Received: 28 February 2020 | Revised: 3 July 2020 | Accepted: 3 July 2020
DOI: 10.1111/gcb.15293

PRIMARY RESEARCH ARTICLE

Global Change Biology WILEY

Vulnerability of global coral reef habitat suitability to ocean warming, acidification and eutrophication

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Funding information
China Scholarship Council

Abstract

Coral reefs are threatened by global and local stressors. Yet, reefs appear to respond differently to different environmental stressors. Using a global dataset of coral reef occurrence as a proxy for the long-term adaptation of corals to environmental conditions in combination with global environmental data, we show here how global (warming: sea surface temperature; acidification: aragonite saturation state, Ω_{arag}) and local (eutrophication: nitrate concentration, and phosphate concentration) stressors influence coral reef habitat suitability. We analyse the relative distance of coral communities to their regional environmental optima. In addition, we calculate the expected change of coral reef habitat suitability across the tropics in relation to an increase of 0.1°C in temperature, an increase of 0.02 μmol/L in nitrate, an increase of 0.01 μmol/L in phosphate and a decrease of 0.04 in Ω_{arag}. Our findings reveal that only 6% of the reefs worldwide will be unaffected by local and global stressors and can thus act as temporary refugia. Local stressors, driven by nutrient increase, will affect 22% of the reefs worldwide, whereas global stressors will affect 11% of these reefs. The remaining 61% of the reefs will be simultaneously affected by local and global stressors. Appropriate wastewater treatments can mitigate local eutrophication and could increase areas of temporary refugia to 28%, allowing us to 'buy time', while international agreements are found to abate global stressors.

KEYWORDS
coral reef, eutrophication, global warming, habitat suitability, ocean acidification, temporary refugia

1 | INTRODUCTION

Coral reefs are among the most productive and diverse ecosystems on Earth and have enormous ecological, social and economic importance (Cesar & Chong, 2004; Moberg & Folke, 1999). They provide habitat for almost one quarter of the world's marine species (Fisher et al., 2015) and contribute billions of dollars in economic value through coastal protection, food and tourism (Beck, Losada, Reguero, Mendendez, & Burke, 2017; Costanza et al., 2014; Martínez et al., 2007; Pauly et al., 2002). However, the ecosystems and ecological services coral reefs provide are being degraded (Hughes et al., 2003) by various anthropogenic stressors, including global warming (Carpenter et al., 2008; Kornder, Riegl, & Figueiredo, 2018), ocean acidification (Anthony et al., 2011; De'ath, Lough, & Fabricius, 2009), eutrophication (Brodie, Fabricius, De'ath, & Okaji, 2005; Bruno, Petes, Harvell, & Hettinger, 2003) and overfishing (Zaneveld et al., 2016). Global (ocean acidification and global warming) and local (nutrient enrichment) stressors can have negative effects on coral reef systems at both organism and ecosystem levels (Cooper, De'ath, Fabricius, & Lough, 2008; Eakin et al., 2010; Ferrier-Pagès, Gattuso, Dallot, & Jaubert, 2000). It is therefore of crucial importance to identify the current ecological status of coral reefs and to evaluate the impacts that changes in environmental conditions will have on coral reefs, especially for developing appropriate conservation and restoration strategies.

In this respect, a classic result is represented by the vulnerability map of global reef ecosystems by the Reefs at Risk Project (Bryant, Burke, McManus, & Spalding, 1998; Burke, Reytar, Spalding, & Perrry, 2011). This project produced a threat index that combined destructive fishing, coastal development, marine pollution and other types of stressors. Another prominent study (Selkoe et al., 2009) estimated the cumulative human impacts on coral reef ecosystems of the Northwestern Hawaiian Islands by using information of anthropogenic threats in combination with habitat maps and expert judgment on the vulnerability of different habitat types. The subjective opinions of experts are relevant contributions (Kappel, Halpern, Selkoe, & Cooke, 2011) in relation to the social and institutional conditions characterising the region of interest, especially when based on observational data or direct experience. However, bias may exist (Halpern, Selkoe, Micheli, & Kappel, 2007), for example, due to the individual backgrounds of the people sharing their experience, the research focus areas of the institutions and researchers conducting the analysis, or to a phenomenon called 'shifting baseline', in which an individual's perception of the state of an ecosystem is based on recent experience rather than on a long-term, historical perspective (Knowlton & Jackson, 2008; Pauly, 1995). Expert opinions, therefore, provide a rather qualitative assessment of coral reef status instead of quantitative information.

In response to the heat waves of 2016 and 2017, corals of the northern Great Barrier Reef (GBR) underwent severe bleaching, but no substantial impacts were observed in the southern regions of the GBR (Hughes, Kerry, & Simpson, 2018). These different responses and the possibility that certain regions can constitute ecological refugia for corals, call for studies aiming at assessing the status of coral reef habitats and at identifying areas where such habitats may remain suitable for coral reefs under changing local and global threats. Physical and chemical conditions can be measured with accuracy and precision, and robust methods can be developed to identify the habitat suitability range of ecological communities in relation to these conditions. Species distribution models (SDMs), such as those based on Maximum Entropy (Maxent), Boosted Regression Trees or Generalized Linear Models, are typically used to forecast changes in coral reef habitat suitability under climate change (Cacciapaglia & van Woesik, 2015; Couce, Ridgwell, & Hendy, 2013; Descombes et al., 2015; Freeman, Kleypas, & Miller, 2013). However, because they extrapolate to future conditions, these models cannot be easily validated, especially when projections are made to conditions outside the training range imposed by the available data. Moreover, most of these studies focus on the consequences of global warming and/or ocean acidification so that comparatively less is known about habitat suitability changes due to eutrophication.

Here, we present a new quantitative method for calculating a habitat suitability index for coral reefs that is based on global biogeochemical data and the current position of coral reefs within their global and regional suitability ranges of physical and chemical conditions, which are: (a) sea surface temperature (SST), (b) aragonite saturation state (Ω_{arag}), (c) nitrate concentration $[NO_3^-]$ and (d) phosphate concentration $[PO_4^{3-}]$. We assume that coral reefs have adapted to these environmental ranges over evolutionary time scales and that the conditions under which they occur in the modern ocean can provide relevant information about their habitat suitability. Although, like other organisms, corals can be affected by many different factors, including physical (e.g. salinity, light availability and waves) and biological (e.g. larval dispersal and diversity) factors, our study is focused on the four factors considered among the first-order determinants of coral reef distributions worldwide (Kleypas, Mcmanus, & Meñez, 1999). Being limited to these four factors, the results of our study are to be considered as conservative.

Given the difficulties of measuring the physiological and ecological performances of coral reefs on a global scale and in relation to a diverse array of environmental factors, also due to the broad varieties of species forming coral communities, we use the global dataset of coral reef occurrence as a proxy for their long-term adaptation to contextual environmental conditions and for defining their habitat suitability ranges. We infer coral habitat suitability ranges from the number of coral reefs occurring at given environmental conditions. According to this approach, coral communities living near the limits of their habitat suitability ranges are more vulnerable than those living close to their optimum.

