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Environmental controls on the global distribution of shallow-water coral reefs

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ABSTRACT

Aim

Elucidating the environmental limits of coral reefs is central to projecting future climate change impacts on these ecosystems and their global distribution. Recent developments in Species Distribution Modelling (SDM) and the availability of comprehensive global environmental datasets provide an opportunity to reassess the environmental factors that control coral reef distribution at the global scale as well as compare the performance of different SDM techniques.

Location

Shallow waters worldwide.

Methods

The SDM methods used include a presence-only technique: Maximum Entropy (MaxEnt), and two presence/absence methods: Classification and Regression Trees (CART) and Boosted Regression Trees (BRT). The predictive variables considered include sea surface temperature (SST), salinity, aragonite saturation state (Ω_{Arag}), nutrients, irradiance, water transparency, dust, and cyclone frequency and intensity. For many variables both mean and SD were considered, and at weekly, monthly and annually-averaged timescales. All were transformed to a global 1°x1° grid to generate coral reef probability maps for comparison with known locations in the ReefBase (2000) dataset.

Results

Model performance was compared in terms of Receiver-Operating-Characteristic (ROC) curves and Area-Under-the-Curve (AUC) scores. BRT consistently outperformed other methods (AUC 0.90), although MaxEnt was also within acceptable performance limits (AUC 0.88). The dominant environmental predictors were the temperature variables; annual mean SST, and monthly and weekly minimum SST, followed by and with their relative importance differing between regions; nutrients, light availability and aragonite saturation. Potential geographical bias was explored via misclassification maps of false positive and negative errors on test data. While no systematic bias was found between major coral provinces, false negatives were more likely for cells that corresponded to 'marginal' non-reef-forming coral communities e.g. southern Queensland, Australia and Bermuda.

Main conclusions

Although SST-related variables dominate the coral reef distribution models, contributions from nutrient concentration, aragonite saturation and light availability were critical in developing models of reef presence in regions such as the Bahamas, south Pacific and Coral Triangle (particularly Sulu Sea and Spratly Is.). Agreement between BRT and MaxEnt models gives predictive confidence that they can be used to explore the environmental limits of coral reef ecosystems at a spatial scale relevant to global climate models (~1°x1°).

Keywords

Boosted Regression Trees (BRT), Classification and Regression Trees (CART), coral reef biogeography, environmental limits, Maximum Entropy (MaxEnt), Species Distribution Modelling (SDM).

INTRODUCTION

Coral reefs cover less than 0.1% of the world's oceans (Spalding & Grenfell, 1997) but constitute one of the most biologically diverse and economically valuable ecosystems on Earth (e.g. Reaka-Kudla, 1997; Moberg & Folke, 1999). These 'oases' support levels of productivity several hundred times higher than that of surrounding generally nutrient-poor areas (Hatcher, 1988). Symbiosis between scleractinian 'stony' coral and photosynthesising unicellular algae (*Symbiodinium spp.*) make this possible, but also limit coral reefs to the warm, shallow and clear waters of the tropics where sunlight is readily available.

Reefs are vulnerable to anthropogenic disturbance, including overfishing and overharvesting of coral, physical damage from destructive fishing and shipping, increased sedimentation due to land use changes, and reduced water quality resulting from coastal runoff. Combinations of these stresses are highly likely responsible for observed declines of these emblematic ecosystems (reviewed in Carpenter *et al.*, 2008). Coral reefs now face additional pressures exerted by climate change. The increase in global mean Sea Surface Temperature (SST) of at least 0.5°C since 1850 (Rayner *et al.*, 2006) has been implicated in widespread coral bleaching events, and hence increased mortality (Carpenter *et al.*, 2008). At the same time, the ocean uptake of CO_2 has decreased seawater pH by an estimated -0.1 units since 1750 (Bindoff *et al.*, 2007). Ocean acidification may compromise the ability of reef-building corals and other carbonate-producing organisms to calcify rapidly enough to maintain reef structures (Kleypas *et al.*, 2006). Recent observations of reduced calcification rates in massive

Porites colonies from the Great Barrier Reef (GBR) are consistent with this already occurring (Cooper *et al.*, 2008; De'ath *et al.*, 2009), and in the near future, calcification could potentially become marginal or strongly inhibited in most areas where reefs are found today (Hoegh-Guldberg *et al.*, 2007; Cao & Caldeira, 2008).

Central to projecting future impacts of climate change and ocean acidification on these ecosystems is a better understanding of what controls the biogeography of coral reefs today. This question has been pursued since Dana (1843), but the seminal study of global reef distribution as a function of environmental factors is Kleypas *et al*. (1999), in which lower limits of SST, aragonite saturation state (Ω_{Arag}) and light availability were identified as key factors determining coral reef distribution. The range of Ω_{Arag} values within which current coral reefs were found has proved particularly influential, and has been adopted as a critical threshold on coral reef distribution under future climate change and ocean acidification scenarios (e.g., Hoegh-Guldberg *et al.*, 2007; Cao & Caldeira, 2008).

