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# Future loss of local-scale thermal refugia in coral reef ecosystems

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## Abstract

Thermal refugia underpin climate-smart management of coral reefs, but whether current thermal refugia will remain so under future warming is uncertain. We use statistical downscaling to provide the highest resolution thermal stress projections (0.01˚/1 km, >230,000 reef pixels) currently available for coral reefs and identify future refugia on locally manageable scales. Here, we show that climate change will overwhelm current local-scale refugia, with declines in global thermal refugia from 84% of global coral reef pixels in the present-day climate to 0.2% at 1.5˚C, and 0% at 2.0˚C of global warming. Local-scale oceanographic features such as upwelling and strong ocean currents only rarely provide future thermal refugia. We confirm that warming of 1.5˚C relative to pre-industrial levels will be catastrophic for coral reefs. Focusing management efforts on thermal refugia may only be effective in the short-term. Promoting adaptation to higher temperatures and facilitating migration will instead be needed to secure coral reef survival.

## Introduction

Coral reefs in every region of the world are threatened by climate change, no matter how remote or well protected [1]. Identifying and protecting climate refugia is a popular recommendation for coral reef management [2–5]. Climate refugia are locations that maintain suitable environmental conditions for a resident species even when surrounding areas become inhospitable [6]. An effective climate refugium is characterised by an ability to provide long-term protection from multiple climate stressors [6]. One of the most pervasive climate threats to coral reefs is ocean warming. Identifying coral reef locations that can buffer the effects of rising ocean temperatures, hereafter "thermal refugia", is a crucial first step to identifying multi-stressor climate refugia. Upwelling areas and reefs with strong ocean currents have been proposed as potential thermal refugia that protect coral reefs from warming conditions [7–10]. However, climate projections are often too coarse to capture the smaller scale oceanographic features that characterise thermal refugia [6]. By missing oceanographic features that lower variability for global 1 km reef pixels is in the S2 Dataset.

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local temperatures, large coral reef declines are projected globally [11, 12]. Whether smaller scale features will provide hidden refugia in the future remains an open question. As climate change progresses, the number of coral reef refugia is expected to diminish [13], particularly as global warming of 1.5˚C set by the Paris Agreement becomes increasingly ambitious. Success of thermal refugia conservation hinges on the ability of local-scale oceanographic features to maintain environmental conditions suitable for coral reef survival under future warming of at least 2.0˚C, generating an urgent need to identify such features at management scales.

Thermal exposure projections using the previous generation of climate models involved in the fifth Coupled Model Intercomparison Project (CMIP5) are available at 4 km resolution [14]. The projections were generated using statistical downscaling techniques that use the relationship between fine and coarse-scale climate variables to increase the resolution of coarse climate model projections and capture observed climate variability [15]. Here, we use the latest generation of climate model projections (CMIP6) to project future thermal exposure on shallow-water coral reefs globally and identify thermal refugia at the highest spatial resolution available (1 km). We use the Multi-scale Ultra-high Resolution (MUR) Sea Surface Temperature (SST) Analysis observational dataset at 1 km spatial resolution [16] as the training dataset to statistically downscale CMIP6 projections of daily SSTs. In satellite-derived observational datasets, the resolution of the grid is often finer than the resolution of the input data. The MUR dataset uses different sized time windows of night-time SST data to reconstruct small-scale SST features, resulting in a feature resolution up to ten times finer than 5–25 km products [17]. Downscaling using the MUR dataset allows us to identify areas where local oceanographic conditions promote thermal refugia and provide information at an unprecedented scale (1 km) to inform reef management.

The CMIP6 models better simulate climate system features influencing thermal stress on corals than CMIP5 models, including elements of El Niño Southern Oscillation and Indian Ocean Dipole [18]. The new models generally have a higher spatial resolution (as high as ~25 km [19]) than their CMIP5 counterparts (typically ~100 km). Some CMIP6 models have a higher equilibrium climate sensitivity (1.8–5.6˚C; i.e. the temperature change resulting from a doubling of $CO_2$) than those of CMIP5 (1.5–4.5˚C) [20–22]. Most models with an equilibrium climate sensitivity $> 4.5$˚C do not reproduce observed warming trends, suggesting that $> 4.5$˚C values are unlikely [21–23] and ensemble means including these models may be biased high. To avoid this bias, we use the models' response at prescribed future global warming levels (e.g. 1.5 or 2.0˚C) in our downscaling approach. Thus, models with high equilibrium climate sensitivity can be included in our model ensembles without our method overestimating future warming. This level-analysis approach uses large ensembles of multiple models and emissions experiments to project local climatic changes associated with each future global warming level [24]. This approach removes most of the uncertainty associated with different climate model sensitivities and displaces the uncertainty due to future emissions trajectories onto an uncertainty as to when a global warming level will be passed [25].

Refugia are defined by their ability to maintain favourable conditions. As such, high thermal stress tolerance of species in a location does not influence whether the area is classified as a refugia [6]. However, various biological and ecological factors can influence the level of impact on corals from thermal exposure. To model the assumption that global coral reefs will adapt to warmer conditions over time, some projections of thermal stress on coral reefs have applied a global increase in the thermal stress threshold [11, 26–28]. Coral reefs living in variable temperature environments have exhibited higher thermal tolerance than those in low variability environments [29–34]. Reefs with high historical thermal exposure and temporal variability have been used to identify coral reef refugia on the basis that these reefs have been able to acclimate/adapt to thermal stress [35, 36].

Here, we examine historical and future thermal exposure to present local-scale (1 km) predictions of whether present-day thermal refugia will persist into the future and provide the context of seasonal and inter-annual SST variability as indicators of the susceptibility of reefs to thermal exposure.

## Results and discussion

### Thermal refugia in the future

Coral recovery following extensive thermal stress-induced mortality is spatially variable but on average is thought to require at least 10 years to re-establish coral communities [37]. To represent sites where coral communities can be maintained and/or re-established, we define thermal refugia as 1 km reef pixels with a probability of thermal stress events less than 0.1 $yr^{-1}$ (one event every 10 years; Fig 1). Exposed reefs are defined as 1 km reef pixels with a probability of thermal stress events greater than 0.2 $yr^{-1}$ (one event every five years). A probabilistic frequency of 0.2 $yr^{-1}$ corresponds to an intolerable level of thermal stress [11, 28, 38]. All other reef pixels are described as intermediate which indicates reefs where the level of thermal stress may be too high to maintain pre-disturbance communities and coral cover, but where species with high recovery rates might proliferate.

