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Future habitat suitability for coral reef ecosystems under global warming and ocean acidification

ELENA COUCE*†, ANDY RIDGWELL* and ERICA J. HENDY†‡

School of Geographical Sciences, University of Bristol, Bristol, BS8 1SS, UK, †School of Earth Sciences, University of Bristol, Bristol, BS8 1RJ, UK, ‡School of Biological Sciences, University of Bristol, Bristol, BS8 1UG, UK

Abstract

Rising atmospheric CO₂ concentrations are placing spatially divergent stresses on the world’s tropical coral reefs through increasing ocean surface temperatures and ocean acidification. We show how these two stressors combine to alter the global habitat suitability for shallow coral reef ecosystems, using statistical Bioclimatic Envelope Models rather than basing projections on any a priori assumptions of physiological tolerances or fixed thresholds. We apply two different modeling approaches (Maximum Entropy and Boosted Regression Trees) with two levels of complexity (one a simplified and reduced environmental variable version of the other). Our models project a marked temperature-driven decline in habitat suitability for many of the most significant and bio-diverse tropical coral regions, particularly in the central Indo-Pacific. This is accompanied by a temperature-driven poleward range expansion of favorable conditions accelerating up to 40–70 km per decade by 2070. We find that ocean acidification is less influential for determining future habitat suitability than warming, and its deleterious effects are centered evenly in both hemispheres between 5° and 20° latitude. Contrary to expectations, the combined impact of ocean surface temperature rise and acidification leads to little, if any, degradation in future habitat suitability across much of the Atlantic and areas currently considered ‘marginal’ for tropical corals, such as the eastern Equatorial Pacific. These results are consistent with fossil evidence of range expansions during past warm periods. In addition, the simplified models are particularly sensitive to short-term temperature variations and their projections correlate well with reported locations of bleaching events. Our approach offers new insights into the relative impact of two global environmental pressures associated with rising atmospheric CO₂ on potential future habitats, but greater understanding of past and current controls on coral reef ecosystems is essential to their conservation and management under a changing climate.

Keywords: Bioclimatic Envelope Modeling, boosted regression trees, coral reef ecosystems, global warming, MaxEnt, maximum entropy, ocean acidification

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Introduction

Anthropogenic climate change has emerged as a serious global-scale threat to the future viability of coral reef ecosystems (e.g., Hoegh-Guldberg et al., 2007; Riegl et al., 2009; Veron et al., 2009; Glynn, 2012), with studies linking widespread bleaching events to increasing sea surface temperatures (SSTs; Hoegh-Guldberg, 1999). There is concern that the growing frequency and severity of mass bleaching episodes may lead to species composition shifts and functional collapse in coral reefs in the near future (Hughes et al., 2003; Baker et al., 2008; Glynn, 2012; van Hooidonk et al., 2013), although this is likely to be strongly influenced by the extent of other anthropogenic stresses and the corals’ capacity for thermal adaptation (e.g., Baskett et al., 2009; Kennedy et al., 2013). In contrast, global warming also has the potential to improve currently marginal environmental conditions and extend the range of tropical coral reefs into higher latitudes (e.g., Precht & Aronson, 2004; Yamano et al., 2011), as demonstrated in the fossil record in response to warmer geological periods (e.g., Lighty et al., 1978; Veron, 1992; Precht & Aronson, 2004; Greenstein & Pandolfi, 2008; Woodroffe et al., 2010; Kiessling et al., 2012). If expansion is not limited by additional factors, higher latitude reefs could provide ‘refuges’ for many coral reef species as increasing temperatures cause ecosystem failure at low-latitude reef sites (e.g., Zamagni et al., 2012; Halfar et al., 2005; Vargas-Ángel et al., 2003; Glynn, 1996; though see, e.g., Lybolt et al., 2011).

A second global environmental pressure associated with rising atmospheric CO₂ – ‘ocean acidification’ – complicates the temperature-only picture of a shift of suitable habitats to high latitudes and contraction in the tropics. Ocean acidification is the chemical consequence of the excess dissolution of CO₂ derived from fossil fuel combustion in surface seawater (Turley et al., 2010). In addition to lower seawater pH, anthropogenic ocean...
acidification is also characterized by a reduction in the saturation state of calcium carbonate (Hönisch et al., 2012). Corals precipitate skeletons of the CaCO$_3$ polymorph aragonite, and declining aragonite saturation ($\Omega_{\text{Arag}}$) increases the metabolic cost of skeletogenesis. Ocean acidification may thus lead to weaker reef structures that are more susceptible to erosion and competitive advantages for bioeroding organisms (Kleypas et al., 1999b; Smith & Buddemeier, 1992; e.g., Manzello et al., 2008). On the basis of this parameter (aragonite saturation) alone, it has been noted that for atmospheric CO$_2$ concentrations beyond ca. 550 ppm, the expected open ocean surface $\Omega_{\text{Arag}}$ value for most reef locations will be below that associated with the limits of coral distributions today (ca. 3.25; Cao & Caldeira, 2008; Hoegh-Guldberg et al., 2007). This has raised concerns over the corals’ ability to maintain reef structures, pushing the view that declining aragonite saturation represents a pressing threat (e.g., Cao & Caldeira, 2008; Silverman et al., 2009; Ricke et al., 2013). However, the actual effect of increased acidification on calcification rates is complex and species dependent (Chan & Connolly, 2013; Kroeker et al., 2013), with many scleractinian corals being capable of buffering their internal pH for instance (e.g., Krief et al., 2010; McCulloch et al., 2012). The present-day relationship between coral reef locations and aragonite saturation is hence very likely modulated by other environmental factors such as temperature and nutrient availability (e.g., Cohen & Holcomb, 2009; Chauvin et al., 2011), meaning that habitat suitability implications cannot be drawn from future aragonite saturation changes in isolation.