Since the 1999 Kleypas *et al*. study, new global ocean environmental datasets have become available and significant advances have been made in the emerging field of Species Distribution Modelling (SDM, see Guisan & Zimmermann, 2000; Elith *et al.*, 2006; and Franklin, 2009 for an overview). These new statistical methods have been developed to meet an increasing demand from conservation planning, ecological and risk assessments, and ecosystem management amongst other fields. Assessment tools to evaluate and compare models' performance in different contexts have been developed and improved (Fielding & Bell, 1997; Manel *et al.*, 2001; Johnson & Gillingham, 2005), and the limitations of SDM better assessed and documented. The latter include the effects of sample size (Hernandez *et al.*, 2006) and sample bias (Costa *et al.*, 2010), spatial scale (Seo *et al.*, 2009), species prevalence (Manel *et al.*, 2001), variations amongst predictions from different models (Johnson & Gillingham, 2005), and limitations of their use in global change studies (Thuiller, 2004; Botkin *et al.*, 2007). SDM methods have been used to analyse environmental controls on coral reef distribution on a regional scale, for example cross-shelf and latitudinal changes of water quality measures within the GBR (De'ath & Fabricius, 2010), and deep water azooxanthellate coral on a global scale (Tittensor *et al.*, 2009).

Here we make use of recent methodological developments to revisit the question of what environmental factors control surface water coral reef distribution at the global scale. The predictive variables we have considered that may directly influence (or co-vary with other driving factors) coral reef distributions, include: temperature, aragonite saturation state, salinity, nutrients, indicators of upwelling (e.g. dissolved oxygen and nutrient concentrations below the photic zone), irradiance, water transparency, dust, and cyclone frequency and intensity. For many of these variables we considered both mean and SD at weekly, monthly, and annual time periods. We compare the predictions and performance of three different SDM statistical methods: Maximum Entropy (MaxEnt), Classification And Regression Trees (CART) and Boosted Regression Trees (BRT). The dominant environmental controls in different geographical areas were identified by studying a series of different variable combinations and mapping the predicted coral reef distribution. Although too coarse for elucidating detailed biological requirements of coral organisms, the 1°x1° spatial scale we use in our analysis is compatible with current global climate models. Combining climate model output with these statistical environmental models of potential reef distribution could provide a valuable tool for projecting future reef distributions under anthropogenic global warming and ocean acidification.

MATERIALS AND METHODS

Reef location data

The point coordinates of over 11,000 coral reefs used in the study were obtained from 'ReefBase', version 2000 (ReefBase, 2000). ReefBase is a composite of published and unpublished sources (e.g. peer-reviewed journal articles, field surveys, and other reports) of coral reef presence. The database includes entries for both 'reef' and 'non-reef coral communities'; the latter characterised by the inability to accumulate calcium carbonate. The presence records were mapped onto a 1°x1° global grid, with the cells designated as 'presence' sites if they contained one or more 'ReefBase' entries (a total of 1242 presence sites), and 'absence' sites if the grid cell did not contain any ReefBase entries. A fixed-degree projection was used instead of equal-area for convenience because most environmental datasets are provided on degree-based grids. A similar global analysis for stony corals on seamounts by Tittensor et al. (2009) found no difference between using 1°x1° resolution and an equal-area projection.

Environmental data

The environmental variables tested in our analysis are listed in Table 1. This includes variables previously considered by Kleypas *et al*. (1999), plus nitrate and phosphate concentrations at 100m water depth, dissolved oxygen concentrations on the surface and 100m water depth, current strength, cyclone activity, atmospheric dust content, and SST variability at various time scales. Of these, nutrient and dissolved oxygen concentrations at 100m water depth were tested as proxies for upwelling regions. Surface dissolved oxygen provides an additional non-linear response to temperature via its solubility. Current strength and cyclone action were considered as proxies for potential physical destruction of structural framework and inhibition of carbonate accumulation (Riegl, 2001), while high levels of dust have previously been linked to reef decline and reduced coral settlement (e.g. Shinn *et al.*, 2000). Finally, weekly, monthly, and inter-annual standard deviation (SD) of SST captures the degree to which a site is exposed to highly variable conditions. For example, SST fluctuations can be associated with stratification and high UV penetration, or climate phenomena such as the El Niño Southern Oscillation, all contributing factors to recent mass bleaching events (e.g. Glynn & Colgan, 1992; Fitt *et al.*, 2001; Berkelmans *et al.*, 2004).