Thermal stress is calculated using the cumulative thermal stress metric Degree Heating Weeks (DHW), which is the rolling 12-week sum of SST anomalies at least 1˚C higher than the long-term maximum monthly mean (MMM) [39]. Thermal stress events are identified as those with a DHW value above 4˚C-weeks, which is the threshold commonly used to indicate thermal stress high enough to cause significant coral bleaching and some mortality, whereas the 8˚C-weeks threshold indicates severe thermal stress leading to broad-scale catastrophic

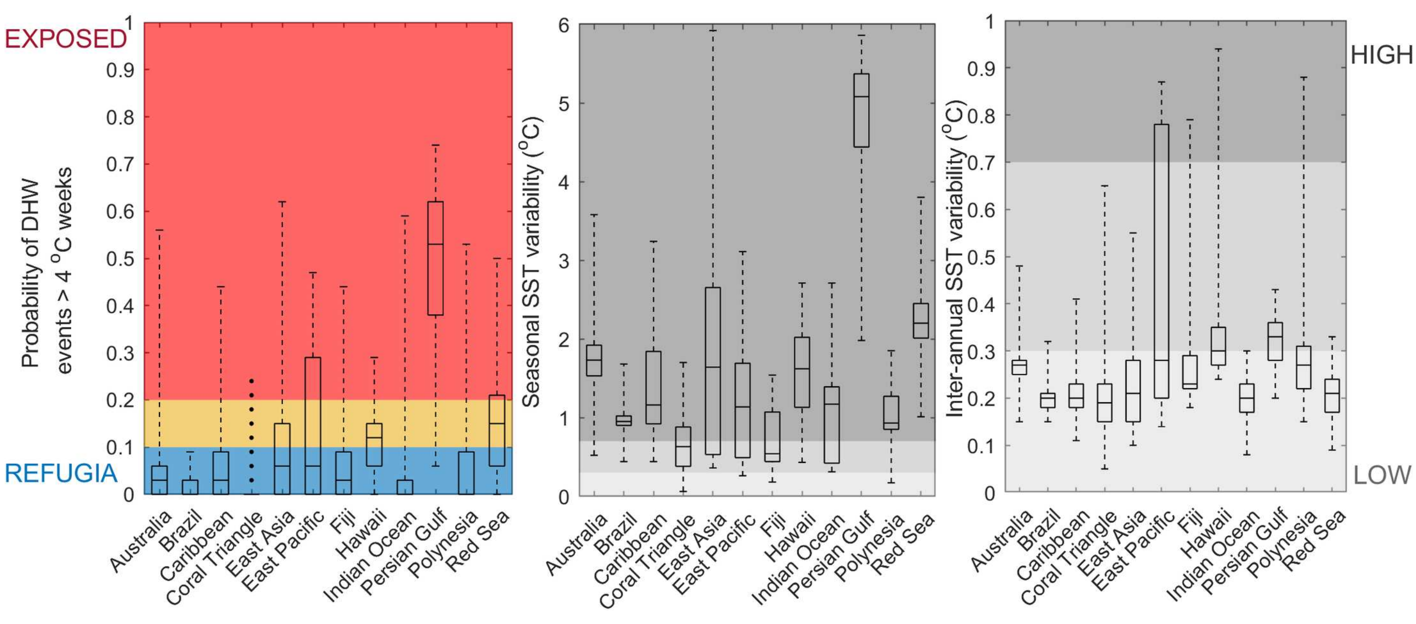


**Fig 1. Probability of DHW events > 4˚C-weeks, seasonal SST variability and inter-annual SST variability in 12 coral reef regions during the period 1986–2019.** Outliers (>100 * interquartile range) are shown by the black dots. Thresholds for determining thermal refugia (probability of DHW events > 4˚C-weeks less than 0.1 $yr^{-1}$) and exposed reefs (probability of DHW events > 4˚C-weeks greater than 0.2 $yr^{-1}$) are represented by the blue and red shaded areas, respectively. Thresholds for determining high SST variability (> 0.7˚C) and low SST variability (< 0.3˚C) are represented by the dark and light grey shaded areas, respectively.

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coral mortality [40]. The long-term MMM calculated here is slightly higher (up to 1˚C) for much of the world's coral reefs than those calculated by previous studies (S1 Fig). We use the European Space Agency Climate Change Initiative (CCI) 5 km SST Analysis product [41] for the early part of the time series, instead of the more-commonly used NOAA Coral Reef Watch product, due to its consistency with in situ SST measurements for coral reef regions [42]. The 5 km SST is then downscaled to 1 km by replacing the CCI 5 km monthly SST climatology with that of the 1 km MUR dataset (S1 Appendix). Together, these factors result in small changes to the MMM which can then lead to larger changes in accumulated thermal stress. The 4˚C-weeks threshold we use therefore indicates more severe bleaching than described in previous studies. We define low variability reefs as those with seasonal and inter-annual SST variability less than 0.3˚C and high variability reefs as those with seasonal or inter-annual SST variability greater than 0.7˚C [26] (Fig 1).

In the recent era (1986–2019), 84.1% of reef pixels globally are thermal refugia (Fig 2). The percentage of global thermal refugia drops to 0.2% (0–57.8%) at 1.5˚C of warming, relative to

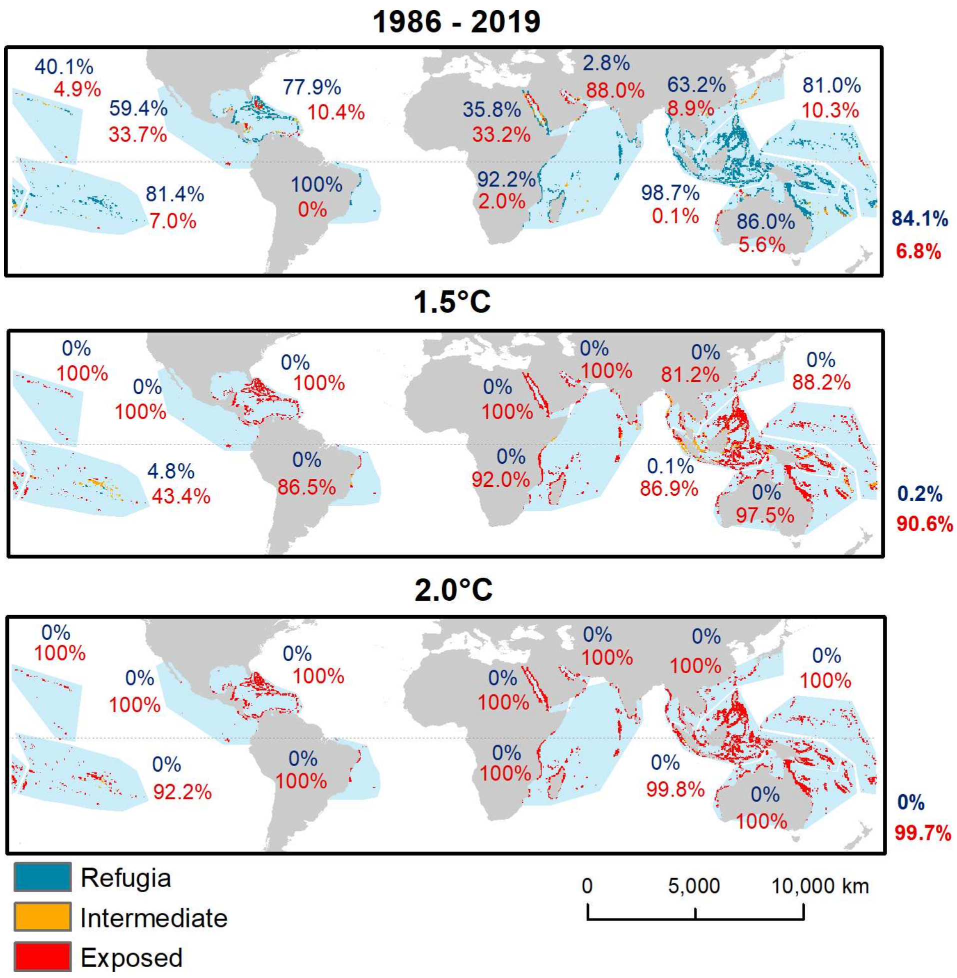


**Fig 2. Global distribution of exposure category in the 1986–2019 climate and at 1.5 and 2.0˚C of future global warming.** Exposure categories are thermal refugia (probability of DHW events > 4˚C-weeks less than 0.1 $yr^{-1}$), intermediate (probability of DHW events > 4˚C-weeks from 0.1–0.2 $yr^{-1}$) and exposed (probability of DHW events > 4˚C-weeks greater than 0.2 $yr^{-1}$). Percentages indicate the regional (on map) and global (right of map) proportion of thermal refugia (blue) and exposed reefs (red). The 12 coral reef regions are outlined in light blue. The base map is made with Natural Earth.