We quantify coral reef habitat suitability with respect to each environmental variable individually. This approach separates local threats (e.g. nutrient eutrophication, which is manageable with local and relatively straightforward solutions) from global threats (e.g. global warming and ocean acidification, which require challenging global solutions for decreasing greenhouse gas emissions). We further provide an overview about the changes in coral reef habitat suitability across all the tropics in relation to expected shifts in environmental conditions. The changes in habitat suitability are calculated within the environmental ranges of present-day analogues and do not extend into unknown conditions. We identify areas that, under environmental change, can (a) remain suitable habitats or even improve their habitat suitability (temporary refugia), (b) become unsuitable habitats in relation to local stressors (eutrophication), (c) become unsuitable habitats in relation to global stressors (warming and acidification) and (d) become unsuitable habitats in relation to both local and global stressors (eutrophication combined with warming and/or acidification).

2 | MATERIALS AND METHODS

2.1 | Coral reef data

Charted reef data were obtained from the Global Distribution of Coral Reefs 2010. The data were originally recorded as polygons in DBF format, with the majority (85%) of them mapped at a 30 m resolution.

We used these data to create an 'observed' reef habitat distribution map at a 30″ × 30″ grid cell resolution. Specifically, we overlaid the charted reef polygons onto a 21,600 × 43,200 matrix of the bathymetric profile (obtained from GEBCO_08 Grid, version 2010, available at http://www.gebco.net in netCDF format). Any grid cell that contained one or more points of a reef polygon was assigned the value of 1, reflecting the presence of coral reefs or a suitable reef habitat. The value 0 was assigned to grid cells that did not contain reefs.

2.2 | Environmental data

We considered global data of temperature (SST; Locarnini et al., 2019), nitrate (NO_3^-; Garcia et al., 2019), phosphate (PO_4^{3-}; Garcia et al., 2019) and aragonite saturation state (Ω_{arag}) at the sea surface. Temperature data are provided on a spatial resolution of 0.25° × 0.25°, while nitrate and phosphate data are on a 1° × 1° spatial resolution. The Ω_{arag} was obtained from the Global Ocean Data Analysis Project (GLODAP) version 2 (GLODAPv2) and a 17 year dataset of surface water Ω_{arag} in the Caribbean Sea. We choose mapped climatologies (GLODAPv2.2016b; Lauvset et al., 2016) and annual mapped data in the Caribbean Sea (Wanninkhof, Pierrot, Sullivan, Barbero, & Trinanes, 2020) for Ω_{arag}. Reef locations not covered by GLODAPv2 and annual mapped data in the Caribbean Sea (they include the Red Sea and some parts of the Caribbean regions) are filled with data using interpolation. The interpolation algorithm is based on discrete cosine transforms (Garcia, 2010; Wang, Garcia, Liu, de Jeu, & Dolman, 2012). The Ω_{arag} has a 1° × 1° spatial resolution. The resolution of all environmental data was then adapted to match the spatial resolution of the coral reef data (i.e. 30″ × 30″). This was done by subdividing the 0.25° × 0.25° grid cells of SST into 30 × 30 sub-grid cells and the 1° × 1° grid cells of $[NO_3^-]$, $[PO_4^{3-}]$ and Ω_{arag} into 120 × 120 sub-grid cells. The sub-grid cells are assigned the same environmental conditions according to the value of the original cell subdivision. Due to a topographic mismatch problem (Guan, Hohn, & Merico, 2015), the environmental variables along coastlines were also interpolated based on discrete cosine transforms.

Since autocorrelations among the chosen environmental variables could constitute a limitation to our study, we investigated this possibility with a Principle Component Analysis on data at reef locations and, for comparison, on data at global ocean scale (but excluding reef location data). The results of this analysis show that, at reef locations, the chosen environmental variables are only weakly correlated or uncorrelated (Figure S1a). This is in contrast with the results obtained at the global ocean scale, where the chosen variables are expectedly strongly correlated (Figure S1b), especially SST and Ω_{arag} and the two nutrients.

2.3 | Suitability index

We combined the observed spatial distribution of coral reefs with each environmental variable and analysed the frequency distribution of reef occurrence for each environmental variable at the global scale. We constructed histograms between the minimum and maximum of each environmental variable x at the corresponding charted coral reef location. The bin size of each histogram was determined by the Freedman–Diaconis' rule (Freedman & Diaconis, 1981) using the following formula:

$$\text{Bin size} = 2\left[\frac{(q_{75} - q_{25})}{\sqrt[3]{n}}\right],$$

where $q_{75} - q_{25}$ is the interquartile range of the data and n is the number of observations of each environmental variable.

We then used a skewed normal distribution model to fit each histogram. The skewed normal distribution was chosen due to the hump-shaped relationship between each environmental variable and frequency distribution of reef occurrence showed in each histogram.

The standard normal probability density function $\varnothing(x)$ is defined as

$$\varnothing(x) = \frac{1}{\sqrt{2\pi}} e^{-\frac{x^2}{2}}. \tag{1}$$

The cumulative distribution function is defined as

$$\Phi(x) = \int_{-\infty}^{x} \varnothing(t)\,dt = \frac{1}{2}\left[1 + \text{erf}\left(\frac{x}{\sqrt{2}}\right)\right], \tag{2}$$

where erf is the error function, defined as

$$\text{erf}(x) = \frac{2}{\sqrt{\pi}} \int_0^x e^{-t^2} dt, \tag{3}$$

The frequency distribution function of a skewed normal distribution is given by

$$F(x) = 2\varnothing(x)\,\Phi(\alpha x), \tag{4}$$

where the parameter α defines the skewness of the distribution. When $\alpha = 0$, the frequency distribution equals a normal distribution. The distribution is right-skewed when $\alpha > 0$ and left-skewed when $\alpha < 0$. The skewness increases as the absolute value of α increases.

By applying the transformation $x \rightarrow (x - \xi)/\omega$, we obtain:

$$F(x) = \frac{2}{\omega}\varnothing\left(\frac{x-\xi}{\omega}\right)\Phi\left[\alpha\left(\frac{x-\xi}{\omega}\right)\right]. \tag{5}$$

The statistical parameters ξ, α and ω represent, respectively, location, skew and scale. We introduced a fourth parameter κ representing the amplitude of $F(x)$, so that:

$$F(x) = \frac{2}{\omega}\varnothing\left(\frac{x-\xi}{\omega}\right)\Phi\left[\alpha\left(\frac{x-\xi}{\omega}\right)\right]\kappa. \tag{6}$$

The best values of the four statistical parameters were derived numerically by fitting the histograms iteratively, starting with initial guessed values and iterating until a minimum sum of the variation from the original data was obtained. The best values for ξ, α and ω and κ are reported in Table S1.

The fitted frequency distributions $F(x)$ were then normalized to the range 0 and 1 by scaling the function to the minimum and maximum values as follows:

$$F(x)_n = \frac{F(x) - \min(F(x))}{\max(F(x)) - \min(F(x))}. \tag{7}$$

The value of the normalized frequency distribution $F(x)_n$ is 1 when reef occurrence is highest and is 0 when reef occurrence is lowest.

We assume that coral reefs have adapted to their environments over evolutionary time scales and that the conditions under which they thrive in the modern ocean can reflect the relevant habitat suitability, $S(x)_n$, for coral reefs.

Thus,

$$S(x)_n = F(x)_n \times 100\%, \tag{8}$$

with $S(x)_n = 100\%$ indicating an optimum condition (i.e. environmental values at which most of the reefs are found and thus suitable for coral growth) and $S(x)_n = 0\%$ indicating an unsuitable environmental condition (i.e. the condition least suitable for coral growth).