With continuing fossil fuel CO$_2$ emissions, these two main global marine environmental changes – surface warming and acidification, create a biogeographical tension, with warming tending to drive the zone of suitable coral reef habitat polewards, and decreasing saturation forcing it to contract toward the equator (Meissner et al., 2012; Yara et al., 2012). The net outcome is far from trivial, as the physiological responses of corals vary between regions, species, and even experimental manipulations, with interactions between stressors that are complex and nonlinear (e.g., Lough & Barnes, 1997; Silverman et al., 2007; Anthony et al., 2008; Chauvin et al., 2011; Edmunds et al., 2012). Despite a pressing need for a better understanding of the ongoing impact of environmental change on coral reef ecosystems (Pandolfi et al., 2011), few quantitative modeling studies have taken into account changes in SST and $\Omega_{\text{Arag}}$ simultaneously. Buddemeier et al. (2011) modeled the response to warming and acidification of eastern Caribbean reefs and projected that 95% coral cover would be lost by 2035, or delayed until 2065 if thermal tolerance of corals increases by 1–1.5 °C. Hoeke et al. (2011) found similar results for the Hawaiian region, with a precipitous decline in coral cover expected sometime between 2030 and 2050 unless corals are able to adapt to higher temperatures. They also predicted a temperature-driven increase in coral growth rates, particularly toward higher latitudes and despite the lower aragonite saturation levels there. Yara et al. (2012) explored changes in SST and $\Omega_{\text{Arag}}$ along the Japanese coastline. On the basis of a minimum $\Omega_{\text{Arag}}$ cutoff value of 3 (2.3) for tropical (temperate) corals, they found that a possible SST-driven range expansion into higher latitudes would be strongly limited by ocean acidification, and projected that all potential habitats in Japan might become unsuitable for tropical/subtropical coral reefs by 2040.

In this study, we assess global patterns of short-term range shifts in potential coral reef habitat under the spatially divergent stresses of ocean warming and acidification at the spatial scale of 1° × 1°. We employ a suite of statistical models based on the environmental factors thought to be limiting to the present equilibrium distribution of shallow-water coral reefs (Fig. 1, see Couce et al., 2012), perturbing them with Earth System Model projected future SST and aragonite saturation changes (the simulations used in Turley et al., 2010). We considered a range of potential future CO$_2$ emissions scenarios, but focus here on the consequences of the ‘A2’ scenario (characterized by regionally oriented economic development and high population growth, expecting ca. 850 atmospheric CO$_2$ by 2100). Significantly, the coral suitability models are not based on specific predetermined cutoff values for either $\Omega_{\text{Arag}}$ or SST, but instead seek to encapsulate the multidimensional climate envelope where the synergies between all relevant drivers favor the presence of coral reefs. Based on equilibrium relationships, these models do not incorporate information on coral responses or potential adaptation to dynamic environmental drivers, such as warming-induced bleaching and sea-level rise. Instead, the models identify where environmental conditions become adverse for coral reef presence based on the range of conditions in which they are currently found. The purpose of the study is thus not to predict the fate of existing coral reefs, but to identify the broad net impacts of warming and acidification on the potential future habitat suitability of these emblematic ecosystems.

Materials and methods

Habitat suitability models

Bioclimatic Envelope Modeling establishes relationships between environmental factors and the distribution of a species or ecosystem through statistical analysis. It defines an n-dimensional volume (or ‘envelope’) in the space of all
relevant environmental factors where conditions are adequate
for a species or ecosystem, identifying the relative significance
of the different factors and the changes in environmental suit-
able across climatic gradients. We employed two different
techniques: Maximum Entropy (MaxEnt; Phillips & Dudık,
2008; Phillips et al., 2006), and Boosted Regression Trees (BRT;
De’ath, 2007; Friedman, 2001). Further details on these model-
ing approaches are provided in Table 1. Both MaxEnt and
BRT are machine-learning techniques, able to handle nonlin-
ear relationships and to take into account synergistic effects
between the different factors affecting a species’ distribution.
This flexible approach is advantageous for studying ecosys-
tems because the tolerance limits of an ecosystem are influ-
enced by contributions from many species and would be
expected to give rise to more complicated relationships with
climatic variables. MaxEnt is widely used in ecological stud-
ies, including the prediction of climate change impacts on a
species or ecosystem’s potential distribution (e.g., tree spar-
rows within North America, Graham et al., 2011a; sagebrush
ecosystems in Nevada, Bradley, 2010; or invasive weeds spe-
cies in Australia, Wilson et al., 2009). To date, BRT is less
widely used, despite having comparable predictive capabi-
lities (e.g., Elith et al., 2006; De’ath, 2007).
All models were trained with coral location data from ‘Reef-
Base’ (version 2000; http://www.reefbase.org; Vergara et al.,
2000). This database was chosen for consistency and ease of
comparison with previous studies: Kleypas et al. (1999a),
Couce et al. (2012, 2013). At the 1° × 1° spatial resolution of
our study, previous testing has shown the results are insensi-
tive to the reef location data set used. For example, BRT and
MaxEnt models developed using the UNEP-WCMC compila-
tion (http://data.unep-wcmc.org/datasets/13; UNEP-
WCMC, WorldFish Centre, WRI, TNC, 2010; IMaRS-USF,
IRD, 2005; IMaRS-USF, 2005) replicated model performance
and environmental variable relevance with insignificant dif-
ferences to the equivalent ReefBase-trained models (E. Couce,
unpublished data).