As summarised in Table 1, mean annual and monthly values of SST (Locarnini *et al.*, 2006), and salinity (Antonov *et al.*, 2006), together with the annual averages of nitrate, phosphate (Garcia *et al.*, 2006a) and dissolved oxygen concentrations (Garcia *et al.*, 2006b) were obtained from the World Ocean Atlas (WOA) 2005 database. Satellite-derived daily irradiance (1991-1993) is from the ISCCP project (Bishop & Rossow, 1991; Bishop *et al.*, 1997) while depth of light penetration was estimated following Kleypas *et al.* (1999), using light irradiance and satellite measurements of the diffuse attenuation coefficient of (490 nm) light from GlobColour (2008). Aragonite saturation (Ω_{Arag}) data was calculated using 'CO2sys' version 1.05 (van Heuven *et al.*, 2009) from GLODAP (Key *et al.*, 2004) alkalinity and total CO_2 together with WOA (2005) temperature, salinity, silicate and phosphate and the carbonate dissociation constants of Dickson and Millero (1987) (Mehrbach et al's 1973 refit, see CO2sys' documentation for details). Areas missing GLODAP data (e.g. Caribbean) were given Ω_{Arag} values taken from the UVic Earth system model (Weaver *et al.*, 2001; Turley *et al.*, 2010) following the methodology of Cao and Caldeira (2008). Global dust data was obtained from NCAR CCSM3 model output (Mahowald *et al.*, 2006). The intensity of cyclone activity was the "sum of wind" product obtained from UNEP/GRID-Europe (2009) and based on data of >2800 historical cyclone events and modelled wind speed for 1977-2006. Weekly SST data (1982-2009) was from NCEP Reynolds Optimally Interpolated SST product (Reynolds *et al.*, 2002) and was used to estimate the SD of average monthly SST in both January and July and to obtain average maximum and minimum weekly temperatures. Finally, annual average, monthly maximum and minimum current speeds (2002-2006) were calculated from SODA version 2.0.4 (Carton & Giese, 2008).

Grid and Mask

All environmental variables were implemented on a 1°x1° grid between -60° and 60° latitude. A shallow-water mask (Fig. 1) was created from 30 second resolution SRTM30 Plus bathymetry data (Becker *et al.*, 2009). The ±60° latitude study region was restricted to areas with a benthic substrate depth that solar light could reach, as computed from the amount of Photosynthetically Active Radiation (PAR) reaching the surface and the water's attenuation coefficient at a wavelength of 490 nm. To minimise the number of isolated sea-mounts not resolved due to limitations in the resolution of the bathymetry data, the mask was established as the grid cells with regions shallow enough to be within twice the mean annual depth of light penetration. A total of 4649 grid cells passed the mask and contained 1115 of the 1242 designated reef presence sites (see Fig. 1). The remaining 127 presence cells falling outside the mask were discarded (>90% plotted on land or were incorrect/incomplete entries in the ReefBase dataset). Variables missing information on a reef cell were approximated by linear interpolation of neighbouring cells.

SDM methods

Three statistical methods were used to determine the relationship between the global distribution of reefs and the environmental variables studied. These were Maximum Entropy Modelling (MaxEnt), Classification and Regression Tree (CART), and Boosted Regression Trees (BRT).

MaxEnt (Phillips *et al.*, 2006; Phillips & Dudik, 2008) is a widely used (e.g. Tittensor *et al.*, 2009; Bradley, 2010; Ficetola *et al.*, 2010) presence-only technique for the prediction of species geographic distributions (i.e. predictions are based only on the environmental conditions of sites of known occurrence). The method assumes that environmental factors act as constraints on the distribution of a species, and that within those constraints, the species will tend to occupy all available habitat in a way that maximises entropy (i.e., the species distribution is not restricted by any additional unknown constraints). We used MaxEnt version 3.3.2, with the convergence threshold value set to 10^{-5} and a maximum number of iterations of 500. The output was obtained as the logistic prediction for presence of reefs, with values ranging from 0 (unsuitable) to 1 (optimal conditions). MaxEnt's logistic prediction can be interpreted as the probability of finding the species for a sampling effort similar to the one that produced the training dataset (see Phillips & Dudik, 2008). As the sampling effort is typically unknown, MaxEnt defaults to assuming an average 50% probability in locations where conditions are favourable.

CART (Breiman *et al.*, 1984; De'ath & Fabricius, 2000) and BRT (Friedman, 2001; De'ath, 2007) are decision-tree based statistical techniques. A single tree (CART) is built by repeatedly splitting the data using a simple rule each time, so that the homogeneity of the resulting groups is maximised. The optimal size of the tree can be chosen from different stopping criteria, such as cross-validation, to avoid over-fitting to training data (De'ath & Fabricius, 2000). Decision trees have the advantages of being able to handle non-linear relationships, high-order interactions, categorical or numerical data, and missing data. For the BRT method a series of trees is produced instead of a single one. Each tree is grown on reweighted versions of the original data, with an ever-increasing weight being assigned 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 have been shown to be extremely good predictors in ecological studies (Leathwick *et al.*, 2006; Moisen *et al.*, 2006).