We also analysed the frequency distributions of reef occurrences for each environmental variable at a regional scale for six major regions (geographic information for the select regions are reported in Table S2). Regional histograms and normalized frequency distributions of reef occurrences were obtained following the same procedure described above for the global case. The six regions contained a total of 24,644 reef pixels (reefs in the Pacific side of the Great Caribbean Region fell outside the six regions), 85% of the global reef cover (accounting for 28,924 reef pixels).

2.4 | Habitat suitability change

We calculated derivatives of the regional habitat suitability to quantify the relative change in habitat suitability with respect to a bin size change in each environmental variable, independently of time. Therefore, these calculations are not related to ‘environmental change over time’ but simply to ‘environmental change’. The advantage of this simple approach is that it does not require knowledge on the exact environmental change trajectories that will unfold over time in the future. These calculations provide the habitat suitability change with respect to a potential 0.1°C warming, 0.04 decrease in Ω_{arag}, 0.02 μmol/L increase in $[NO_3^-]$ or 0.01 μmol/L increase in $[PO_4^{3-}]$ (Figure S6).

2.5 | Reef habitat classification

Within the six regions, areas were classified as follows. Areas showing a positive habitat suitability change with respect to all four environmental variables were classified as temporary refugia. Areas showing no habitat suitability change, and SST, $[NO_3^-]$ and $[PO_4^{3-}]$ are below optimal conditions, and Ω_{arag} is above optimal conditions, were also classified as temporary refugia. Areas showing a negative habitat suitability change under warming and/or decrease in Ω_{arag} were considered under global threats. Areas showing no habitat suitability change, where SST is above optimal conditions, and/or Ω_{arag} is below the optimal conditions, are also considered under global threats. Areas showing a negative habitat suitability change with respect to increase of $[NO_3^-]$ and/or $[PO_4^{3-}]$ were considered under local threats. Areas showing no habitat suitability change where $[NO_3^-]$ is above optimal conditions, and/or $[PO_4^{3-}]$ is above optimal conditions, are also considered under local threats. Areas showing a negative habitat suitability change due to warming and/or decrease in Ω_{arag} and increase in $[NO_3^-]$ and/or $[PO_4^{3-}]$ were considered under global and local threats. Finally, areas showing no habitat suitability change and SST, $[NO_3^-]$ and/or $[PO_4^{3-}]$ are above optimal conditions, and/or Ω_{arag} is under optimal conditions, are also considered under global and local threats.

3 | RESULTS

3.1 | Environmental optima for reef occurrences

We analysed the occurrences of coral reefs with respect to SST, Ω_{arag}, $[NO_3^-]$ and $\left[PO_4^{3-}\right]$ on a global scale considering all coral reefs worldwide. As mentioned in Section 1, we assumed that the environmental conditions under which the majority of reefs are found reflect the most suitable conditions (i.e. the optimal conditions) for coral reef growth and we produced histograms of global reef presence in relation to each environmental condition (Figure S2). The normalized frequency distributions derived from such histograms (see Section 2) show clear optima, that is, environmental conditions at which the occurrence of coral reefs is highest (Figure 1). These optima are 28.7°C, 3.8, 0.23 μmol/L and 0.15 μmol/L for SST, Ω_{arag}, $[NO_3^-]$ and $\left[PO_4^{3-}\right]$ respectively (Figure 1; Table 1).

Since the global frequency distributions are representative of an aggregation of multiple species over a larger scale, they can mask potential adaptations of coral communities to local environmental conditions. To identify regional differences, we assessed reef distributions in six specified regions of the tropical oceans. These regions contained a total of 24,644 reef pixels, representing 85% of the reef pixels found worldwide (see Section 2).

When the regional frequency distributions (all statistical parameters of the frequency distributions are reported in Table S1) are compared and related to the global environmental optima, clear differences among regions emerge (Figure 1). For example, the GBR is the region with the lowest SST optimum, 27.0°C (Figure 1a; Table 1), a Ω_{arag} optimum, 3.7, slightly lower than the global value

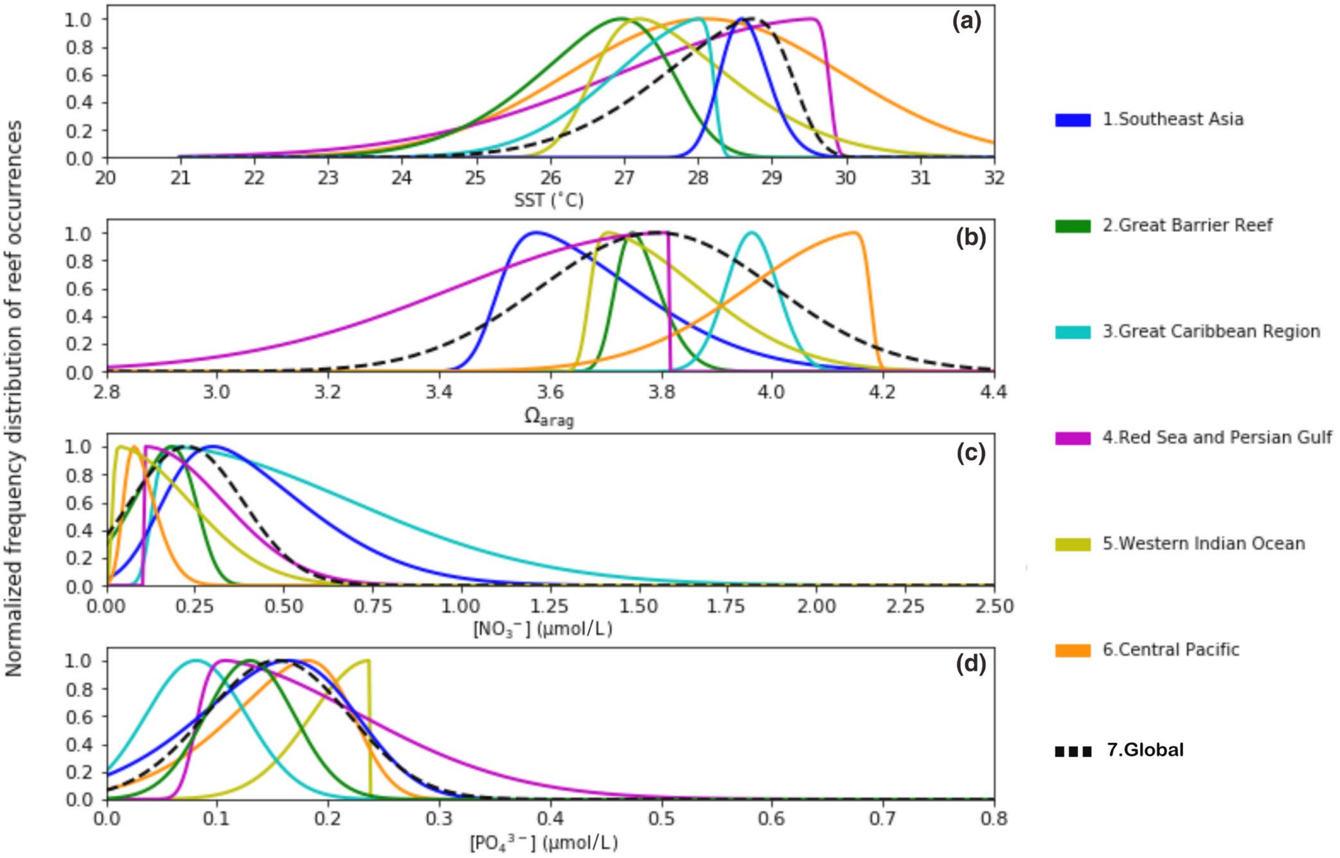

FIGURE 1 Normalized frequency distributions of reef occurrences for (a) SST, (b) Ω_{arag}, (c) $[NO_3^-]$ and (d) $[PO_4^{3-}]$ and for specific regions. The statistical parameters of the frequency distributions are reported in Table S1