The optimal ‘OPT’ models were trained with a complete
suite of relevant environmental fields identified in Couce
et al., 2012 (a total of 27 parameters; these are the MaxEntOPT
and BRTOPT models), whereas the simple ‘SIM’ models were
trained with a reduced subset of 6 of the most significant vari-
bles (the MaxEntSIM and BRTSIM models) – see Table 1 for
complete variable list. Annual average SST and ΩArag values
were obtained from climate and marine carbon cycle projec-
tions made using the University of Victoria (UVic) Earth
System Model (Weaver et al., 2001), while most of the remain-
ing variables were observationally based. The UVic mean
annual data were interpolated to the 1° × 1° resolution of the
reef suitability models using the Inverse Distance Weighted
method (2nd degree). Maximum and minimum SST values
were computed by adding observed present-day anomalies to
UVic 1990 mean SST. Additional information and analysis of
the model development, data sources, and variables’ contribu-
tion to predictions are available in the Supporting Data S1 and
is described in further detail in Couce et al. (2012).

Grid and mask
All fields, including coral reef presence data, were mapped onto
a 1° × 1° global grid between −60° and 60° latitude. The suit-
ability models were trained on a shallow water mask established
as the grid cells with regions shallow enough for adequate light
penetration. The shallowest depth of a grid cell was determined
from 30′ resolution SRTM30 Plus bathymetry data (Becker et al.,
2009). The mask was defined as the grid cells for which the shal-
lowest point fell within twice the mean annual depth of penetra-
tion of light (Z), estimated after Kleypas et al. (1999a):
Z = \frac{\ln(\text{PAR}_{\text{cell}}/\text{PAR}_{\text{min}})}{K_{490\text{cell}}},

where \text{PAR}_{\text{cell}} was the monthly mean Photosynthetically Active Radiation (PAR) using data from ISCCP (Bishop & Rossow, 1991; Bishop et al., 1997), \text{PAR}_{\text{min}} was 125 dWm\(^{-2}\) (to encapsulate mesophotic reefs; Gattuso et al., 2006) and \text{K}_{490\text{cell}} was the monthly mean diffuse attenuation coefficient of light (wavelength 490 nm) obtained from Globcolour (2008) satellite measurements.

In addition, the study region was further constrained to the open-ocean areas covered by UVic projections (i.e., excluding the Red Sea and Arabian Gulf; Fig. S1.1 in Data S1). The environmental fields were extrapolated 1° shoreward by linear average of nearest neighbors to cover near-shore coral reef locations. This process resulted in a total of 32,582 oceanic grid cells, 4,002 of which were located within the shallow-water mask. A total of 1,124 cells contained at least one entry from the ReefBase v2000 data set (Fig. 1) and were designated ‘presence’ cells.

| Model Description | Model name | Variables |
|-------------------|------------|-----------|
| Boosted regression trees (BRT; Friedman, 2001) is a decision-tree-based statistical technique. A single tree is built by repeatedly splitting the data finding a cutoff value for one of the environmental variables so that the homogeneity of the resulting two groups is maximized. For BRT models, a sequence of trees (typically >1000) is produced, each grown on reweighted versions of the data, assigning ever-increasing weight to the cases misclassified by previous trees. The final prediction is obtained by the weighted average of predicted values across the sequence of trees. BRT models were fitted in R, with version 1.6-3.1 of the gbm library (Ridgeway, 2007). Different values for the Tree Complexity (TC), Learning Rate (LR) and Bagging Fraction (BF) were considered, and the combination that minimized the predictive deviance was chosen in each case (for BRT\(_{\text{OPT}}\): TC = 10, LR = 0.01 and BF = 75; for BRT\(_{\text{SIM}}\): TC = 7, LR = 0.01 and BF = 50). See Couce et al. (2012) for more details. | BRT\(_{\text{OPT}}\) | 27 environmental variables:  
- Sea surface temperatures (SST; annual average, monthly maximum and minimum, annual range, standard deviation of monthly means, weekly maximum and minimum, and standard deviation of January and July means)  
- Salinity (annual average, and monthly maximum and minimum)  
- Nutrients (annual average phosphate and nitrate concentrations)  
- Irradiance (annual average, and monthly maximum and minimum), attenuation coefficient at 490 nm wavelength (annual average), and depth of light penetration (annual average, and monthly maximum and minimum)  
- Aragonite saturation (annual average \(\Omega_{\text{Arag}}\))  
- Dust level (annual average)  
- Cyclone activity (30-year average)  
- Current speed (annual average, and monthly maximum and minimum). For data sources see Couce et al. (2012) |
| Maximum entropy modeling (MaxEnt; Phillips et al., 2006) is a presence-only technique for the prediction of species geographic distributions, based on the environmental conditions of sites of known occurrence. Assumes environmental factors act as constraints on the distribution of a species and that within those constraints, the species will occupy the available habitat in a way that maximizes entropy. Our models were developed with Maxent version 3.3.3e, with default values for the convergence threshold (10\(^{-5}\)) and maximum number of iterations (500). | MaxEnt\(_{\text{OPT}}\) | Same variable set as BRT\(_{\text{OPT}}\) |
| MaxEnt\(_{\text{SIM}}\) | Same variable set as BRT\(_{\text{SIM}}\) |
**Future projections**