Both CART and BRT were fitted in R (version 2.10.1, R Development Core Team, 2009). The spatial data was processed using the *sp* library, version 0.9-65 (Pebesma & Bivand, 2005; Bivand *et al.*, 2008), while single trees were generated with version 3.1-46 of the *rpart* library (Therneau & Atkinson, 2010) and boosted trees with version 1.6-3.1 of the *gbm* library (Ridgeway, 2007). The method adopted to generate boosted trees is the one proposed by Elith *et al.* (2008). Generating a BRT model requires specifying a number of parameters that control the process. These include the Tree Complexity (TC), which determines the size of each individual tree, the Learning Rate (LR), which establishes each tree's contribution to the final prediction, and the Bagging Fraction (BF), or percentage of random test data used to generate each of the trees. For this study, in order to generate each BRT model we tested TC values of 1, 3, 5, 7, and 10, LR values of 0.5, 0.1, 0.05, 0.01, 0.005, and 0.001, and BF of 0.5, 0.6 and 0.75 (values suggested by Elith *et al.*, 2008). The combination that optimised the model's predictive deviance from coral reef observations within reasonable time constraints was chosen in each case. An example of the procedure is given in Appendix S1.1 in Supporting Information.

Methods for model comparison

The output from the three models was compared in terms of Receiver Operating Characteristic (ROC) curves (reviewed in Zweig & Campbell, 1993); graphical plots of the true positives versus false positives for a binary classifier system. A curve in true-positives vs. false-positive space is obtained as the cut-off value for the probability at which a cell is considered a presence site (the 'discrimination threshold') is allowed to change. The ROC method, in addition to being independent of the discrimination threshold, is less biased by the prevalence of the species under study than other methods commonly used to test SDM output (Manel *et al.*, 2001). Although ROC was originally developed for presence/absence techniques, it can also be applied to presence-only models. Typically this involves comparing prediction at presence sites with prediction at sites chosen randomly from the study region (called 'pseudo-absences'). In our case, as absence data was available and used in the development of the presence/absence models, in order to establish a meaningful comparison, MaxEnt's ROC curve was also generated using true absence data. For techniques based on decision trees (CART and BRT), model performance is indicated by a single point in ROC-space, corresponding to a 50% probability of presence of the species/ecosystem being studied. While the discrimination threshold has an obvious cut-off, the rest of the ROC curve can still be obtained if the value is allowed to change. Average Area Under the Curve (AUC) scores (Bradley, 1997) were obtained from the output of 10 different model runs, generated each time from a random choice of 75% of the total data (training data) and tested on the remaining 25% (evaluation data).

Methods for assessing environmental variables as model predictors

Some of the 31 environmental variables used in this study (Table 1) are strongly correlated (Appendix S3; Fig. S3.1). In order to explore whether all potential environmental variables were necessary to the overall prediction and assess how the importance of different variables differ geographically, we created an ensemble of models using different combinations of environmental variables (Table 1). In Appendices S1 and S2 we included the results of a number of standard tests for exploring SDM output, such as 'variables' contribution indices' (Tables S1.1 and S2.1), which aim to measure the relative relevance of each variable to the model, and 'marginal response curves' (Figs. S1.6 S2.2, S2.3), which are graphical representation of the effect on the model's output of variations of a single variable while keeping the rest fixed at their average value.

RESULTS

Prediction maps

The results from all three SDM techniques (Fig. 2) are consistent with the observed major regions of coral reef presence (Fig 1). The probability maps (Fig. 2) use the *OPTIMAL* set of variables (Table 1), identified as the optimal combination of environmental variables to study present coral distribution (results from other models will be discussed below). Modelled coral reef probabilities are plotted for the shallow water mask with values from 0 (low probability; blue) to 1 (high probability; red). MaxEnt (Fig. 2b) differs from the BRT model (Fig. 2a) in having a compressed probability distribution, with predicted coral reef regions predominantly assigned logistic predictions close to 0.5 with limited high-probability sites. This is a characteristic of the MaxEnt method's default logistic output, which assumes that typical presence localities have an average probability of presence of about 0.5. Tree-based methods, in contrast, attempt to assign high values to presence sites, and their predictions are not directly comparable to MaxEnt's. In addition, the CART approach demonstrates noticeable discretisation as a result of the small number of final states (or terminal nodes) available (Fig 2c). Enlargements of the BRT and MaxEnt prediction maps for the Coral Triangle region are given in Supporting Information (Fig. S1.9 & S2.7).

Histograms and misclassification maps

The predicted probability values for each model can also be visualised as histograms (Fig. 3). These histograms separate the presence and absence sites according to ReefBase data, and were obtained from 30 model runs, each using a randomly chosen 75% of the data for training, and the remaining 25% for model evaluation. The values assigned to each cell correspond to the average of all runs in which the cell was selected to evaluate the model. Fig. 3 also shows the percentage of false positives (cells without reefs where the model predicts presence) and false negatives (cells with reefs where the model predicts absence). BRT correctly predicted coral presence in over 60% of actual reef cells, a percentage that dropped to 50% for CART. MaxEnt distribution has a clear peak at 0.5, with 65% of reef cells being assigned logistic prediction values between 0.4 and 0.6. Prediction errors (false positives and negatives) have also been mapped in Fig. 4, to investigate possible spatial bias.