TABLE 1 Global and regional optima (i.e. environmental values corresponding to the highest number of coral reef occurrences) for different environmental variables

Variable	SST (°C)	Ω_{arag}	$[NO_3^-]$ (µmol/L)	$[PO_4^{3-}]$ (µmol/L)
Global	28.7	3.8	0.23	0.15
Southeast Asia	28.6	3.6	0.30	0.17
Great Barrier Reef	27.0	3.7	0.18	0.13
Great Caribbean Region	28.0	4.0	0.19	0.08
Red Sea & Persian Gulf	29.5	3.8	0.11	0.11
Western Indian Ocean	27.2	3.7	0.04	0.24
Central Pacific	28.1	4.1	0.08	0.18

of 3.8 (Figure 1b; Table 1), a $[PO_4^{3-}]$ optimum, 0.13 µmol/L, slightly lower than the global value of 0.15 µmol/L (Figure 1d; Table 1), and a $[NO_3^-]$ optimum, 0.18 µmol/L, well below the global optimum of 0.23 µmol/L (Figure 1c; Table 1). In contrast, the Red Sea and Persian Gulf show the highest SST optimum, 29.5°C (Figure 1a; Table 1), a Ω_{arag} optimum, 3.8, equal to the global Ω_{arag} optimum of 3.8 (Figure 1b; Table 1), a $[NO_3^-]$ optimum, 0.11 µmol/L, lower than the global optimum of 0.23 µmol/L (Figure 1c; Table 1), and a $[PO_4^{3-}]$ optimum, 0.11 µmol/L below the global optimum of 0.15 µmol/L (Figure 1d; Table 1).

3.2 | Habitat suitability in relation to current conditions and future environmental shifts

Environmental conditions at reef locations in combination with habitat suitability maps provide visual overviews about the current status of reef communities. Here we used the normalized frequency distributions of reef counts in relation to each environmental parameter as a proxy for habitat suitability. We quantified the changes in habitat suitability with respect to ocean warming by 0.1°C, ocean acidification by 0.04 reduction in Ω_{arag} and eutrophication characterized by increases in $[NO_3^-]$ and $[PO_4^{3-}]$ by 0.02 and 0.01 µmol/L respectively.

In general, reef locations at higher latitudes and several reef locations along the equator show lower habitat suitability in relation to SST (Figure 2a). Low habitat suitability in reef locations along the equator results from SSTs higher than the corresponding regional optima, whereas low suitability at higher latitudes is generated by SST values below the corresponding regional optima. Most reef locations exhibit high habitat suitability for Ω_{arag} (Figure 2b). However, reef locations in Vietnam, Thailand, the Molukka Sea (Figure 2b, box 1), the northern part of the GBR (Figure 2b, box 2), the Great Caribbean Region (excluded the Bahamas and Cuba; Figure 2b, box 3), the Persian Gulf and the coast of Oman (Figure 2b, box 4) and equatorial islands in the Central Pacific (Figure 2b, box 6) show low habitat

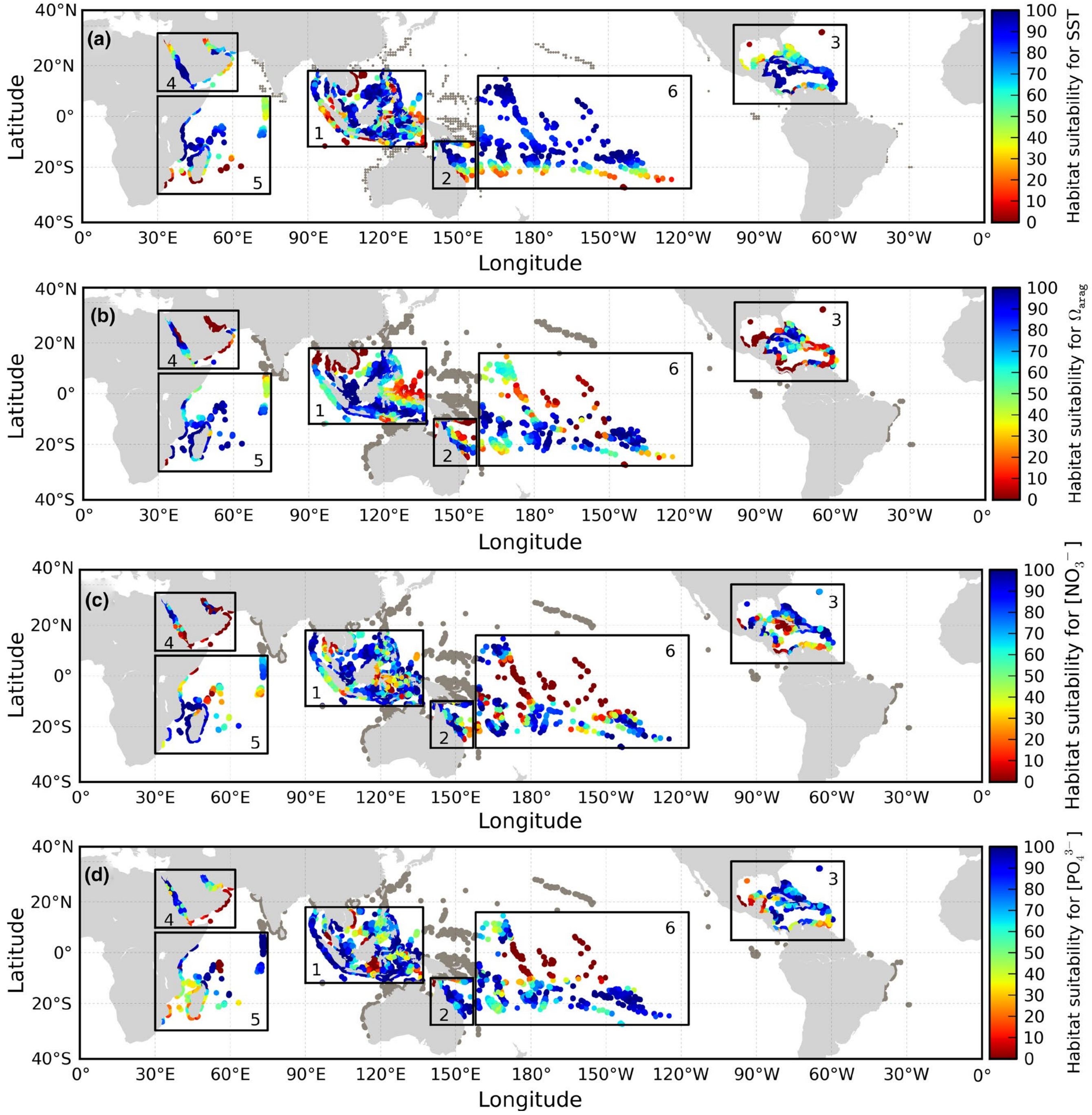

FIGURE 2 Habitat suitability in per cent in relation to (a) SST, (b) Ω_{arag}, (c) [NO_3^-] and (d) [PO_4^{3-}] and specific to each region. A more suitable habitat is indicated in blue, whereas a less suitable habitat is indicated in red

suitability with respect to their corresponding regional Ω_{arag} optima. Reef locations in the Makassar Strait, Gulf of Thailand (Figure 2c, box 1), Cuba, Coast Rica and Panama (Figure 2c, box 3), the southern Red Sea, the Persian Gulf and the coast of Oman (Figure 2c, box 4) and equatorial islands in the Central Pacific (Figure 2c, box 6) show a lower habitat suitability with respect to [NO_3^-]. Reef locations in the Makassar Strait (Figure 2d, box 1), Mexico and Belize (Figure 2d, box 3), the coast of Oman (Figure 2d, box 4) and equatorial islands in the Central Pacific (Figure 2d, box 6) show low habitat suitability with respect to [PO_4^{3-}].

