. https://doi.org/10.1016/j.marpolbul.2012.03.031

Loya, Y., Sakai, K., Yamazato, K., Nakano, Y., Sambali, H., & van Woesik, R. (2001). Coral bleaching: the winners and the losers. *Ecology Letters*, *4*(2), 122–131. https://doi.org/10.1046/j.1461-0248.2001.00203.x

Madin, J. S., Anderson, K. D., Andreasen, M. H., Bridge, T. C. L., Cairns, S. D., Connolly, S. R., … Baird, A. H. (2016). The Coral Trait Database, a curated database of trait information for coral species from the global oceans. *Scientific Data*, *3*(1), 16. https://doi.org/10.1038/sdata.2016.17

Matz, M. V., Treml, E. A., & Haller, B. C. (2020). Estimating the potential for coral adaptation to global warming across the Indo-West Pacific. *Global Change Biology*, *26*(6), 3473–3481. https://doi.org/10.1111/gcb.15060

McClanahan, T. R., Darling, E., Maina, J., Muthiga, N., D'agata, S., Leblond, J., … Grimsditch, G. (2020). Highly variable taxa-specific coral bleaching responses to thermal stresses. *Marine Ecology Progress Series*, *648*, 135–151. https://doi.org/10.3354/meps13402

McClanahan, T. R., Darling, E. S., Maina, J. M., Muthiga, N. A., 'agata, S. D., Jupiter, S. D., … Leblond, J. (2019, November 1). Temperature patterns and mechanisms influencing coral bleaching during the 2016 El Niño. *Nature Climate Change*. Nature Publishing Group. https://doi.org/10.1038/s41558-019-0576-8

McClanahan, T. R., Maina, J. M., Darling, E. S., Guillaume, M. M. M., Muthiga, N. A., D'agata, S., … Grimsditch, G. (2020). Large geographic variability in the resistance of corals to thermal stress. *Global Ecology and Biogeography*, *29*(12), 2229–2247. https://doi.org/10.1111/geb.13191

Mollica, N. R., Guo, W., Cohen, A. L., Huang, K. F., Foster, G. L., Donald, H. K., & Solow, A. R. (2018). Ocean acidification affects coral growth by reducing skeletal density. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(8), 1754–1759. https://doi.org/10.1073/pnas.1712806115

Mydlarz, L. D., McGinty, E. S., & Harvell, C. D. (2010). What are the physiological and immunological responses of coral to climate warming and disease? *The Journal of Experimental Biology*, *213*(6), 934–945. https://doi.org/10.1242/jeb.037580

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., … Wagner, H. (2019). Vegan: community ecology package Vegan: community ecology package, 2006. R package.

Osborne, K., Thompson, A. A., Cheal, A. J., Emslie, M. J., Johns, K. A., Jonker, M. J., … Sweatman, H. P. A. (2017). Delayed coral recovery in a warming ocean. *Global Change Biology*, *23*(9), 3869–3881. https://doi.org/10.1111/gcb.13707

Palumbi, S. R., Barshis, D. J., Traylor-Knowles, N., & Bay, R. A. (2014). Mechanisms of reef coral resistance to future climate change. *Science*, *344*(6186). Retrieved from http://science.sciencemag.org/content/344/6186/895

Pratchett, M. S., Anderson, K. D., Hoogenboom, M. O., Widman, E., Baird, A. H., Pandolfi, J. M., … Lough, J. M. (2015). Spatial, temporal and taxonomic variation in coral growth-implications for the structure and function of coral reef ecosystems. In *Oceanography and Marine Biology* (Vol. 53, pp. 166–223). CRC Press. https://doi.org/10.1201/b18733-7

Pratchett, M. S., Thompson, C. A., Hoey, A. S., Cowman, P. F., & Wilson, S. K. (2018). Effects of Coral Bleaching and Coral Loss on the Structure and Function of Reef Fish Assemblages (pp. 265–293). Springer, Cham. https://doi.org/10.1007/978-3-319-75393-5_11

Quigley, K. M., Bay, L. K., & van Oppen, M. J. H. (2019). The active spread of adaptive variation for reef resilience. *Ecology and Evolution*, *9*(19), 11122–11135. https://doi.org/10.1002/ece3.5616

R Core Team. (2021). R: A Language and Environment for Statistical Computing. Retrieved

from https://www.r-project.org/

Romero-Torres, M., Acosta, A., Palacio-Castro, A. M., Treml, E. A., Zapata, F. A., Paz-García, D. A., & Porter, J. W. (2020). Coral reef resilience to thermal stress in the Eastern Tropical Pacific. *Global Change Biology*, *26*(7), 3880–3890. https://doi.org/10.1111/gcb.15126