Future habitat suitability was computed by applying the Bioclimatic Envelope Models to UVic-generated projections for annual average SST and aragonite saturation under the IPCC TAR scenarios A2, B1, and A1B. Future maximum and minimum SST values were computed by adding observed present anomalies to UVic mean SST data (i.e., assuming future variability will remain the same). All other environmental fields were kept fixed at present values. Projections were then generated at 10-year intervals from 2010 to 2070.

To isolate the impacts of warming and ocean acidification, changes in SST variables and $\Omega_{\text{Arag}}$ were considered first separately and then in combination, while all other environmental variables were kept constant at modern observed values. Future projections can involve novel environmental conditions, exceeding the values of the models' training range. Understanding the way in which the model deals with these data is critical for the correct interpretation of the results. The four models used in this study (Table 1) extrapolate by maintaining a constant response outside the training range (i.e., treating variables exceeding the values present in the training range as if they remained at the limit of the training range; see Data S2 for a detailed discussion on extrapolating to novel conditions and the impact on the predictions). In the results presented here, we explicitly indicate regions with novel SST or $\Omega_{\text{Arag}}$ conditions where the method of extrapolation significantly affects the projections and statistical relationships observed in training may no longer hold. These regions were defined as areas where MaxEnt$_{\text{OPT}}$'s projected suitability was found to vary by 0.1 or more when extrapolation was carried out using a different method (i.e., by simple linear extrapolation of the model’s response curves to each climatic variable, instead of maintaining a constant response). The 2070 cutoff for future projections was chosen because over 10% of coral reef cells are out of training range by this date.

**Model evaluation**

Model performance on 1990 training data was tested via Receiver Operating Characteristic curves (ROC curves; Peterson et al., 1954) and Area-Under-the-Curve scores (AUC; Swets, 1988; Fig. S1.2 in Data S1). To assess the models' predictive ability we considered published reports of fossil evidence from past warm geological periods and reports of present-day range expansion. We also explored whether rapid changes in equilibrium habitat suitability were correlated with areas where conditions have already been identified as challenging for existing coral reefs as evidenced by recent bleaching episodes. The data set of bleaching events was obtained from ReefBase (www.reefbase.org); it was originally developed by the WCMC and the WorldFish Center and subsequently extended to include published records and reports of personal observations. The changes in suitability between 2010 and training (1990) conditions on cells where bleaching episodes had been reported (between 2008 and 2012) were compared with the changes predicted in all reef presence cells; distributions and p-values of the two populations were compared via a Welsh's t-test, after testing the data for colinearity.

**Results**

**Impact of future surface warming**

Considering changes in SST variables only, sea surface warming has a marked impact on habitat suitability for coral reef ecosystems in currently favorable areas (defined as suitability $\geq 0.5$), especially in the central Indo-Pacific region (Fig. 2). The percentage of presence cells (those currently with reefs or nonreef coral communities) for which the model is predicting suitability above a value of 0.5 falls from 77% in 2010 to 66% in 2040 and 54% by 2070 (BRT$_{\text{OPT}}$ projections). This reduction is particularly pronounced in the Western Pacific Warm Pool (WPWP) region, affecting the Coral Triangle and some of the most biodiverse coral reef regions in the world. Suitability elsewhere either declines slightly (e.g., most of the Indian Ocean), or slightly increases (e.g., some areas of the Atlantic, including the Caribbean, and high latitudes). By 2070, SST conditions move out of training range for a large fraction of the Indo-Pacific region, with the area of less reliable model projection (as defined in ‘Methods’) affecting up to ca. 13% of coral reef cells under the A2 scenario (hashed areas in Fig. 2 maps and histograms). If areas requiring extrapolation into novel conditions are excluded from the analysis, the observed patterns of change to 2070 remains robust (e.g., the decrease in habitat suitability among presence cells in the histograms in Fig. 2 is still evident).