An increase in SST by 0.1°C produces a strongest reduction in habitat suitability at reef locations of Southeast Asia (Figure 3a, box 1). Reef locations of GBR (Figure 3a, box 2), Caribbean region (Figure 3a, box 3) and Madagascar (Figure 3a, box 5) exhibit an increase in habitat suitability. The habitats of other regions, such as Red Sea and Persian Gulf (Figure 3a, box 4) and Central Pacific (Figure 3a, box 6) remain relatively unchanged or become slightly more suitable with warming. A change in Ω_{arag} by −0.04 produces a strongest decrease in habitat suitability in Nansha Islands, Java and Lesser Sunda Islands (Figure 3b, box 1), far northern and southern GBR (Figure 3b, box 2) and Great Caribbean

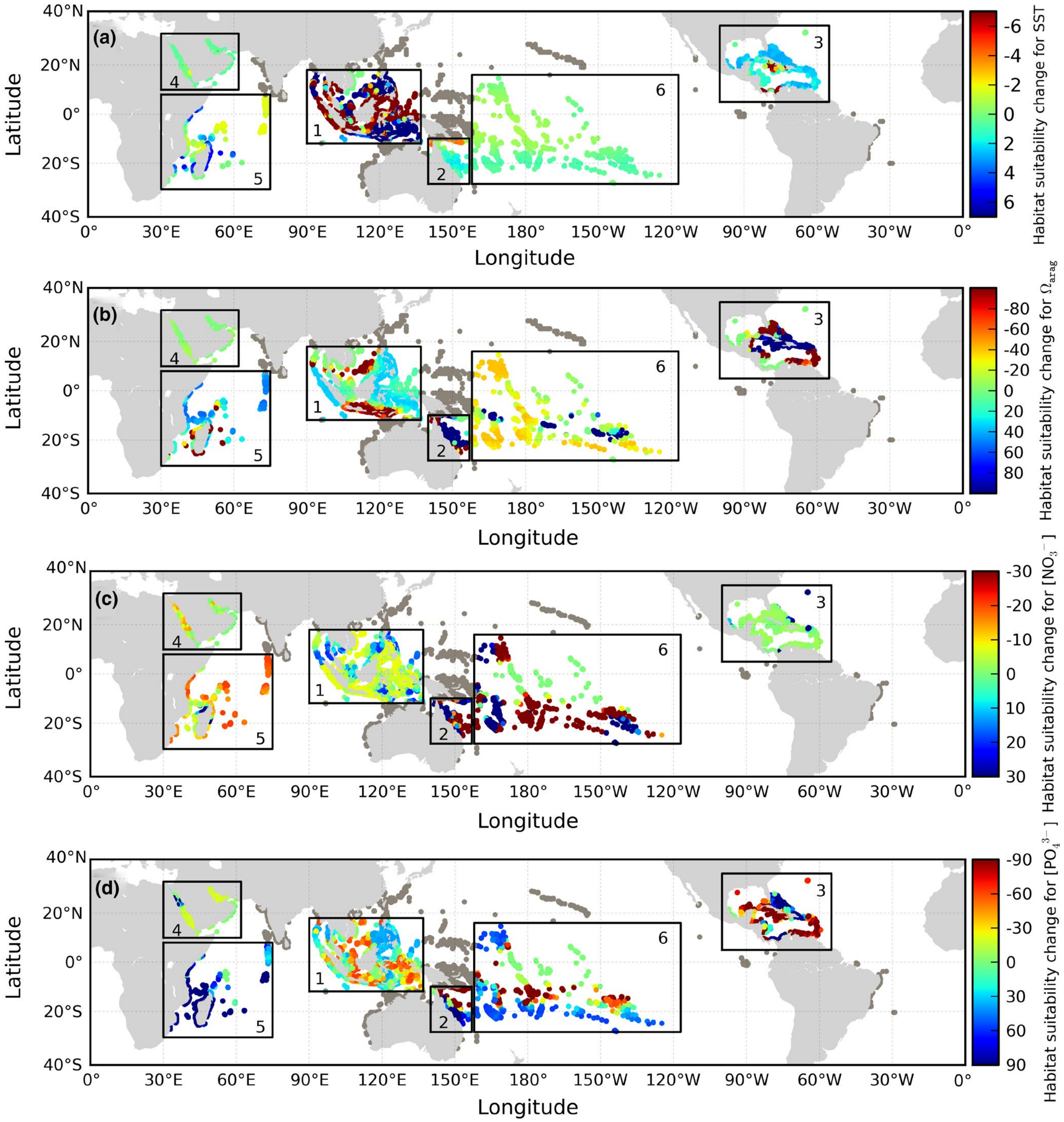

FIGURE 3 Change in habitat suitability with respect to (a) a warming by +0.1°C, (b) a decrease in Ω_{arag} by −0.04, (c) an increase in [NO_3^-] by +0.02 µmol/L and (d) an increase in [PO_4^{3-}] by 0.01 µmol/L respectively. Blue colours indicate improved habitat suitability whereas a decline in habitat suitability is indicated in red

Region (e.g. the Bahamas, Venezuela; Figure 3b, box 3). Reef locations in areas such as Philippines (Figure 3b, box 1), GBR (Figure 3b, box 2), Cuba (Figure 3b, box 3) and northern Mozambique Channel (Figure 3b, box 4), however, show an increase in habitat suitability with respect to a 0.04 decrease in Ω_{arag}.