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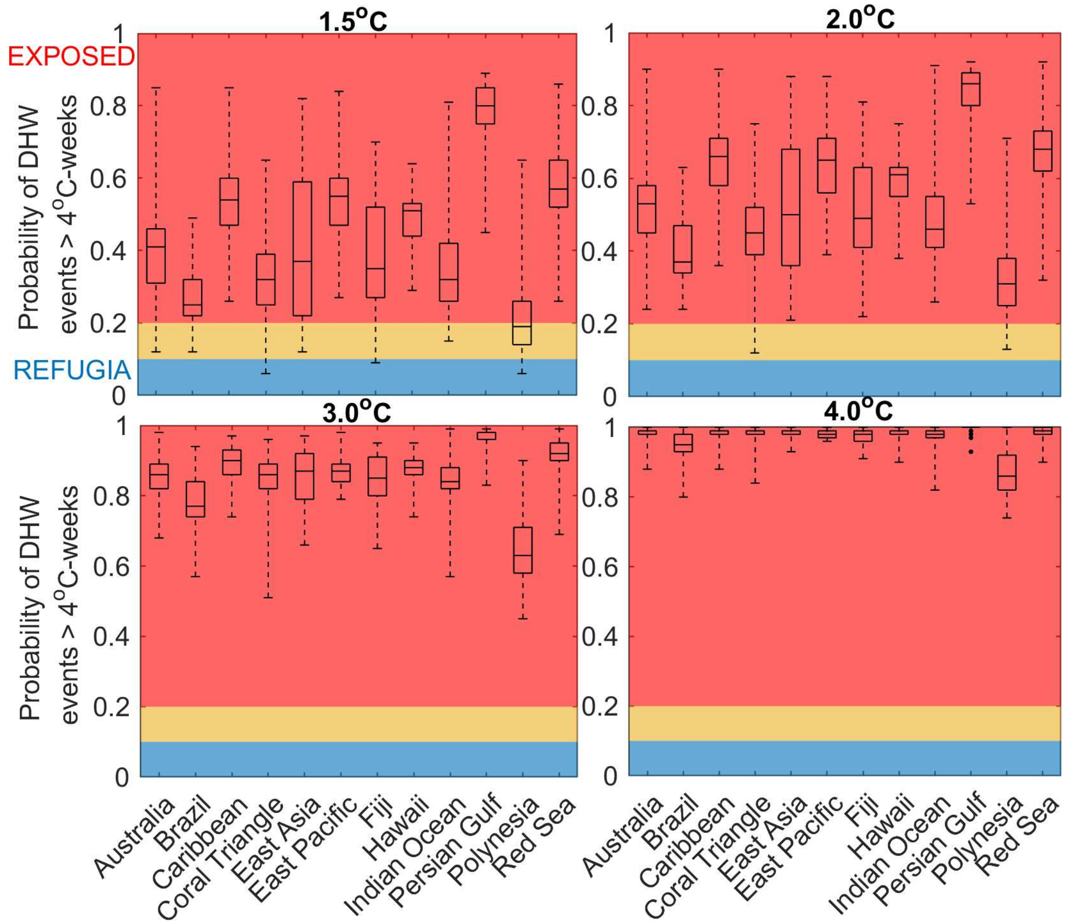


**Fig 3. Probability of DHW events > 4˚C-weeks across 12 coral reef regions under 1.5, 2.0, 3.0 and 4.0˚C of global warming relative to pre-industrial levels.** Thresholds for determining thermal refugia (probability of DHW events > 4˚C-weeks less than 0.1 $yr^{-1}$) and exposed reefs (probability of DHW events > 4˚C-weeks greater than 0.2 $yr^{-1}$) are represented by the blue and red shaded areas, respectively.

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pre-industrial levels, and to 0% (0–45.2%) at 2.0˚C of warming (Fig 2). Only 6.8% of reef pixels are exposed in the 1986–2019 period, increasing to 90.6% (12.1–100%) and 99.7% (16.3–100%) at 1.5˚C and 2.0˚C of warming, respectively. At 3.0˚C and 4.0˚C, there are no thermal refugia and all global reef pixels are exposed (Fig 3). Coarse resolution (50 km) CMIP3 projections for the global coral reef area estimated that 100% (4˚C-weeks threshold) and 89% (8˚C-weeks threshold) of coral reefs will be exposed (> 0.2 $yr^{-1}$) at 1.5˚C of global warming [11]. Our findings provide further support that the Paris Agreement target of limiting warming to 1.5˚C will not be enough to save most coral reefs [11, 28, 43]. However, by capturing fine-scale SST features that have been known to prevent bleaching mortality in the past, we locate small reef areas where the probability of thermal stress under future warming is lower than in adjacent areas.

We find thermal refugia in all 12 coral reef regions in the 1986–2019 climate (Fig 2). At 1.5˚C, thermal refugia are only present in two coral reef regions (Fig 2): Polynesia and the Coral Triangle. For most coral reef areas, current thermal refugia are not projected to remain so. Many known upwelling areas in Oman [7, 44], Colombia [7], Indonesia (Lesser Sunda) [9] and the Caribbean [8] are projected to have no thermal refugia remaining at 1.5˚C of warming

(Fig 2). The exception is in the East Indian Ocean Sumatra-Java upwelling region, which has some thermal refugia remaining at 1.5˚C of warming. While upwelling areas can provide respite from coral bleaching and mortality in the present-day climate, local upwelling is only enough to mitigate thermal stress on coral reefs in very rare cases and under the smallest projected change in future warming. Similarly, there are no thermal refugia at 1.5˚C of global warming in areas with high currents known to influence bleaching dynamics in the past, such as Panama, Florida [8] and Lesser Sunda, Indonesia [9]. Some small reef areas influenced by upwelling or high currents in Lesser Sunda and Oman are rated intermediate for exposure at 1.5˚C of warming rather than exposed, but they are not thermal refugia given our refugia criteria. Similar patterns emerge when using an 8˚C-weeks threshold to define thermal refugia, with a slightly slower decline to 0% thermal refugia (S2 Fig).