**Impact of future ocean acidification**

A reduction of surface $\Omega_{\text{Arag}}$ – while maintaining all other variables fixed at present values – leads to a decline in suitability for all areas currently favorable to coral reef formation (Fig. 3). However, the reduction is more subdued than that due to future SSTs (Fig. 2). For instance, whereas the projected SST rise caused the average suitability of presence cells to fall by 17%, from 0.69 in training (1990) conditions to 0.52 in 2070, the projected change in $\Omega_{\text{Arag}}$ over the same period caused a decrease of 10%, to an average of 0.59 (BRT$_{\text{OPT}}$). The projected decline is also more uniformly distributed globally (Fig. 3) in contrast to the more extreme pattern of warming-induced impact. However, some geographical differences are still apparent, with regions most affected by increased acidification corresponding to equatorial zones in the Pacific, adjacent to the WPWP zone most affected by warming, and to a lesser degree in localized regions of the central Indian Ocean and the Caribbean. Unlike SST, changing $\Omega_{\text{Arag}}$ alone does not lead to extrapolation uncertainties (Fig. 3), as the areas with novel $\Omega_{\text{Arag}}$ conditions are confined to high lati-
Synergistic impacts of warming and acidification

On a zonally averaged basis, ocean acidification reduces the environmental suitability for reef presence across all latitudes, but maximal influence is in the off-equatorial zone (ca. 5° to 20° in both hemispheres, Fig. 4a). The projected rise in SST significantly reduces coral reef suitability for all latitudes between 15°S and 15°N, while driving slight increases at latitudes above ca. 20° (Fig. 4b). With simultaneous changes in SST and \( \Omega_{Arag} \), the suitability for coral reef presence drops across all latitudes between 20°S and 20°N (Fig. 4c). This reduction is more extreme when the analysis is
restricted to the grid cells with substrate within the euphotic zone adequate for reef formation (Fig. 4d). The SST-driven expansion at latitudes above 20° still persists, although it is restricted by the countereffect of acidification.

The zonal averaged changes (Fig. 4) conceal a more heterogeneous geographical response, with the 2070 projections forecasting decreased suitability for coral reef ecosystems in nearly all reef areas (including the Caribbean, GBR, and Coral Triangle region) and with the greatest decline in suitability taking place in the western Pacific (Fig. 5). All four models project a 27–30% decline within shallow waters over the next 60 years (Fig. 6). The three CO₂ emission scenarios considered (A2, A1B, B1) produce very similar projected changes in suitability, corresponding to the consistent levels of warming to 2070 expected across all scenarios (IPCC, 2007).

Fig. 3  Predicted changes in suitability for coral reef ecosystems under the A2 scenario for future change in aragonite saturation only; 2010 (a), 2040 (b) and 2070 (c). Histograms show predicted suitability values for the 1124 presence sites of the study grid (i.e., cells currently with reefs according to the ReefBase v2000 data). All environmental fields apart from $\Omega_{\text{Arag}}$ were kept constant at their present values (used in model training). Unlike the SST results (Fig. 2), changes in $\Omega_{\text{Arag}}$ do not give rise to extrapolation uncertainties by producing novel conditions. The figure shows BRT$_{\text{OPT}}$ results (see figure S3.2 in Data S3 for MaxEnt$_{\text{OPT}}$ projections).

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**Model performance, comparison with fossil data and recent bleaching episodes**

All models performed adequately on training data, with average AUC scores close to 0.9 when evaluated on a random 25% subset data that had been excluded for model training (Fig. S1.2 in Supporting Data S1). The simple MaxEnt*SIM* model, based on a reduced set of climatic variables, showed the poorest performance in ROC space, with an AUC score of 0.84 ± 0.01. There is a clear correspondence between the changes in suitability predicted for present-day (2010) by the ‘SIM’ versions of the models and the locations of over 3500 reported bleaching episodes from 2008 to 2012 (Fig. 7). However, this correlation was not present in the forecasts obtained with the full ‘OPT’ models. In general, there was good agreement between forecasts obtained with the different models (Data S3), with the exception of BRT*SIM*.

Sites of observed range expansion and fossil evidence from warmer periods in the past (based on data from Kiessling*et al.*, 2012; Woodroffe*et al.*, 2010; Greenstein & Pandolfi, 2008; Veron, 1992; Lighty*et al.*, 1978) are consistent with the areas showing improved environmental suitability in our future projections (Fig. 5). In addition, the SST-driven decline projected at low latitudes is consistent with the equatorial decline described by Kiessling*et al.* (2012) from analysis of locations of coral fossil records from the last interglacial period.