Increases in [NO_3^-] and [PO_4^{3-}] by, respectively, 0.02 µmol/L and 0.01 µmol/L do not alter the habitat suitability of the regions already characterized by low habitat suitability with respect to [NO_3^-] and $\left[PO_4^{3-}\right]$ (Figure 2c,d) because they are already well above the corresponding regional optima. An increase in [NO_3^-] by 0.02 µmol/L produces a decline in habitat suitability in Southeast Asia (Figure 3c, box 1), central and southern GBR (Figure 3c, box 2), Western Indian Ocean (Figure 3c, box 5) and islands of the Central Pacific between 10°S and 20°S (Figure 3c, box 6). An increase in [PO_4^{3-}] by 0.01 µmol/L decreases habitat suitability in Southeast Asia (Figure 3d, box 1), Caribbean (Figure 3d, box3) and

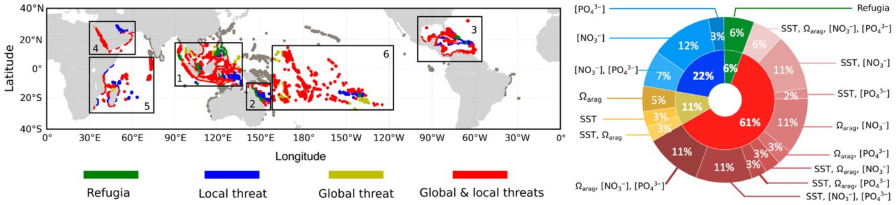

FIGURE 4 Classification of coral reef habitat locations with respect to an increase in SST by 0.1°C, a decrease in Ω_{arag} by 0.04, an increase in [NO_3^-] by 0.02 μmol/L or an increase in [PO_4^{3-}] by 0.01 μmol/L. Temporary refugia (green), only 6% of the reefs in the six regions, are locations in which these changes in environmental conditions will maintain or increase habitat suitability. Locations that will face a decline in habitat suitability due to increase in [NO_3^-] and/or [PO_4^{3-}] are classified as local threat (blue) and cover 22% of the reefs in the six regions. Locations that will face a negative habitat suitability change with respect to warming and/or decreasing Ω_{arag} are classified as global threat (yellow), 11% of the reefs in the six regions. Locations that will face a decrease in habitat suitability due to warming and/or decreasing Ω_{arag} and increase in [NO_3^-] and/or [PO_4^{3-}] are classified as global and local threats (red), 61% of the reefs in the six regions. For more details about classification of coral reef habitat, see Section 2

Central Pacific islands, between 10°S and 20°S (Figure 3d, box 6). In contrast, the habitat suitability of southern GBR (Figure 3d, box 2), Bahamas (Figure 3d, box 3), western Indian Ocean (Figure 3d, box 5) and Central Pacific islands along 20°S (Figure 3d, box 6) increase as [PO_4^{3-}] increases because these reefs are below their regional optima (Figure 3d, box 5).

3.3 | Reef vulnerability classification to global and regional threats

The results of habitat suitability change with respect to 0.1°C warming, −0.04 change in Ω_{arag}, 0.02 μmol/L increase in [NO_3^-] and 0.01 μmol/L increase in [PO_4^{3-}], can be used to classify coral reef locations into four major categories: (a) temporary refugia, if regional conditions in relation to all four environmental variables change in direction towards the corresponding optima; (b) local threat, if regional conditions in [NO_3^-] and/or [PO_4^{3-}] concentrations shift away from the corresponding optima; (c) global threat, if regional conditions in SST and/or Ω_{arag} shift away from the corresponding optima or (d) global and local threats, if regional conditions in SST and/or Ω_{arag} and [NO_3^-] and/or [PO_4^{3-}] shift away from corresponding optima.

This classification shows that the Andaman and Nicobar Islands, Philippines, inner GBR, and the Turks and Caicos Islands can be considered as temporary refugia (Figure 4). These reefs account for only 6% of the total number of reef locations in the six regions. Under changing environmental conditions, about 61% of the total number of reefs will likely be affected by both local and global threats. These reefs are found in all six major regions we considered (Figure 4). We also found that 11% of the total number of reefs in the six regions, mainly in Marshall Islands, New Caledonia and French Polynesia will experience a decline in habitat suitability due to global threats. Furthermore, 22% of the total number of reefs in the six regions will experience negative habitat suitability changes under increasing nutrient concentrations (Figure 4). These areas are Persian Gulf, coast of Somalis and Kenya, Mauritius, Banda Sea, outer GBR and Puerto Rico (Figure 4).

4 | DISCUSSION

4.1 | Global and regional habitat suitability

Experimental studies showed that optimal conditions might vary for different coral species. For example, the coral *Galaxea fascicularis* exhibits a maximum calcification rate at 25°C (Marshall & Clode, 2004), whereas the optimal temperature for *Pocillopora verrucosa* calcification is between 28°C and 29°C (Sawall et al., 2015). The optimal conditions reported in the present study, however, should be regarded as species-aggregated ecological optima and not as species-specific optima.

The performance curves with respect to temperature tend to be left-skewed (Figure 1), indicating that the thermal optima in many regions are close to the upper tolerance limits. This implies that small shifts towards increasing temperature will have a detrimental impact on the performance of corals currently living close to their optimal temperature, similar to what has been reported for other marine and terrestrial organisms (Deutsch et al., 2008; Huey et al., 2012; Pörtner & Knust, 2007; Tewksbury, Huey, & Deutsch, 2008). In contrast, coral communities living at temperatures below global optima are in the conditions to adapt towards more thermotolerant communities via shifts in species composition. The performance curves with respect to temperature for Southeast Asia and Western Indian Ocean are right-skewed. The differences in the particular shape of the thermal tolerance curves may be explained by community-specific relationships of photosynthesis to temperature (Farquhar, von Caemmerer, & Berry, 1980; Leuning, 2002) and by the way Rubisco is regulated in response to temperature variations. More specifically, the activation and deactivation processes of Rubisco increase with temperature following an exponential, Arrhenius-type function (Farquhar et al., 1980). Different realizations of these two processes in communities with different species compositions may give rise to the different responses observed in Figure 1.

The relationship between coral calcification and Ω_{arag} can range from exponential (Ries, Cohen, & McCorkle, 2009, 2010) to linear (Langdon et al., 2000; Ohde & Hossain, 2004). Our method is not designed to estimate the shape of coral physiological responses to Ω_{arag}.

The method is based on the distribution of Ω_{arag} values extracted at coral reef locations to estimate habitat suitability. According to this, a decrease in Ω_{arag} to values that remain above 3.8 does not produce a decrease in habitat suitability because Ω_{arag} rarely exceeds 4 in the modern ocean (Figure S3b). However, when Ω_{arag} values fall below 3.8, habitat suitability is negatively impacted. Past studies showed that a decrease in Ω_{arag} will decrease rates of coral calcification (Albright, Langdon, & Anthony, 2013; Doo, Edmunds, & Carpenter, 2019; Kline et al., 2019; Ohde & Hossain, 2004). In addition, decreasing Ω_{arag} increases rates of $CaCO_3$ dissolution both in perforate coral skeletons (Kline et al., 2019; van Woesik et al., 2014) and reef structures (Eyre, Andersson, & Cyronak, 2014; Eyre et al., 2018). Decreased calcification and increased dissolution, both driven by reductions in Ω_{arag}, make coral reefs among the most vulnerable ecosystems on the planet in relation to ocean acidification. The primary impacts of ocean acidification include reductions in structural complexity (Fabricius et al., 2011), skeleton density (Mollica et al., 2018) and coral recruitment (Doropoulos & Diaz-Pulido, 2013; Fabricius, Noonan, Abrego, Harrington, & De'Ath, 2017), as well as increases in bioeroders (Wisshak, Schönberg, Form, & Freiwald, 2012). While certain corals can tolerate low pH (Venn et al., 2013) via local adaptations (McCulloch, D'Olivo, Falter, Holcomb, & Trotter, 2017), most of the evidence available to date suggests that coral reef communities will not be able to adapt or acclimate to future ocean acidification scenarios (Langdon et al., 2000).