Assessment of model performance

The performance of the three SDM methods was assessed by means of Receiver Operating Characteristic (ROC) curves. The curves in Fig. 5 correspond to the *OPTIMAL* variable set (see Table 1 for variable choice). Ten models were developed, each using a randomly chosen 75% of all the available data for model training; the curves (Fig. 5) correspond to each model's performance evaluation on the remaining 25% data. The average AUC-scores obtained from these curves are shown in Table 2. The presence/absence BRT model was the most successful, with an AUC score of 0.9, while the presence-only MaxEnt model performed almost as well (Fig. 5, Table 2). AUC scores above 0.9 correspond to 'highly accurate' models according to Swets (1988), with the 0.7-0.9 range corresponding to models with some useful applications and scores below 0.7 indicating 'low accuracy. BRT represents an upgrade of CART and clearly outperforms it.

Prediction maps of coral reef distribution were developed with different subsets of the predictive variables using both BRT and MaxEnt (Fig. 6). Table 1 lists the model names and the selected variables used to develop each of the models. The probability histograms for each model and the comparison of their performance in ROC space are also provided in Appendix S3 (Figs. S3.2 and S3.3). Despite very similar, often overlapping results in ROC space, the models developed from different variable combinations display distinct spatial distribution predictions of coral reefs presence.

Discussion

Coral biogeography and the spatial structure of environmental control

All SDM models indicate that coral reef distribution is primarily limited to regions of high SST, with high light availability, salinity, aragonite saturation state, and low nutrient concentrations being of secondary significance. Levels of dust, current speed, cyclone intensities, and inter-annual SST variability, are all typically assigned to be of minor importance. The mean percentage contribution values and SD in 10 model runs are given for both BRT and MaxEnt outputs (Tables S1.1 and S2.1). The BRT estimation of percentage contribution takes into account the number of times each variables is selected for splitting weighted by the square improvement of the model as a result of those split and averaged across the sequence of trees (Friedman & Meulman, 2003). Whereas, MaxEnt keeps track of the increase in gain due to each of the variables used in fitting the model, and the normalised percentage contribution of all variables are considered a measure of each variable's relevance to the final result (Phillips, 2006). However, because some of the variables are highly correlated, caution is required in the interpretation of these contribution values. An alternative for MaxEnt is Jackknife tests (Appendix S2; Figs. S2.4-6). In order to explore the spatial structure of environmental controls on coral reef biogeography, the relative contribution of each variable can also be analysed in conjunction with the probability maps (Figs. 6 & 7). Testing different combinations of potential predictive environmental variables provides insight into the control of these highly correlated variables on model response and global distribution of coral reefs.

In combination, SST variables contribute close to 50%-60% of the environmental controls on coral distributions according to all SDM methods (using *OPTIMAL* model variables; output Fig. 3). This is not surprising. First described in the 19th century (Dana, 1843), the high correlation between elevated surface temperature and coral distribution has been well documented (e.g. Stoddart, 1969; Rosen, 1984; Veron & Minchin, 1992). The majority of coral reefs are found in water temperatures with an annual minimum SST greater than 18°C and average minimum weekly temperature above 16°C (reviewed in Kleypas, 2007). The marginal response curves for both BRT and MaxEnt methods indicate threshold values for minimum monthly and weekly SST that are consistent with these estimates (S2 and S3). Mechanisms through which high SST favours the presence of coral reefs include positive physiological effects on growth and calcification rates (Harriott, 1999; Lough & Barnes, 2000), increased reproductive viability (reviewed in Harriott & Banks, 2002), and ecological advantages in the competition with macro-algae (Johannes *et al.*, 1983) linked to nutrient availability and herbivory pressures (McCook *et al.*, 2001; Smith, 2008).

Models based on SST variables alone (Table 1 model *SST*), however, provide limited explanation of the global distribution of coral reefs (Figs. 6a & 7a) because they fail to account for reefs in higher latitudes, such as the Southern GBR, New Caledonia, South French Polynesia, and Northern Red Sea, South Japan and Ryukyu Islands. The predictions for certain high-temperature regions (e.g. South China Sea/Sulu Sea and South East Papua New Guinea) were also poor. Identifying what environmental factors in addition to SST control distribution at these sites is particularly critical for understanding how reefs will respond under future global change scenarios. Modelled reef distribution is improved by the inclusion of light availability (Figs. 6d & 7d; model *SST_LDepth*), nutrients (Figs. 6e & 7e; model *SST_Nutr*), aragonite saturation (Figs. 6b & 7b; model *SST_Arag*), and secondary SST variables (Figs. 6f & 7f; model *SST_2ndSST*).

Each model tends to reinforce *SST* predictions due to synergistic interactions, but also demonstrates critical addition information that is needed for correctly modelling particular geographical locations.

Water clarity, together with solar PAR irradiance, determine the amount of light available and hence limit the depth of reef formation via depth-related control of coral primary productivity and calcification rates (Gattuso *et al.*, 2006). Light availability, and therefore the maximum depth of reef formation, decreases with increasing latitude (Gattuso *et al.*, 2006). However, the addition of light penetration depth variables improves predictions in both the Pacific and Caribbean regions (Figs. 6d & 7d) by extending the latitudinal range of predicted reef habitats (e.g. to include southern islands of French Polynesia). Including light availability also improves predictions for the South China Sea/ Sulu Sea region and the Bahamas.