Bleaching risk is heavily influenced by inter-annual and seasonal SST variability [26, 45]. Here, we find that areas with moderate to high inter-annual variability have a lower bleaching risk with future warming (S3 Fig) because cooler years, influenced by natural climate variability, provide respite between thermal stress events [26]. For example, the probability of thermal stress events $>$ 4˚C-weeks is lower along the Sumatra-Java coast, resulting in small areas of thermal refugia at 1.5˚C of warming with some intermediate reefs remaining at 2.0˚C of warming in West Sumatra. This pattern most likely arises from positive Indian Ocean Dipole events that drive upwelling that results in cold SST anomalies along the Sumatra-Java coastline [18], which may provide respite from future warming in Sumatra facilitating coral reef recovery. However, some CMIP6 models simulate more regular Indian Ocean Dipole events during the historical period compared to observations, indicating that this cool respite might be less frequent than projected here [18]. Furthermore, upwelling is associated with the transport of nutrients to surface waters which can have harmful effects on coral reef ecosystems [46]. Thermal refugia in South Sumatra are associated with bay areas influenced by river input which also contribute high nutrient loading [47], potentially exacerbated by increased extreme rainfall with future warming and land use change [48].

The probability of thermal stress events $>$ 4˚C-weeks is lower in the Polynesia region under future warming than in other coral reef regions (Fig 3). The region has the highest number of thermal refugia at 1.5˚C of global warming (Fig 2). CMIP6 models simulate relatively low rates of future warming in the southern Pacific compared to the rest of the world [49, 50]. Weakening of equatorial trade winds due to global warming will slow ocean circulation and equatorial upwelling [51] causing less warm water being transported away from the equator resulting in higher rates of warming in the equatorial Pacific compared to regions off the equator (e.g. French Polynesia). However, rates of warming in the southern Pacific are uncertain. SST warming rates in the tropical Pacific are affected by long-standing climate model biases in oceanographic SST features (e.g. the equatorial cold tongue bias [52]) although this bias is reduced in CMIP6 compared to CMIP5 [50].

High latitude reefs are among the first areas to lose thermal refugia under future global warming (Fig 2). These regions are characterised by high seasonal variability (Fig 1). We find that reef pixels with high seasonal SST variability have a larger increase in the probability of thermal stress between the 1986–2019 climate and 1.5˚C of warming (S4 Fig). Chronic warming in highly seasonally variable regions results in summer temperatures exceeding thermal stress thresholds annually under small changes in global mean temperature [26]. High latitude reefs may therefore provide a thermal refugia for range shifting corals adapted to warmer baseline temperatures [53] but are unlikely to provide a thermal refugia for the species currently living there, unless they are able to sufficiently increase their thermal tolerance under the highly variable environmental conditions.

## Thermal refugia and variability

Variable environmental conditions are thought to indicate more resistant or adaptable coral reef communities [29–34]. Seasonal variability is the dominant SST variability (Fig 1). A large percentage (68.7%) of the global coral reef area has seasonal variability above the high ($> 0.7^{\circ}C$ [26]) SST variability threshold. Only 0.7% of the global coral reef area has inter-annual variability above the high SST variability threshold. Reefs with the highest inter-annual variability, influenced by El Niño, are located in the tropical East Pacific [31]. We divide thermal refugia, intermediate and exposed reefs into high (seasonal or inter-annual variability $> 0.7^{\circ}C$), moderate and low (seasonal and inter-annual variability $< 0.3^{\circ}C$) SST variability categories [26] (Fig 4 and S5 Fig) to identify locations where high SST variability might lead to more rapid adaptation of species and communities.

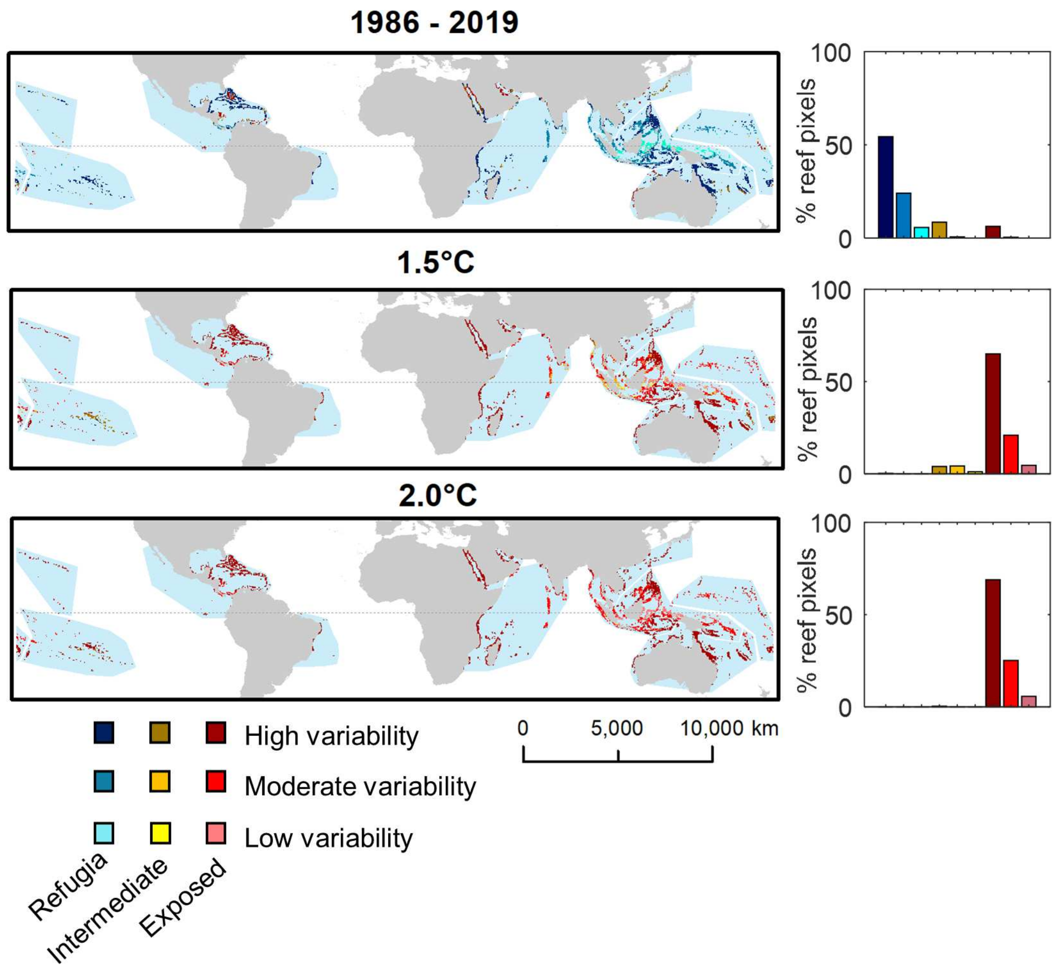


**Fig 4. Global distribution of exposure category and SST variability level in the 1986–2019 climate and at 1.5 and 2.0˚C of future global warming relative to pre-industrial levels.** Exposure categories are thermal refugia (probability of DHW events $> 4^{\circ}C$-weeks less than 0.1 $yr^{-1}$), intermediate (probability of DHW events $> 4^{\circ}C$-weeks from 0.1–0.2 $yr^{-1}$) and exposed (probability of DHW events $> 4^{\circ}C$-weeks greater than 0.2 $yr^{-1}$). Exposure categories are split by the level of SST variability (high = seasonal OR inter-annual variability $> 0.7^{\circ}C$, low = seasonal AND inter-annual variability $< 0.3^{\circ}C$, moderate = all others). The 12 coral reef regions are outlined in light blue. Bars indicate the percentage of 1 km reef pixels in each exposure category. The base map is made with Natural Earth.