Savary, R., Barshis, D. J., Voolstra, C. R., Cárdenas, A., Evensen, N. R., Banc-Prandi, G., … Meibom, A. (2021). Fast and pervasive transcriptomic resilience and acclimation of extremely heat-tolerant coral holobionts from the northern Red Sea. *Proceedings of the National Academy of Sciences*, *118*(19), e2023298118. https://doi.org/10.1073/pnas.2023298118

Schoepf, V., Carrion, S. A., Pfeifer, S. M., Naugle, M., Dugal, L., Bruyn, J., & McCulloch, M. T. (2019). Stress-resistant corals may not acclimatize to ocean warming but maintain heat tolerance under cooler temperatures. *Nature Communications*, *10*(1), 1–10. https://doi.org/10.1038/s41467-019-12065-0

Schoepf, V., Stat, M., Falter, J. L., & McCulloch, M. T. (2015). Limits to the thermal tolerance of corals adapted to a highly fluctuating, naturally extreme temperature environment. *Scientific Reports*, *5*(1), 17639. https://doi.org/10.1038/srep17639

Selig, E. R., Casey, K. S., & Bruno, J. F. (2012). Temperature-driven coral decline: the role of marine protected areas. *Global Change Biology*, *18*(5), 1561–1570. https://doi.org/10.1111/j.1365-2486.2012.02658.x

Selmoni, O., Lecellier, G., Magalon, H., Vigliola, L., Oury, N., Benzoni, F., … Berteaux-Lecellier, V. (2021). Seascape genomics reveals candidate molecular targets of heat stress adaptation in three coral species. *Molecular Ecology*, mec.15857. https://doi.org/10.1111/mec.15857

Selmoni, O., Lecellier, G., Vigliola, L., Berteaux-Lecellier, V., & Joost, S. (2020). Coral cover surveys corroborate predictions on reef adaptive potential to thermal stress. *Scientific Reports*, *10*(1), 1–13. https://doi.org/10.1038/s41598-020-76604-2

Selmoni, O., Rochat, E., Lecellier, G., Berteaux-Lecellier, V., & Joost, S. (2020). Seascape genomics as a new tool to empower coral reef conservation strategies: an example on north-western Pacific Acropora digitifera. *Evolutionary Applications*, 588228. https://doi.org/10.1101/588228

Simpson, E. H. (1949). Measurement of diversity. *Nature*. Nature Publishing Group. https://doi.org/10.1038/163688a0

Skirving, W., Marsh, B., De La Cour, J., Liu, G., Harris, A., Maturi, E., … Eakin, C. M. (2020). CoralTemp and the Coral Reef Watch Coral Bleaching Heat Stress Product Suite Version 3.1. *Remote Sensing*, *12*(23), 3856. https://doi.org/10.3390/rs12233856

Soto, I. M., Muller Karger, F. E., Hallock, P., & Hu, C. (2011). Sea Surface Temperature Variability in the Florida Keys and Its Relationship to Coral Cover. *Journal of Marine Biology*, *2011*, 1–10. https://doi.org/10.1155/2011/981723

Sully, S., Burkepile, D. E., Donovan, M. K., Hodgson, G., & van Woesik, R. (2019). A global analysis of coral bleaching over the past two decades. *Nature Communications*, *10*(1), 1–5. https://doi.org/10.1038/s41467-019-09238-2

UNEP-WCMC, WorldFish-Center, WRI, & TNC. (2021). Global distribution of warm-water coral reefs, compiled from multiple sources including the Millennium Coral Reef Mapping Project. Version 4.1. Retrieved May 9, 2017, from http://data.unep-wcmc.org/datasets/1

Van Hooidonk, R., Maynard, J. A., & Planes, S. (2013). Temporary refugia for coral reefs in a warming world. *Nature Climate Change*, *3*(5), 508–511. https://doi.org/10.1038/nclimate1829

van Oppen, M. J. H., & Lough, J. M. (2009). Coral Bleaching — Patterns, Processes, Causes and Consequences (pp. 298–201). Springer. https://doi.org/10.1007/978-3-540-69775-6_11

van Woesik, R., Franklin, E. C., O'Leary, J., McClanahan, T. R., Klaus, J. S., & Budd, A. F. (2012). Hosts of the plio-pleistocene past reflect modern-day coral vulnerability. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1737), 2448–2456. https://doi.org/10.1098/rspb.2011.2621

van Woesik, R., Sakai, K., Ganase, A., & Loya, Y. (2011). Revisiting the winners and the losers a decade after coral bleaching. *Marine Ecology Progress Series*, *434*, 67–76. https://doi.org/10.3354/meps09203

Veron, J. E. N. (2000). *Corals of the world*. (M. Stafford-Smith, Ed.) (Vol. 1–3). Townsville: Australian Institute of Marine Science.