In general terms the inclusion of seawater nutrient (phosphate and nitrate) concentrations is expected to exclude modelled reefs from areas enriched by riverine discharge, upwelling along eastern equatorial ocean boundaries and higher latitudes in response to the latitudinal gradient of increasing nutrients. Coral reef manipulation studies reveal a more complex relationship, which is often species and region-dependant and with responses that are typically subtle (e.g. Koop *et al.*, 2001; Dizon & Yap, 2005; Smith *et al.*, 2005). Instead, macroalgae abundance, which generally correlates with nutrient concentrations, may play a decisive controlling role (e.g. Johannes *et al.*, 1983; Birkeland, 1988; De'ath & Fabricius, 2010). Macroalgae have been shown to directly interfere with coral recruitment, suppress coral growth and fecundity, increase disease-related mortality, and compete with coral for space (reviewed in McCook *et al.*, 2001; Smith *et al.*, 2006; Mumby & Steneck, 2008). The inclusion of surface nutrient concentrations is critical for modelling sites in the Southern GBR and Southern Japan (Figs. 6e & 7e). These parameters also have the strongest influence on improving SDM predictions across the Caribbean.

Aragonite saturation has the largest effect in both BRT and MaxEnt after SST, light and nutrient variables (Figs. 6b & 7b; Appendix Tables S1.1 & S2.1). There is a well-documented relationship between low Ω_{Arag} and reduced coral calcification rates (experimental studies reviewed in Kleypas *et al.*, 2006; e.g. field studies Cooper *et al.*, 2008; De'ath *et al.*, 2009). Low cementation of reef framework and high bioerosion rates are also associated with low Ω_{Arag} (e.g. Manzello *et al.*, 2008; Silverman *et al.*, 2009). In addition, high magnesium calcite precipitating coralline algae, which play a key role in the cementation of coral rubble into solid reef, are particularly sensitive to carbonate saturation state (Kuffner *et al.*, 2008). The *SST_Arag* model reinforces predictions of reef presence in areas already picked up by the *SST* model, as expected since both datasets are highly correlated (Appendix S3; Fig. S3.1). Although the addition of Ω_{Arag} dramatically improves predictions in areas such as the Spratly Islands / Sulu Sea and Southern French Polynesia (Figs. 6b & 7b), predictions for the Northern GBR deteriorate in the BRT model. The latter result potentially highlights an issue with the quality of the Ω_{Arag} dataset for this region.

Modelling probability of reef presence in the Southern GBR proves particularly challenging (Figs. 6 &7), although the *OPTIMAL* variable selection is capable of providing the information needed (Fig. 2). Reef formation in this area is apparently controlled by a different combination of conditions than those acting on the Northern section. Of all the variable models presented in Figs. 6 and 7, only the inclusion of nutrients and secondary SST variables improve predictions for the Southern GBR. Other regions challenging to model include the Galapagos Islands and Bermuda. In a sense it is reassuring that the SDMs are failing to pick up these areas, because they correspond to regions with known adverse conditions for present-day formation of reefs and currently support low coral biodiversity (Glynn *et al.*, 1983; Logan & Tomascik, 1991).

With a large enough number of explanatory variables, a statistical model may succeed in explaining data by 'finding' causal relationships that are in fact dubious or nonexistent. The process is known as over-fitting, and weakens the utility and applicability of the model. Environmental variables having an effect which appear in conflict with biological knowledge of coral habitat and physiology may indicate this occurring and hence can be identified (and omitted) on this basis. This appears to be the case with the variables included as indicators of upwelling (nutrients at 100m depth and dissolved oxygen both at the surface and at 100m). By comparing the prediction maps for the *SST* and the *SST_upwllng* models (Figs. 6a & c and 7a & c) it is obvious that the addition of the upwelling indicators give an improved model 'prediction'. The prediction of habitat suitability for coral reefs improves most, however, in areas that are either distant to upwelling processes (such as Bermuda or Northern Red Sea) or where upwelling conditions are expected to pose a serious challenge to reef presence, rather than be an asset (e.g. Galapagos Islands). We highlight this example as a warning of how overfitting could obscure important variables and responses in SDM. As a result we have opted for not including these variables in our final predictor set and 'optimal' model (*OPTIMAL*).