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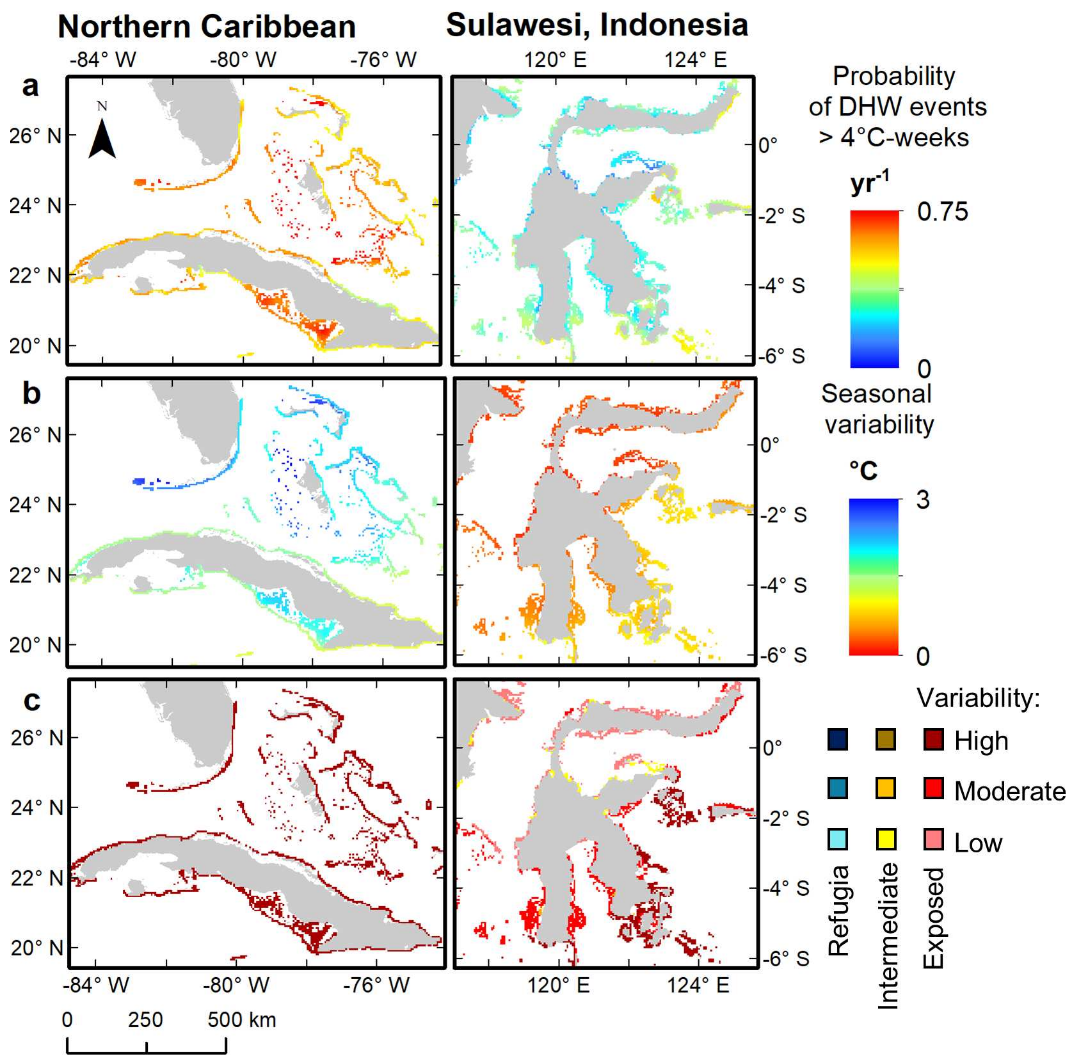


**Fig 5. Probability of DHW events > 4˚C-weeks (a), seasonal SST variability (b) and exposure category (c) in the Northern Caribbean and Sulawesi, Indonesia at 1.5˚C of global warming.** Exposure categories are thermal refugia (probability of DHW events > 4˚C-weeks less than 0.1 $yr^{-1}$), intermediate (probability of DHW events > 4˚C-weeks from 0.1–0.2 $yr^{-1}$) and exposed (probability of DHW events > 4˚C-weeks greater than 0.2 $yr^{-1}$). Exposure categories are split by the level of SST variability (high = seasonal OR inter-annual variability > 0.7˚C, low = seasonal AND inter-annual variability < 0.3˚C, moderate = all others). The base map is made with Natural Earth.

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Reef pixels with high SST variability (Fig 4) are the most promising candidates for corals surviving through adaptation. In areas of high variability, species are better equipped, both physiologically [54] and genetically [29], to cope with thermal stress. However, the variable conditions that increase thermal tolerance also drive bleaching risk [26]. Regions with high inter-annual variability are already some of the most thermally stressed due to periodic high temperatures associated with El Niño [32]. High latitude regions with high seasonal variability experience frequent thermal stress with relatively low background warming (e.g. the Northern Caribbean, Fig 5). As a result, thermal refugia with high variability are rare at 1.5˚C of warming (407 global coral reef pixels, 0.17%), and are mostly located in French Polynesia, likely due to lower rates of warming.

Low variability reef areas have a low bleaching risk under low levels of background warming, but as global warming increases, these regions rapidly transition to experiencing very frequent thermal stress that leads to bleaching [26]. This is the case in much of the equatorial Coral Triangle (Fig 4); where thermal refugia in the 1986–2019 climate transition to exposed at 1.5˚C. Despite having high susceptibility to future thermal stress, low variability thermal refugia in South Sumatra and intermediate reefs in Sulawesi (Fig 5) may act as very short-term thermal refuges. Less exposed reefs in Central Sulawesi occur where river input influences local SST [55, 56]. Reefs in these thermal refugia are in poor health [57]. River input and nearby coastal developments result in high levels of marine pollution and sedimentation [55, 56], alongside overfishing and destructive fishing practices [57]. Management of anthropogenic pressures in low variability, less exposed reefs may however allow these areas to reseed in the short term and facilitate the recovery of the thermally exposed surrounding areas [2].

Higher thermal tolerance of corals in more variable regions facilitates the notion of a higher thermal threshold [31]. We sum SST $>$ 1˚C above the maximum monthly mean to calculate DHWs, following the commonly used NOAA Coral Reef Watch metric [39]. Donner [31] developed an offset to replace the 1˚C threshold with a spatially varying value determined by the variability in summer maximum SST. Using this thermal stress metric lowers the thermal exposure in regions where summer SST is highly variable, for example in the Persian Gulf that experiences wind-driven variability in summer SST [58], and in tropical East Pacific regions affected by El Niño [32]. Here, we use the standard (constant) 1˚C thermal threshold as the variability offset underestimates the observed thermal stress in these high maximum SST variability regions [31]. For example, we find no thermal stress events $>$ 4˚C-weeks in 1986–2019 in the Persian Gulf when thermal stress is calculated using the variability offset (S6 Fig), yet Persian Gulf reefs have experienced high thermal stress leading to bleaching in multiple years [58]. Our projections for these regions are therefore likely to be conservative.

## Thermal refugia in coral conservation

Future warming will quickly result in thermal stress events that are, without adaptation by corals, too frequent for the persistence of corals currently living in thermal refugia (Fig 6). Thermal refugia at 1.5˚C of global warming are very rare, and non-existent for 2.0˚C. We demonstrate that thermal refugia in upwelling areas (e.g. Sumatra-Java) are not widespread, and clearly not enough to save contemporary coral reef ecosystems. Many known upwelling and high-current areas previously identified as refugia are not thermal refugia under future warming. Future thermal refugia in existing coral locations are predicted for a very limited number of coral reef areas.