The shapes of the global distributions for nitrate and phosphate are in good agreement with the conceptual understanding of coral physiology, suggesting that the performance of these organisms can be sub-optimal at very low nutrient concentrations and that corals can benefit from slight nutrient enrichments (D'Angelo & Wiedenmann, 2014). Most coral reefs, however, are found at low inorganic nutrient concentrations because of physiological adaptations that provide corals with competitive advantages over macroalgae in low nutrient environments (Falkowski, Dubinsky, Muscatine, & McCloskey, 1993; Muscatine & Porter, 1977). Corals are polytrophic and opportunistic feeders and exhibit two primary feeding modes: (a) via capture of plankton and organic particles by polyps and (b) via translocation of photosynthetic products from their endosymbiotic algae (Symbiodiniaceae or 'zooxanthellae'). Symbiodiniaceae (LaJeunesse et al., 2018) have relatively low growth rates and are nutrient limited within the coral host (Cook & D'elia, 1987; Muscatine & Pool, 1979). Accordingly, an increase in nutrient concentration should enhance the growth rate and biomass of Symbiodiniaceae (Hoegh-Guldberg, 1994), with destabilizing effects to the symbiotic relationship. Corals are, however, unable to cope with continuous and severe inputs of nutrients and generally compete poorly with benthic macroalgae under such conditions (Vermeij et al., 2010).

Coral communities of different regions are thus adapted to distinct environmental conditions (Figure 1). This suggests that high temperature-adapted corals of the Red Sea and Persian Gulf could be transplanted, in theory, to the GBR or to other regions with lower SST optima such as Southeast Asia, where they could form communities able to cope with locally rising SST (Anthony et al., 2017; Coles & Riegl, 2013). However, the costs and the technical challenges involved in coordinating the international translocation of corals could be daunting (Coles & Riegl, 2013). Translocations may also prove ineffective given the current evidence of high mortality among transplanted corals due to shifts in microbiome (Casey, Connolly, & Ainsworth, 2015) and given the problems associated with invasiveness (Coles & Riegl, 2013), and introduction of alien pathogens (Hoegh-Guldberg et al., 2008). Transplant of conspecific corals within the current distribution range of species is another option on the table (van Oppen, Oliver, Putnam, & Gates, 2015). However, our results show that coral communities of the Red Sea and Persian Gulf are adapted to high Ω_{arag} (Figure 1b). Therefore, while transplanting these corals to locations characterized by an increasing trend in temperature may conserve the reefs there, other environmental conditions such as Ω_{arag} may not be suitable for the transplanted corals (Prada et al., 2017). In addition, transplants come with the risk of maladaptation to other nonclimate-related conditions (Anthony et al., 2017). The success of transplants may also depend on nutrient concentrations, an additional factor that can alter the susceptibility of corals to bleaching (D'Angelo & Wiedenmann, 2014; Pogoreutz et al., 2017; Wiedenmann et al., 2013; Wooldridge, 2009). We found, for example, that corals in the Western Indian Ocean are adapted to a low N:P ratio (about 0.2), whereas corals in the Caribbean are adapted to a relatively higher N:P ratio (about 2.4; Figure 1).

4.2 | Habitat suitability change under environmental shifts

Previous studies classified Southeast Asia as a hotspot for future coral bleaching due to high temperature (Couce et al., 2013; van Hooidonk, Maynard, Manzello, & Planes, 2014; van Hooidonk, Maynard, & Planes, 2013). We also show that ocean acidification will negatively affect habitat suitability in this region (Figure 3b). Increasing both SST and ocean acidification can lead to alteration of coral communities via shifts towards more competitive, weedy, stress-tolerant corals (Darling, Alvarez-Filip, Oliver, Mcclanahan, & Côté, 2012; Fabricius et al., 2011). For example, data collected from CO_2 seeps in Papua New Guinea showed that coral cover was similar in the low and the high pCO_2 sites. However, the cover of massive *Porites* corals doubled with decreasing distance from the seeps, whereas the cover of structurally complex corals (branching, foliose and tabulate) reduced by threefold with decreasing distance from the seeps (Fabricius et al., 2011). In addition, most Southeast Asian reefs currently occur under optimal nutrient conditions (Figure 2c,d; Figure S3c,d), but are nonetheless very close to the threshold value at which the frequency of reef occurrences drastically declines (Figure 3c,d). Eutrophication has been reported as one of the most prevalent and destructive factor in Southeast Asia, and it has already caused severe coral biodiversity loss, up to 60% in parts of Indonesia (Edinger, Jompa, Limmon, Widjatmoko, & Risk, 1998; Todd, Ong, & Chou, 2010).

Coral reef locations characterized by temperatures below regional optima (e.g. southern GBR, Caribbean) will become more suitable habitats with a +0.1°C change in temperature (Figure 3c). An increase in habitat suitability in relation to SST is confirmed, for example, by increasing growth rate of massive *Porites* along a latitudinal gradient in Western Australia (Cooper, O'Leary, & Lough, 2012) and by previous model studies (Couce et al., 2013; Descombes et al., 2015). This trend is also confirmed by a decline in coral recruitment in tropical waters accompanied by an increase in subtropical waters becoming warmer (Price et al., 2019). However, large-scale bleaching events that occurred in the GBR and in the Caribbean over the last decades (Berkelmans & Oliver, 1998; Eakin et al., 2010; Hughes, Anderson, et al., 2018; Hughes, Kerry, et al., 2018; Hughes et al., 2017; McWilliams, Côté, Gill, Sutherland, & Watkinson, 2005) indicate that temperature is not the only factor responsible for coral bleaching. Nutrient enrichment could be a co-occurring factor and could act synergistically with temperature to lower the coral bleaching thresholds in the GBR and in the Caribbean (Figure 3c,d; D'Angelo & Wiedenmann, 2014; Pogoreutz et al., 2017; Wiedenmann et al., 2013; Wooldridge, 2009). In fact, mean annual loads of nitrogen and phosphorus have increased by 5.7 and 8.9 times, respectively, in the GBR since pre-European times (Kroon et al., 2012).

A decline in Ω_{arag} by 0.04 in the GBR is mainly associated (with the exclusion of regions in the far north and far south) to an increase in habitat suitability (Figure 3b), indicating that ocean acidification is unlikely to increase corals' susceptibility to bleaching in this region. Anthony, Kline, Diaz-Pulido, Dove, and Hoegh-Guldberg (2008) found that at ecologically relevant values of irradiance (1,000 μmol photons m^{-2} s^{-1}), an 8 week incubation of crustose coralline algae and branching (*Acropora*) and massive (*Porites*) corals at 1,010–1,350 ppm CO_2 (pH = 7.6–7.7) reduced productivity and induced bleaching (loss of pigmentation). In contrast, productivity and thermal bleaching (loss of *Symbiodinium* and/or chlorophyll content) in *Seriatopora caliendrum* was unaffected by high $p\mathrm{CO}_2$ (Wall, Fan, & Edmunds, 2013). Noonan and Fabricius (2016) surveyed corals at CO_2 seeps during a minor regional bleaching event. The elevated $p\mathrm{CO}_2$ had little impact on the susceptibility of *Acroporidae*, *Faviidae*, *Pocilloporidae*, *Poritidae* or *Seriatopora hystrix* to bleaching. Their tank experiments also showed no effect of elevated $p\mathrm{CO}_2$ (780 μatm) on bleaching sensitivity in *Acropora millepora* or *S. hystrix* (Noonan & Fabricius, 2016). *Stylophora pistillata* from the Gulf of Aqaba showed no signs of bleaching after 1.5 months of exposure to 1°C–2°C above long-term summer maximum SST and a seawater pH of 7.8 (Krueger et al., 2017). Therefore, a role of ocean acidification in coral bleaching is questionable. Massive *Porites* continued to calcify under at high $p\mathrm{CO}_2$ (750 μatm), even when temperature increased from 25°C to 28°C, indicating that raising temperature, below the thermal stress threshold, may reduce the effects of ocean acidification on calcification (Cole, Finch, Hintz, Hintz, & Allison, 2018). However, calcification in the coral *S. pistillata* decreased at high $p\mathrm{CO}_2$ (760 μatm) and when temperature increased from 25°C to 28°C (Reynaud et al., 2003). Variable effects to the combined increase of $p\mathrm{CO}_2$ and temperature could be partially explained by species-specific responses and highlight the need for more research on the effects of combined stressors. Furthermore, it is increasingly clear that ocean acidification has the capacity to influence postbleaching recovery by compromising coral fertilization, settlement (Webster, Uthicke, Botté, Flores, & Negri, 2013) and postsettlement growth (Albright, Mason, & Langdon, 2008; Albright, Mason, Miller, & Langdon, 2010; Nakamura, Ohki, Suzuki, & Sakai, 2011).