Geographical bias and error analysis of mapped SDM predictions

Misclassification maps (Fig. 4; based on the false positives and false negatives averaged from evaluation data of 30 model runs) were used to test for geographical bias in the predicted probabilities. From visual inspection, no systematic bias is apparent between major coral provinces (i.e. Caribbean and Indo-Pacific regions); any clustering of errors takes place at lower spatial scales. All three SDM techniques, MaxEnt, CART and BRT, fail to model suitable habitat for coral reefs at certain sites for which there are ReefBase entries (false negatives). Interestingly, the percentage of false negatives is much higher for cells that according to the reef location database correspond to non reef-forming coral communities. For BRT (and MaxEnt), a total of 53% (65%) of cells with non-reef coral communities give false negatives, compared to only 37% (45%) of the remaining presence sites. Non-reef entries largely correspond to sites classified as 'marginal' by Kleypas *et al.* (1999) and include the Pacific coast of Costa Rica and Panama, Bermuda, the southern coasts of the main islands of Japan, southern Queensland, Australia and the Galápagos Islands. Reef formation at these sites is known to be challenging (e.g. mainland Japan, Veron & Minchin, 1992; Solitary Islands, Harriott *et al.*, 1994; Galápagos, Glynn *et al.*, 1983), and typically coral communities are present rather than reefs (ReefBase, 2000) because of an inability to accumulate $CaCO_3$ and a diminished presence of primary reef-building taxa such as *Porites* and *Acropora* (Buddemeier & Smith, 1999; Harriott & Banks, 2002). On the Pacific coast of Costa Rica and Panama, reef development is sporadic and mostly takes place around offshore islands. D'Croz & Robertson (1997) suggest this might be due to temperature extremes associated to El Niño events and frequent cool upwelling episodes, with the formation of reef in the coast further prevented by high concentration of nutrients, likely caused by terrestrial runoff. The consistent SDM results across models hint that this region is currently unsuitable for coral reef accretion. Missing input variable(s) may also explain some consistent SDM output errors. For example, all three methods misclassify cells to give false negatives across the region of the West Timor Sea and Rowley Shoals, off NW Australia, where coral reefs are known to be present (Spalding *et al.*, 2001).

Performance comparison of the different SDM techniques

All three models were able to produce distributions that are consistent with the major regions of coral reef distribution. However, the three SDM techniques used in this paper are static, and therefore our underlying assumption is that surface water coral reefs are in equilibrium (or quasi-equilibrium) with their environment (e.g. Peterson *et al.*, 1999; Pearman *et al.*, 2008). Non-equilibrium situations are often considered more realistic in an ecological context (Guisan & Zimmermann, 2000; Austin, 2002), but the required global environmental datasets do not exist with the temporal frequency required to run dynamic simulation models (Botkin *et al.*, 2007). Instead, we considered transient effects in the analysis by including them as additional predictive variables (e.g. tropical storm frequency and intensity, standard deviations in SST at inter-annual and weekly time scales). None were found to have a significant impact on the models.

Presence-only methods, such as MaxEnt, provide a test of the potential anomalies in model results created by inaccuracies or incompleteness of the input datasets. For example, SDM results for wide-ranging and tolerant species can be particularly sensitive to absence data (Brotons *et al.*, 2004). Hirzel *et al.* (2001) also showed that presence-only models seemed to perform better than presence/absence ones in out-of-equilibrium situations (i.e. when a species does not occupy all suitable habitat) and so such models might be better suited to predict response to environmental change. A limitation of static modelling is that the realised habitat is assumed to equal the 'fundamental' one (i.e. that coral reefs are present in all areas with an environment compatible with requirements). However, even under equilibrium conditions, absence might be due to dispersal limitations. For presence/absence models this can give rise to an *a-priori* bias in the training data (Hutchinson, 1957; Pulliam, 2000; Phillips *et al.*, 2006), and in out-of-equilibrium situations migration limitations can become a significant source of uncertainty that is also difficult to estimate (reviewed in Thuiller *et al.*, 2008). Comparison with the output from presence-only methods can pinpoint the magnitude of some of these effects on model performance (Gu & Swihart, 2004). Encouragingly for our study, the presence-only method, MaxEnt, and the presence/absence method, BRT, perform almost equally well (Table 2) in evaluation tests (e.g. for ability to separate presence/absence signal) and in comparisons between modelled predictions and actual presence/absence data. The application of both SDM approaches in parallel, therefore, increases confidence in the models as predictive tools for understanding the global distribution of surface water coral reefs under present conditions.

Conclusions

We have used three SDM methods to predict coral reef presence/absence based on environmental factors at 1° resolution. At this scale, SST-related variables are found to be dominant in explaining the current biogeography of coral reefs, but alone are insufficient to give an accurate picture of global distribution. Surface nutrient concentration, aragonite saturation and light availability prove critical in accurately defining the limits of coral reef ecosystems in both the Caribbean and Pacific. We find that light availability is particularly crucial for the South Pacific, with the exception of the Southern GBR, where nutrient concentrations are key. The Coral Triangle region is poorly modelled using just SST variables, and an accurate prediction requires a combination of nutrients, light availability and most significantly, aragonite saturation.

We have tested model performance on evaluation data, and find that BRT, a presence/absence technique, performs slightly better than presence-only MaxEnt. Our prediction confidence is strengthened by this result because any major inconsistencies between the two would indicate issues associated with the input data, underlying assumptions, or model selection.

Although the 1°x1° scale of our analysis is too coarse to capture local environmental controls at reef sites and their impact on local-scale distribution, our chosen resolution is consistent with the current generation of global climate models (ca. 1°x1°) and the available global environmental data sets. Aggregation to coarser spatial scales also increases the reliability of a species absence (McPherson *et al.*, 2006), and can thus offset limitations in the reef location database. Explicit linking of environmental-biogeographical and climate models will facilitate the generation of future (and past) projections (and sensitivities) of coral reef biogeography to global environmental change.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 BRT model optimisation, output and analysis.