**Discussion**

**Isolating the impacts of warming and acidification**

Areas where projected coral reef habitat suitability is most critically degraded by ocean surface warming (Fig. 2) correspond to areas with the highest mean annual SSTs today (Fig. 1), and also map onto regions identified as being particularly susceptible to future coral bleaching (e.g., Guinotte*et al.*, 2003; Donner*et al.*, 2005; van Hooidonk*et al.*, 2013). We find that the projected decrease in suitability is most strongly associated with the weekly maximum – and to a lesser degree, minimum – SST variable, and very high values (>32 °C).
are linked to marked declines (see Figs. S1.7–S1.8 in Data S1 and Fig. S2.5 in Data S2). Both BRT and MaxEnt statistical modeling approaches assign a relatively high significance to maximum weekly SST; in 10 randomly generated versions of MaxEnt\textsubscript{OPT}/BRT\textsubscript{OPT}, this parameter ranked 5th/8th of a total of 27 parameters in average relative contribution to model output (however, correlations between variables do make it difficult to clearly establish hierarchy; Couce \textit{et al.}, 2012). The importance placed by the Bioclimatic Envelope Models on SST variables in general, and the negative contribution to modeled suitability at the higher end of the SST range, indicates that the global data set used for model training contains sites where present-day coral reef distribution is already limited by an upper thermal threshold. Although equivalent maximum SSTs are tolerated by Red Sea and Arabian Gulf coral reefs, these sites could not be included in the training data set and analysis because it was not possible to simulate conditions using the UVic model in these enclosed seas. It has been suggested that Red Sea and Arabian Gulf coral are potentially conditioned to extreme SSTs by very high SST variability (Ateweberhan & McClanahan, 2010), however, this is not a characteristic shared with the equatorial regions projected to decline in habitat suitability (Lough, 2012). Adding support to our model projections of an equatorial retraction, in addition to a poleward expansion, is the matching distribution range shift identified in fossil records of coral distribution during the last interglacial period, when the global average temperature exceeded that of today (Kiessling \textit{et al.}, 2012).

The areas most affected by reductions in $\Omega_{\text{Arag}}$ levels correspond to off-equatorial latitudes, particularly in the western Pacific (Fig. 3 and 4b). Generally highly stratified, therefore with little buffering by mixing with subsurface waters, these regions will tend to experience the strongest degree of saturation decline. In addition, these are slightly cooler waters, where other environmental factors, including $\Omega_{\text{Arag}}$, are likely to out-weigh temperature variables in terms of importance. For instance, Cooper \textit{et al.} (2012) argued that, at present, SST was far more significant than $\Omega_{\text{Arag}}$ to explain long-term changes in calcification rates for massive Porites colonies off Western Australia, whereas the GBR has been identified, in modeling studies (McNeil \textit{et al.}, 2004) and skeletal measurements in massive Porites colonies (e.g., Cooper \textit{et al.}, 2008; De’ath \textit{et al.}, 2009), as a region already exceeding the thermal optima for coral calcification and sensitive to reduced $\Omega_{\text{Arag}}$.

**Fig. 5** Projected change in suitability for coral reef ecosystems between 1990 and 2070 under the A2 scenario, considering simultaneous changes in aragonite saturation and surface ocean temperature. The projected response has been averaged across both ‘OPT’ models and the MaxEnt\textsubscript{SIM} model (models defined in Table 1; BRT\textsubscript{SIM}’s results were excluded from the average, as discussed in the text and Data S3). Green dashed line indicates null projected change, whereas the hatched pattern identifies areas with novel conditions where projections are less reliable, due to a significant impact of the chosen extrapolation method (as explained in Methods). The sites of past (green triangles) and present (orange diamonds) range expansion of coral are also indicated, based on data from Lighty \textit{et al.} (1978), Veron (1992), Marsh (1993), Vargas-Ángel \textit{et al.} (2003), Greenstein & Pandolfi (2008), Woodroffe \textit{et al.} (2010), and Yamano \textit{et al.} (2011). Black crosses indicate coral reef distribution during the last interglacial period (data from Kiessling \textit{et al.}, 2012).
Synergistic impacts of warming and acidification

Under the combined influences of ocean surface warming and acidification, habitat suitability for coral reef ecosystems declines across the latitudinal band between 20°N and 20°S, affecting significant reef areas such as the Caribbean, GBR, and Coral Triangle region (Fig. 4c and 5). Areas where shallow water substrate is available are particularly susceptible to the impacts of warming and acidification (e.g., in Fig. 4d, modeled suitability in shallow equatorial regions more than halves by 2070). Although a marginal improvement at higher latitudes is projected by 2070, range expansion is constrained by availability of shallow waters where benthic substrate is present within light penetration depths (Fig. 5). Range expansion is also projected onto areas at the extreme end of oceanographic circulation pathways along the western boundaries, where the most depauperate reefs are found today (e.g., Glynn et al., 2007; Macintyre, 2003; Veron & Minchin, 1992; but see Thomson & Frisch, 2010). Coral reef expansion to higher latitude sites with improved conditions will, therefore, depend on larval influx, introducing a likely limitation for sites situated away from current transport such as the south-eastern Pacific (Wood et al., 2013). The rate of projected range expansion of suitable environmental conditions for coral reef presence varies between models. The MaxEnt_{OPT} model predicts a moderate (ca. 5 km per decade) expansion at present, accelerating to 30–45 km per decade by 2070 (Fig. 4d; calculated as rate at which curve edges intersects a horizontal line at 0.2). In contrast, BRT_{OPT} projects an initial global shrinkage under the effects of acidification (at ca. 25 km per decade), with increasingly rapid expansion from 2020–2030 as the effect of
rising SST becomes dominant (up to 70–80 km per decade by 2070). For comparison, Burrows et al. (2011) found the average poleward speed of surface isotherm movement in the oceans (50°S to 80°N) over the last 50 years was 27.5 km per decade. As already stated, our coral reef range expansion rate estimates do not take into account connectivity limitations related to the dispersal of coral larvae by ocean currents, and thus follow the thermal shift tempered by ocean acidification.