Our projections of future thermal refugia are dependent on the refugia criteria. We use an ecologically relevant threshold based on the capacity of coral communities to recover following bleaching in the past [37]. However, there will likely be regional and local-scale differences in the recovery rate of coral reef ecosystems. Micro-refugia may exist on smaller spatial scales than those projected here ($<$ 100 m) [6], e.g. in unique environments, such as lagoons, not well represented by global SST observations [59]. In addition, corals have found refugia at depth during past thermal stress events [60]. However, deep refugia are not guaranteed as high thermal stress and significant bleaching can still occur [60, 61]. High frequency temporal variability in SST can decrease coral bleaching [62, 63] but higher than daily temporal resolution for global observational SST is lacking. Turbid reefs may act as potential refuges from thermal stress-induced coral bleaching due to reduced irradiance [64]. Our projected probability of thermal stress is calculated using a minimum 30-year period so indicates where long-term thermal refugia might exist under future warming. These projections can then be used

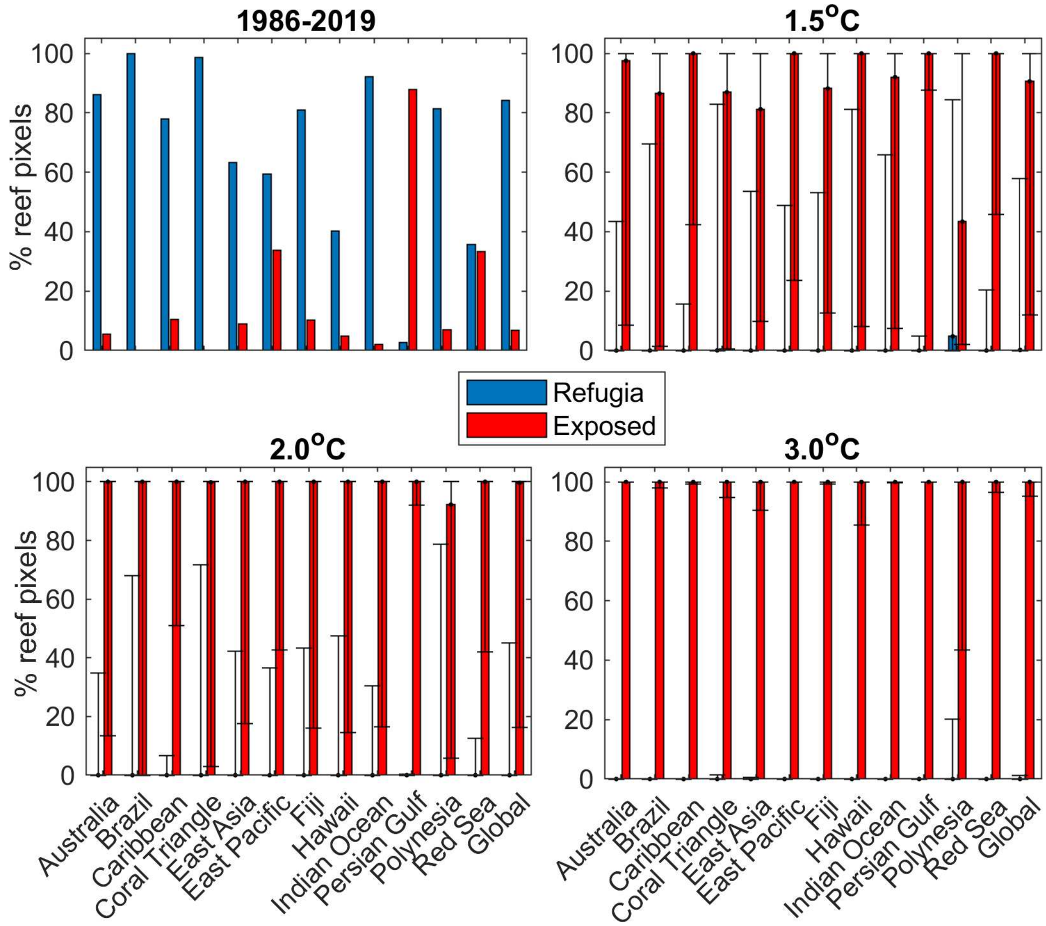


**Fig 6. Percentage of thermal refugia and exposed reef pixels in 12 coral reef regions and globally in the 1986–2019 climate and at 1.5, 2.0 and 3.0˚C of global warming.** As with 3.0˚C, there are 0% thermal refugia and 100% exposed reefs at 4.0˚C of global warming. Error bars are the percentage of thermal refugia and exposed reefs identified using the maximum and minimum probability of DHW events > 4˚C-weeks simulated by the 57 sets of CMIP6 climate projections (15 models and four SSP emissions scenarios: two climate models, GFDL-CM4 and NESM3, had only two and three SSP runs available, respectively).

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alongside other environmental variables, such as water clarity and irradiance, to identify multi-stressor climate refugia.

Corals vary in their bleaching susceptibility depending on species, geographic location and presence of thermally tolerant symbiont clades [64]. While high tolerance to thermal stress does not identify an area as a refugium, knowing which species and locations will be better able to cope with ocean warming can aid conservation decision making [6]. Corals will need to adapt in order to persist in their current locations, but whether they'll be able to do this fast enough is unclear. Refugia have been suggested as "slow lanes" which may allow time for genetic adaptation to warmer conditions [65] but species living in refugia may also have low adaptation potential as it is the inhospitable conditions that drive adaptation [66]. High SST variability reefs are promising candidates for adaptation as variable environments can promote thermal tolerance [30]. Low variability thermal refugia and high variability exposed reefs may be useful in multi-objective management approaches. By supplying coral larval recruits and reef-associated species [2], low variability thermal refugia may promote the recovery of high variability exposed reefs in the next decade as they undergo more frequent thermal stress. As climate change progresses, high variability exposed reefs may be better able to facilitate the recovery of the low variability thermal refugia once they become exposed by supplying more thermally tolerant larval recruits. This approach requires connectivity between the low variability thermal refugia and high variability exposed reefs. Prior exposure can lead to shifts in community composition to more stress-tolerant species rather than adaptation [67]. In some cases, promoting the conservation of high variability reefs may succeed in conserving the most thermally-tolerant coral species but not maintain ecosystems in their present state. Furthermore, prior thermal stress exposure in 1998 and 2002 did not lessen bleaching severity on the Great Barrier Reef in 2016 [1]. As such, prior thermal exposure does not guarantee adaptation.

The rapid increase in the frequency of thermal stress events on corals in their current locations reinforces the need for alternative management approaches [68, 69], alongside the implementation of marine protected areas. Coral reefs are shifting their range to locations with more favourable climate conditions [70]. High latitude reefs may provide a crucial habitat for migrating corals adapted to tropical SST [53]. Corals and their associated species have expanded their ranges poleward in Australia [71, 72] and Japan [73], in a process known as tropicalisation. Dynamic management approaches may facilitate the movement of coral populations over time [68]. Prioritising present thermal refugia in management strategies may provide stepping stones for migrating corals to more favourable habitats [65]. However, concomitant ocean acidification is likely to limit the poleward extent of reef-accreting corals due to reductions in aragonite saturation state [74]. In future research, our projections can be used to estimate future thermal stress at high latitudes for corals adapted to tropical baseline temperatures in different locations around the world. Assisted evolution and the translocation of heat-tolerant corals also require further exploration, especially for the coral reef regions projected to lose all thermal refugia by 1.5˚C of warming. The projections presented here are a valuable tool to be considered alongside other sources of climate exposure, non-climate related stressors, ecological processes and socioeconomic factors for effective coral reef management in the face of future climate change [3, 25].