4.3 | Vulnerability of coral reef habitats

Our analysis shows that, under changing local and global environmental conditions, only 6% of the total number of reef locations in the six regions can be classified as ecological refugia for coral reefs (Figure 4). Hock et al. (2017) suggested that reefs with high connectivity and free of disturbances are ideal 'robust source reefs' to facilitate recovery of disturbed areas. However, these areas are insufficient to save disturbed reefs globally due to their small size and limited spatial distribution. Disturbed reefs will also be exposed to environmental stress such as ocean acidification, tending to lower coral recruitment (Fabricius et al., 2017; Kegler et al., 2017). The reef refugia identified in our study are much less than the 17.4% of the Indo-Pacific reefs identified for protection by the work of Darling et al. (2019). Darling et al. (2019) suggested to protect reefs that were exposed only to a minimal bleaching stress during the years 2014 to 2017 and that were able to maintain at least 10% of coral cover. Coral reefs, however, face several threats simultaneously and focussing on thermal stress only may overestimate the number of coral reefs that could be protected against multiple environmental stressors. The approach adopted in our study considers chemical factors in addition to temperature stress. The reef refugia identified in our study, therefore, include reef habitats that will not be affected by global warming, ocean acidification and eutrophication. These refugia may be considered as ideal habitats for 'super reefs', that is, reefs that have evolved to be naturally resistant to ocean warming. These reef areas should be the prioritized for protection.

We show that 61% of the total number of reefs in the six regions will likely be affected by both local and global threats under changing environmental conditions. These reefs are found in all six major regions we considered (Figure 4). Local management can act to reduce the anthropogenic pressures in these regions. However, although essential, local management programmes may produce little benefits in areas subject to global threats because the impacts of warming and ocean acidification may outweigh the benefits from local management (Hughes et al., 2017). For such areas, combining local management with the reduction of greenhouse gasses remains the only solution. It is also unclear if local management can increase the 'resilience' of coral reefs to climate change. Local stressors could filter out stress sensitive species, and leave stress-tolerant species. Local management aims to reverse reef degradation with the effect of bringing back sensitive taxa and thus decreasing ecosystem resilience to climate change (Bruno & Valdivia, 2016; Côté & Darling, 2010).

Anthropogenic impacts on coral reefs are expected to increase with the number of people living in coastal areas. Excessive human-related nutrients enter the coastal waters from sewage treatment facilities, agricultural fertilizers or livestock waste (Howarth, Sharpley, & Walker, 2002). Nutrient enrichment can increase macroalgae cover (Fabricius, De'ath, McCook, Turak, & Williams, 2005) and the prevalence and severity of coral diseases (Bruno et al., 2003; Voss & Richardson, 2006) and can thus lead to higher frequency of Crown of Thorns Starfish outbreaks (Brodie et al., 2005). Wastewater management programmes can reduce these negative nutrient effects. Local wastewater management can also increase coral reef recovery after disturbances (Jury & Toonen, 2019; Sawall, Jompa, Litaay, Maddusila, & Richter, 2013), which is one important factor of resilience (Côté & Darling, 2010).

Furthermore, we find that 11% of the total number of reefs in the six regions will experience a decline in habitat suitability due to global threats. These reefs can only be saved through reducing carbon emissions on a global scale. The establishment of MPAs has been one of the main tools for protecting coral reef habitats (Sale, 2008) and conserving biodiversity. However, MPAs cannot protect coral reefs from global stressors (Anthony, 2016; Hughes et al., 2017; Selig, Casey, & Bruno, 2012). For example, ocean warming increases local larval retention, potentially weakening the connectivity between coral populations, thus limiting the natural recovery of reefs due to a lack of coral larval supply (Figueiredo, Baird, Harii, & Connolly, 2014). Therefore, active reef restoration may be one of the few options available for these 11% of reefs areas. Restoration approaches such as coral gardening (Epstein, Bak, & Rinkevich, 2001; Rinkevich, 2005, 2008, 2014, 2015), supplementing gardening activities using coral larvae (Chamberland et al., 2015; Lirman & Schopmeyer, 2016), appear promising approaches. However, the costs for large scale restoration remain prohibitive (Bayraktarov et al., 2016; Spurgeon, 1999).

In summary, about 22% of the total number of reefs in the six regions considered will experience negative habitat suitability changes under increasing nutrient concentrations (Figure 4). Reducing local nutrient loads can delay reef loss in these areas for about a decade under very high (RCP8.5) CO_2 emissions (Kennedy et al., 2013). Coral communities that harbour species with moderate tolerance to increased temperature and acidification can rapidly recover after appropriate sewage treatments (Jury & Toonen, 2019). Local wastewater programmes aiming at reducing nutrient loads are amenable to management at regional scales, and therefore represent a rational strategy for mitigating the effects of eutrophication. These programmes can potentially increase areas classifiable as temporary refugia to 28% of the total number of reefs in the six regions considered here, thus buying humanity additional time for producing mutually agreed solutions against global threats such as warming and ocean acidification.

ACKNOWLEDGEMENTS

We thank Dieter Wolf-Gladrow and two anonymous reviewers for valuable comments that improved the presentation of our work, and Zhiqiang Liu and Mingming Li for their suggestions with data interpolation.

AUTHOR CONTRIBUTION

A.M. and S.H. conceived the idea of the study; Y.G. coded the model and performed the statistical analyses; Y.G., S.H., C.W. and A.M. contributed to interpretation of the results and writing the manuscript.

DATA AVAILABILITY STATEMENT

The coral reef data can be accessed from website: http://data.unep-wcmc.org/datasets/1. The environmental data can be downloaded from the website: https://www.nodc.noaa.gov/OC5/woa18/woa18data.html. The GLODAPv2 data can be downloaded from the website: https://cdiac.ess-dive.lbl.gov/ftp/oceans/GLODAPv2/Data_Products/mapped/. The mapped climatology data for Ω_{arag} in the Caribbean can be downloaded from the website: https://www.aoml.noaa.gov/ocd/ocdweb/gridded_caribbean/index.html.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Guan Y, Hohn S, Wild C, Merico A. Vulnerability of global coral reef habitat suitability to ocean warming, acidification and eutrophication. *Glob Change Biol*. 2020;00:1–15. https://doi.org/10.1111/gcb.15293