The combined impacts of increasing SST and acidification have little impact on environmental suitability for coral reef presence in the eastern Pacific, south east Atlantic, and the north Brazilian coast over the coming decades. These are recognized as marginal reef sites (e.g., Smith, 1992; Kleypas et al., 1999a; Glynn et al., 2007; Manzello et al., 2008); however, the decline of Ω_{Arag} is relatively slow in these predominantly upwelling regions, average SST is within tolerance levels, and further increases in SST might actually be advantageous for reef formation. The low Ω_{Arag} values in the eastern Pacific are not a limiting factor according to any of our statistical models, which instead assign constant, or at times increasing, suitability values to areas with Ω_{Arag} values falling below 2.2–2.3. While these levels of Ω_{Arag} will obviously impact reef structure and the balance of carbonate accretion and dissolution (e.g., Kleypas et al., 1999b; Manzello et al., 2008), and is likely to affect species composition and biodiversity (e.g., Fabricius et al., 2011), the region remains suitable for reef presence in our models, potentially assisted by warming where temperatures were previously suboptimal. That conditions remain suitable does not necessarily imply that existing reefs will be able to cope with the changes anticipated by 2070. We have not considered future changes in SST variability in our analysis, and this factor could play a key role for coral reef survival in these marginal areas (Glynn & Colgan, 1992; Toth et al., 2012), which are ranked globally among the slowest in terms of recovering from disturbances (Graham et al., 2011b).

**Model evaluation and limitations**

Empirical evidence is important to increasing our confidence in Bioclimate Envelope Models and projected distribution changes (Araújo et al., 2005) and the fossil coral record can provide a test for the models’ predictive ability. If SST is the stronger limiting factor for the presence of shallow coral reefs at high latitudes, we would expect fossil evidence of such an expansion into higher latitudes during warmer geological periods. In
Fig. 5, we compare our 2070 predictions with relevant fossil records, including reports of extensive reef formations in high-latitude sites in Japan (Veron, 1992), Florida (Lighty et al., 1978), and Lord Howe Island (Woodroffe et al., 2010) dating from the Holocene, and along the Western Australian coast dating back to the Late Pleistocene (Greenstein & Pandolfi, 2008). Kiesling et al. (2012) documented both a range expansion and an equatorial retraction of coral reef distribution during the last interglacial period of the Pleistocene (ca. 125,000 years ago; Fig. 5), when average SST might have been about 1 °C higher than today (McKay et al., 2011). In addition, there is evidence supporting present-day range expansion. Yamano et al. (2011) report several tropical coral species expanding their range into higher latitudes along the coast of Japan, among them two Acropora sp. key for reef formation in the Indo-Pacific region. Veron (1992) also describes a high latitude fossil reef in Japan being re-colonized as a response to increasing temperature andMarsh (1993) reported Acropora sp. growing at a high-latitude site off Perth, Western Australia. In the Atlantic region, Vargas-Ángel et al. (2003) describe thickets of Acropora cervicornis growing off the coast of Florida at higher latitudes than found previously. All these reports of past and present range expansion are consistent with our projections under current environmental change (Fig. 5).

Bioclimatic Envelope Models trained with equilibrium data are not suitable tools for the prediction of transient coral bleaching episodes. In particular, the models employed here have not been trained with the most relevant environmental variables (e.g., Degrees Heating Weeks or other short-term measures of thermal stress), or the location, date, and severity of bleaching episodes. Our projections correspond, instead, to the expected equilibrium response if conditions were maintained constant for sufficient time. Within these limitations, we wanted to establish a comparison of our predictions for the present-day with current observations. Coral bleaching reflects a stress response (Glynn, 1996), and degrading environmental conditions may lead to an increased number of bleaching episodes. To test this hypothesis, we compared the distribution of over 3500 recent bleaching events (observed between 2008 and 2012) with projected changes in suitability between model training conditions (1990) and the present-day (2010). We found bleaching episodes were more frequent in areas to which both MaxEnt_SIM and BRT_SIM’s 2010 projections assign higher decreases in suitability, when compared to the average on presence cells (Fig. 7). This is particularly significant for the BRT ‘SIM’ model; however, no such correlation is present with projections by the ‘OPT’ models, developed from the full suite of 27 predictive variables. Models relying on a limited number of variables are more sensitive to any change in those variables, and thus the responses of the ‘SIM’ models generally amplify that of the ‘OPT’ models, which can help explain why the ‘SIM’ models correlate better to short-term variations. MaxEnt_SIM and BRT_SIM do however differ substantially in their predictions, especially in the WPWP region and surrounding areas, where the highest decrease in suitability is to be found according to MaxEnt_SIM, but where BRT_SIM actually forecasts improved conditions. Few bleaching events are reported for the WPWP, but as it contains some of the least monitored coral sites in the world, this may be due to underreporting. BRT methods tend to overfit to training data, despite careful model development designed to minimize this (e.g., Elith et al., 2008), and models relying on a limited number of variables are more affected. Despite acceptable performance by BRT_SIM within training conditions (similar AUC scores to that of MaxEnt_SIM; Fig. S1.2 in Data S1), overfitting makes its projections unstable, creating an oscillatory response to rising temperatures (e.g., Fig. S1.7) and leading to unreliable projections for anything but the smallest changes in environmental variables, including out-of-range conditions (e.g., the WPWP and surrounding areas in Fig. 7). For this reason, we chose to exclude BRT_SIM projections from the average 2070 change in suitability (Fig. 5). Interestingly, the same qualities that make BRT_SIM a poor long-term predictor may determine its strength in identifying areas that are currently experiencing thermal stress (Fig. 7). The MaxEnt technique is not as prone to overfitting, and we find strong agreement between projections by the ‘SIM’ and ‘OPT’ model versions. In addition, this issue is not present with the full ‘OPT’ version of the BRT model, which has a similar performance to both MaxEnt models (Data S3).