## Materials and methods

### Coral reef area

We obtained the latitudinal and longitudinal coordinates for the global coral reef area at 1 km resolution from the UNEP World Conservation Monitoring Centre dataset [75]. The dataset includes tropical and subtropical coral reefs and spans a latitudinal range of approximately -35 to 35˚N. We divided the global coral reef area into 12 biogeographically distinct regions described by McWilliam *et al.* [76]. These regions vary in their functional redundancy and so indicate susceptibility to ecological changes with climate change [76]. There are 232,828 1 km reef pixels included in the analysis.

### Increasing the resolution of climate model projections

We applied statistical downscaling by linear regression that relates fine and coarse-scale climate variables [77]. The fine-scale local climate conditions are represented by observational historical SST data obtained from two global datasets: the 5 km resolution European Space Agency (ESA) Climate Change Initiative (CCI) SST Analysis daily dataset [41] from 1985–2006 and the 1 km Multi-scale Ultra-high Resolution (MUR) SST Analysis dataset [16] from 2006–2019. SST is an estimate of the upper ocean (1–20+ m) temperature in the absence of diurnal temperature variability [78]. We combined these two observational datasets to provide daily SST data from 1985–2019 for each reef pixel (S1 Appendix). We downscaled the 5 km

CCI dataset to 1 km using the change factor technique [79, 80]. The 1 km MUR dataset is bias adjusted to the 1 km downscaled CCI dataset. For locations where CCI data demonstrably used climatological values, they were replaced by CoralTemp SST data [81] downscaled using the same approach.

The coarse-scale SST refers to the larger-scale atmospheric predictor that is simulated by the CMIP6 climate models [15], downloaded from ESGF-CoG (https://esgf-node.llnl.gov/projects/cmip6/). We obtained simulated daily SST data from 1985 to 2100 for historical and four Shared Socioeconomic Pathway (SSP) experiments (SSP1 2.6, SSP2 4.5, SSP3 7.0 and SSP5 8.5) for 15 CMIP6 models with a spatial resolution of less than 100 km (S2 Appendix). SST data is linearly interpolated longitudinally to fill grid points missing data as in Van Hooidonk *et al.* [14]. Climate model daily SST is converted to 1 km resolution by bilinear interpolation and the SST data extracted for each 1 km reef pixel.

Linear models are generated based on the relationship between observed and simulated historical (1985–2019) daily SST (S3 Appendix). We generated four separate linear models to reflect SST variability by season (Jan-Mar, Apr-Jun, Jul-Sept and Oct-Dec) for each 1 km reef pixel. Observational SST is not well correlated with climate model output because model runs cannot provide correspondence in time between reality and the climate model [15]. The observational and simulated data were therefore ranked in ascending order according to the asynchronous piecewise linear regression technique used by Stoner *et al.* [15]. The approach uses a piecewise linear regression technique to find the relationship between the spread of simulated output and observed data whereby the highest observed SST corresponds to the highest simulated SST. The simple linear regression is suitable for this study due to the relatively low day-to-day, seasonal and inter-annual SST variability in the tropics [15]. We applied these seasonal linear models to the climate model daily ensemble mean projections to modulate local-scale SST projections.

A key assumption of statistical downscaling is that the relationship between large and local scale SST will be unchanged in the future [77]. Our projections capture present-climate local-scale SST features, for example where seasonal upwelling lowers summer SST. However, local-scale features may be altered under future climate change, for example upwelling may be reduced or enhanced. Such changes will not be captured by statistically downscaled projections [14]. Further, we maintain the coarse resolution model-simulated long-term warming trend in our downscaled projections and so may not capture local-scale spatial variation in warming, for example where upwelling areas do not warm as rapidly as non-upwelling reefs nearby [82].

## Identifying thermal refugia

Thermal refugia are reef pixels with a low probability of a thermal stress event occurring in a given year. We calculated the probability of thermal stress events of Degree Heating Week (DHW) values greater than 4˚C-weeks (S7 Fig and S1 Dataset). DHW is the sum of SST anomalies 1˚C higher than the long-term maximum monthly mean (MMM) over a 12-week period [39]. We calculated the long-term (1985–2012) MMM following the NOAA Coral Reef Watch approach by re-centring the monthly mean SST to the 1985–1990 + 1993 period [83]. This approach allows a sufficient (28-year) time period to be used to capture inter-annual variability in the climatology while minimising the effect of chronic warming over the 1985–2012 time period [84]. The 4˚C-week thermal stress threshold is useful for estimating bleaching occurrence [40]. Observed bleaching is likely to vary on less than 1 km scales due to varying tolerances to thermal stress between coral species and other factors influencing bleaching susceptibility such as nutrient input [85], light exposure [86] and diurnal and intra-seasonal temperature variability [62, 63]. The 4˚C-week threshold is not necessarily a predictor of bleaching at the 1 km scale but is useful for comparing thermal exposure between reefs now and in the future.

We calculated seasonal and inter-annual SST variability (S2 Dataset) as indicators of acclimation or adaptation potential [87]. Previous studies have indicated that past elevations in temperature associated with seasonal and inter-annual temperature variability have lowered the bleaching susceptibility of corals [30, 88, 89]. We transformed monthly SST into frequency bands using Fourier transform and calculated the root mean square (RMS) of spectral energy in the seasonal (0.5–1 year) and inter-annual (3–8 year) bands [26]. Changes in seasonal and inter-annual variability with increased global warming are not robust across climate models and emissions scenarios for all global coral reef pixels (S1 Table). The change in inter-annual variability is not robust for reef pixels with the highest inter-annual variability, indicating uncertainty in future changes to El Niño Southern Oscillation. We therefore used observed seasonal and inter-annual variability to identify high variability reef pixels under increased levels of global warming.

Model uncertainty in SST projections is reduced by downscaling all models and SSP experiments separately and creating large ensembles including different models and emissions pathways in each of four global mean temperature change scenarios (1.5, 2.0, 3.0 and 4.0˚C). The global mean temperature change is defined as the change in decadal global mean surface temperature from a pre-industrial baseline (1861–1901). We used a pre-industrial baseline rather than a century-scale baseline due to the greater availability of climate model output for the historical experiments compared to the historical natural climate experiments. All model years in which the decadal global mean surface temperature change is within 0.2˚C of the global warming level (e.g. 1.3–1.7˚C for the 1.5˚C level) [90] are included in the calculation of the ensemble mean probability of DHW events greater than 4˚C-weeks (S8 Fig).