Caveats in the use of Bioclimatic Envelope Models to predict the effect of climate change on the distribution of a species include uncertainties associated with the modelling technique used (e.g., Thuiller, 2004; Lawler et al., 2006), migration limitations (reviewed in Thuiller et al., 2008), the method employed for out-of-range extrapolation (e.g., Webber et al., 2011), the availability of absence data or background selection (e.g., Elith et al., 2010), the spatial scale of the analysis (e.g., Pearson & Dawson, 2003), and the equilibrium hypothesis (e.g., Hirzel et al., 2001). Some of these caveats can be addressed by understanding the limitations of the results, which represent changes in equilibrium habitat suitability. Projections of the fate of existing coral reef ecosystems require the consideration of additional factors, such as local anthropogenic pressures and management, stress responses and recovery, bleaching, mortality, rates of sea-level rise, potential for adapta-
tion, and migration capabilities among others. Instead, the Bioclimatic Envelope Models used here simply identify areas with future conditions similar to those where present-day coral reefs are found. In addition, the 1° × 1° spatial scale of the study may be too coarse to resolve many of the subtleties of the changing environmental conditions; however, this scale is typical of global projections from current climate models. Within those limitations, our results are informative, representing an initial estimation of the magnitude of the impact and providing a basis for future modelling work.

We employed two Bioclimatic Envelope Model approaches that make different use of absence data. MaxEnt is a presence-only technique, meaning it does not assume absence in areas where presence has not been established, unlike BRT. These two approaches have divergent responses to some of the limitations listed above, including performance in out-of-equilibrium situations (Hirzel et al., 2001) and dealing with incompleteness of the training database and/or absences due to factors other than climatic unsuitability (e.g., Pulliam, 2000). In addition, the development of models with two different levels of complexity – the ‘OPT’ and ‘SIM’ versions – helps establish the impact of variable selection in the model output and illustrate model-related performance issues, such as BRTSIM’s poor performance for long-term and out-of-equilibrium predictions. Overall, we find relatively high model agreement between presence-only MaxEnt and presence/absence BRT (for the ‘OPT’ versions) and between the ‘OPT’ and ‘SIM’ model versions in the case of MaxEnt, particularly in areas projected to experience worsening conditions (Fig. 5 and Data S3). This, together with the congruence with the distribution of fossils from warmer geological times, increases our confidence in the predictions.

Despite their limitations, we note that the use of Bioclimatic Envelope techniques together with climate models output remains among the best tools in the study of species or ecosystem responses to changing conditions (e.g., Pearson & Dawson, 2003; Wiens et al., 2009). This study represents a significant advance over previous studies discussing the conflicting effects of warming and acidification because our models do not rely on specified thresholds for SST and ΩArag variables, but instead make simultaneous use of all relevant variables in the definition of an optimal climatic ‘envelope’ based only on the statistical analysis of the current coral reef distribution. This ‘envelope’ allows for the synergetic or antagonistic responses between variables that complicate physiological experimental results of thermal tolerance and ocean acidification studies.

Our main findings for future environmental suitability of coral reef ecosystems in all three CO2 emission scenarios considered are as follows: (i) range expansion at the high-latitude boundaries; (ii) no decreased suitability in currently marginal eastern Equatorial Pacific locations as well as in the Atlantic generally; and (iii) severe temperature-driven impacts in the WPWP and surrounding regions. The potential range expansion at high latitudes, however, may in many places be severely constrained by a lack of suitable benthic environment available for colonization and could additionally be affected by dispersal limitations. Currently, reefs in the Eastern Tropical Pacific will remain marginal, with increased warming offsetting the negative impacts of ocean acidification, while impacts in the suitability of the Atlantic basin as a whole may be minor. However, our models also forecast a significant overall decline in coral reef habitat suitability, with a decrease in suitability for coral reef ecosystems by 2070 of up to 30% in shallow water areas. We find that the decline, driven mainly by short-term SST maxima, is greatest around the WPWP region, and therefore would affect some of the most biodiverse coral reef regions. These results present important implications for future coral reef management, as they suggest that more emphasis should be placed in conservation efforts on marginal reefs as they are not necessarily a ‘lost cause’. They also suggest that coral reef presence is more likely to be preserved throughout much of the central and western Indian Ocean as well as the Atlantic, assuming other anthropogenic stresses are minimized.

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