Coral recovery following bleaching mortality varies spatially but is limited in the first five years and possible in 10 years [37]. We identified thermal refugia as reef pixels with a probability of DHW events > 4˚C-weeks less than 0.1 $yr^{-1}$. Exposed reef pixels have a probability of DHW events > 4˚C-weeks greater than 0.2 $yr^{-1}$. Reef pixels with a probability of DHW events > 4˚C-weeks from 0.1–0.2 $yr^{-1}$ are described as intermediate. The probability is the number of events during a present-day or future time period divided by the length of the period. A probability of 0.1 $yr^{-1}$ corresponds to thermal stress events occurring every 10 years and 0.2 $yr^{-1}$ every five years. A probability of 1.0 $yr^{-1}$ corresponds to annual thermal stress. We calculated the minimum and maximum simulated probability of thermal stress per pixel to calculate the uncertainty in the percentage of reef pixels in each exposure category (refugia, intermediate or exposed).

We defined low variability reefs as those with seasonal and inter-annual variability less than 0.3˚C and high variability reefs as those with seasonal or inter-annual variability greater than 0.7˚C [26]. We lowered the threshold for inter-annual variability from 0.9˚C in Langlais *et al.* [26] to 0.7˚C to incorporate reefs heavily influenced by El Nino across the tropical Pacific [32]. We compared regional thermal refugia and exposed reefs in the present-day climate (1986–2019) and at 1.5, 2.0, 3.0 and 4.0˚C global mean temperature change between 12 coral reef regions.

## Supporting information

**S1 Fig. The difference between the maximum monthly mean (MMM) calculated using the Coral Reef Watch (CRW) CoralTemp product and the MMM calculated using the bias corrected and downscaled Climate Change Initiative (CCI) dataset.** The difference is calculated

as the CCI MMM minus the CoralTemp MMM, therefore values from 0–1˚C indicate where the CCI MMM is higher than CoralTemp and values from -1–0˚C indicate where the CoralTemp MMM is higher than CCI. The 5 km MMM was calculated from the CoralTemp SST and hotspot products and converted to 1 km resolution using bilinear interpolation. The CCI dataset was downscaled and bias corrected to the 1 km Multi-scale Ultra-high Resolution (MUR) dataset and then the MMM calculated. Both MMMs were calculated using the NOAA CRW approach; the monthly mean climatologies were calculated using data from 1985–2012 and re-centered on the period 1985–1990+1993. The hottest monthly mean was then selected as the MMM. The observed Degree Heating Weeks (DHW) calculated using the combined bias corrected CCI and MUR datasets are lower than previously reported for most of the world's coral reefs because the MMM is higher. The base map is made with Natural Earth.
(TIF)

**S2 Fig. Global distribution of exposure category in the 1986–2019 climate and at 1.5 and 2.0˚C of future global warming using the 8˚C-weeks thermal stress threshold.** Exposure categories are thermal refugia (probability of DHW events > 8˚C-weeks less than 0.1 $yr^{-1}$), intermediate (probability of DHW events > 8˚C-weeks from 0.1–0.2 $yr^{-1}$) and exposed (probability of DHW events > 8˚C-weeks greater than 0.2 $yr^{-1}$). There are no thermal refugia and all reef pixels are exposed at 3.0 and 4.0˚C of global warming. Percentages indicate the regional (on map) and global (right of map) proportion of thermal refugia (blue) and exposed reefs (red). The 12 coral reef regions are outlined in light blue. The base map is made with Natural Earth.
(TIF)

**S3 Fig. Correlation between the rate of change in the probability of thermal stress and inter-annual SST variability.** The rate of change in the probability of thermal stress is the linear slope in the probability of thermal stress events > 4˚C-weeks from the 1986–2019 climate to 1.5, 2.0, 3.0 and 4.0˚C. There is a significant negative correlation between the rate of change in the probability of thermal stress and inter-annual SST variability.
(TIF)

**S4 Fig. Correlation between the change in the probability of thermal stress and seasonal SST variability.** The change in the probability of thermal stress is the difference between the probability of thermal stress events > 4˚C-weeks in the 1986–2019 climate and 1.5˚C of global warming relative to pre-industrial levels. The colour indicates the probability of thermal stress events > 4˚C-weeks in the 1986–2019 climate. There is a significant positive correlation between the change in the probability of thermal stress and seasonal SST variability. This relationship breaks down where reef pixels have high seasonal SST variability and the probability of thermal stress is already high in the 1986–2019 climate (e.g. in the Persian Gulf).
(TIF)

**S5 Fig. High resolution image (3,000 dpi) of the global distribution of exposure category and SST variability level in the 1986–2019 climate and at 1.5, 2.0 and 3.0˚C of future global warming relative to pre-industrial levels.** Exposure categories are thermal refugia (probability of DHW events > 4˚C-weeks less than 0.1 $yr^{-1}$), intermediate (probability of DHW events > 4˚C-weeks from 0.1–0.2 $yr^{-1}$) and exposed (probability of DHW events > 4˚C-weeks greater than 0.2 $yr^{-1}$). Exposure categories are split by the level of SST variability (high = seasonal OR inter-annual variability > 0.7˚C, low = seasonal AND inter-annual variability < 0.3˚C, moderate = all others). The 12 coral reef regions are outlined in blue. The base map is made with Natural Earth.
(PDF)

**S6 Fig. Thermal exposure calculated using the variability offset.** a) Global distribution of the variability offset in 12 coral reef regions during the period 1986–2019. The variability offset is the normalised standard deviation in the annual maximum monthly SST. b) Global distribution of the probability of DHW events > 4˚C-weeks. c) Global distribution of the 1986–2019 exposure category: thermal refugia (probability of DHW events > 4˚C-weeks less than 0.1 $yr^{-1}$), intermediate (probability of DHW events > 4˚C-weeks from 0.1–0.2 $yr^{-1}$) and exposed (probability of DHW events > 4˚C-weeks greater than 0.2 $yr^{-1}$). Percentages indicate the regional proportion of thermal refugia (blue) and exposed reefs (red). The base map is made with Natural Earth.
(TIF)

**S7 Fig. Probability of DHW events > 4˚C-weeks in 12 coral reef regions in 1986–2019 and at 1.5, 2.0, 3.0 and 4.0˚C of global warming relative to pre-industrial levels.** The base map is made with Natural Earth.
(TIF)

**S8 Fig. Probability of DHW events > 4˚C-weeks for global coral reef pixels simulated by 15 CMIP6 models and four Socioeconomic Pathways (SSPs) under 1.5, 2.0, 3.0 and 4.0˚C of global warming relative to pre-industrial levels.** Outliers (>1.5 * interquartile range) are shown by the black dots.
(TIF)

**S1 Table. Percentage of global coral reef pixels with a robust (positive: > 0.01˚C or negative: < -0.01˚C) SST variability trend from observed (1985–2019) to future global warming scenario.** A trend is considered robust if simulated by 75% of models. Of those reef pixels with a robust change in inter-annual SST variability, none are those pixels most heavily influenced by El Niño Southern Oscillation in the observed climate (tropical Pacific).
(DOCX)

**S1 Appendix. Combining 5 km and 1 km observational sea surface temperature datasets.**
(DOCX)

**S2 Appendix. Simulated SST data used in statistical downscaling.**
(DOCX)

**S3 Appendix. Statistical downscaling of SST.**
(DOCX)

**S1 Dataset. Probability of thermal stress > 4˚C-weeks in the 1986–2019 climate and at 1.5, 2.0, 3.0 and 4.0˚C of global warming.**
(XLSX)

**S2 Dataset. Seasonal and inter-annual SST variability in the 1986–2019 climate.**
(XLSX)

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