Appendix S2 MaxEnt model output and analysis.

Appendix S3 Environmental variable correlations and contributions.

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Biosketch

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Author contributions: E.C., A.R. and E.J.H. conceived the research idea and collaborated in the interpretation of the analysis, E.C. led the writing, and undertook the data processing and modelling.

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Figure headings:

Figure 1. Mask used for the study (grey), corresponding to shallow waters between -60° and 60° latitude. Presence cells (those containing at least one entry from the ReefBase version 2000 dataset) are shown in black. The areas not included in the analysis are white. Behrmann Projection.

Figure 2. Predicted probability ((a) BRT and (c) CART) or logistic prediction ((b) MaxEnt) of a coral reef being present based on the environmental variables from the *OPTIMAL* model variable dataset (Table 1) and using the complete dataset for training. Each cell is designated a likelihood value for the predicted probability or logistic prediction from 0 (unlikely; in blue) to 1 (highly likely habitat; in red).

Figure 3. Histogram for the average modelled probabilities (BRT and CART), or logistic prediction (MaxEnt), of a coral reef being present in the shallow-water grid cells using BRT (a), MaxEnt (b) or CART (c). Cells where coral reefs or communities are present according to the ReefBase dataset are shown in grey, absence sites in white. The probability (logistic prediction in MaxEnt's case) assigned to each cell is the average of the runs in which it is taken as evaluation data out of a total of 30 random runs. The distribution of model results that are false positives (red) or false negatives (blue) is also shown.

Figure 4. Maps showing the spatial distribution of false positives (red) and false negatives (blue) obtained for evaluation cells in 30 runs of BRT (a), MaxEnt (b) and CART (c) models. Areas in grey in the MaxEnt map indicate cells where environmental data was missing (e.g. areas missing aragonite saturation data) because predictions can not be obtained using MaxEnt at sites with missing environmental data; in contrast tree-based techniques are able to look for alternative variables.

Figure 5. ROC curves for the three model techniques and using 25% evaluation data chosen randomly for each of 10 model runs. The optimal point in ROC space for BRT (circles) and CART (triangles) corresponds to a threshold value of 50% probability of presence.

Figure 6. Prediction maps for BRT models using various combinations of environmental variables to evaluate predictor contributions to model performance. The predictor subset used in each of the models are given in Table 1; SST variables (a), SST variables plus aragonite saturation state (b), SST plus upwelling variables (c), SST plus light variables (d), SST plus nutrient variables, (e) SST plus secondary SST variables capturing SST variability on various timescales (f).

Figure 7. Prediction maps for MaxEnt models (given in Table 1) using various combinations of environmental data to evaluate individual variable contributions to model performance. As for Figure 6, the predictor subset used in each of the models are given in Table 1; SST variables (a), SST variables plus aragonite statuation state (b),

SST plus upwelling variables (c), SST plus light variables (d), SST plus nutrient variables, (e) SST plus secondary SST variables capturing SST variability on various timescales (f).

Figure 1.

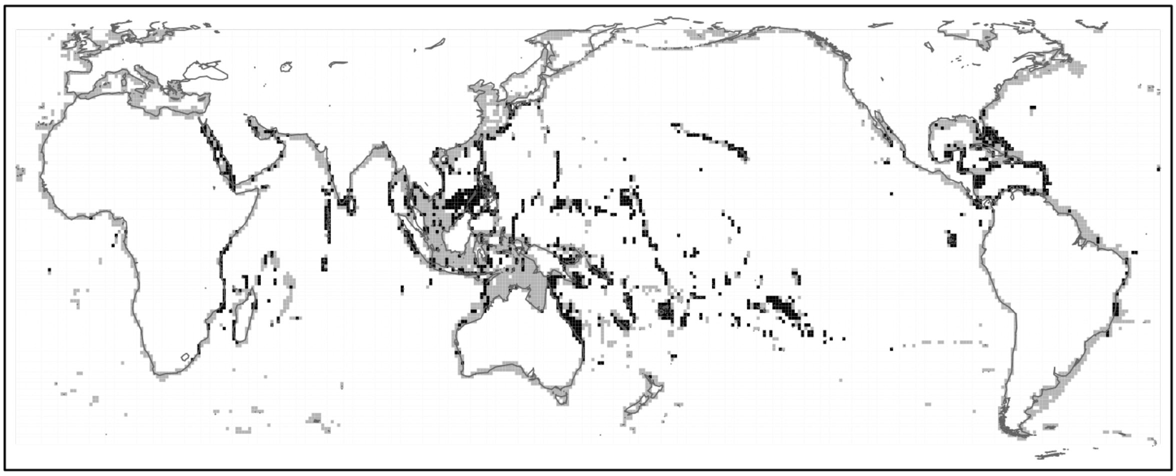

Figure 2.

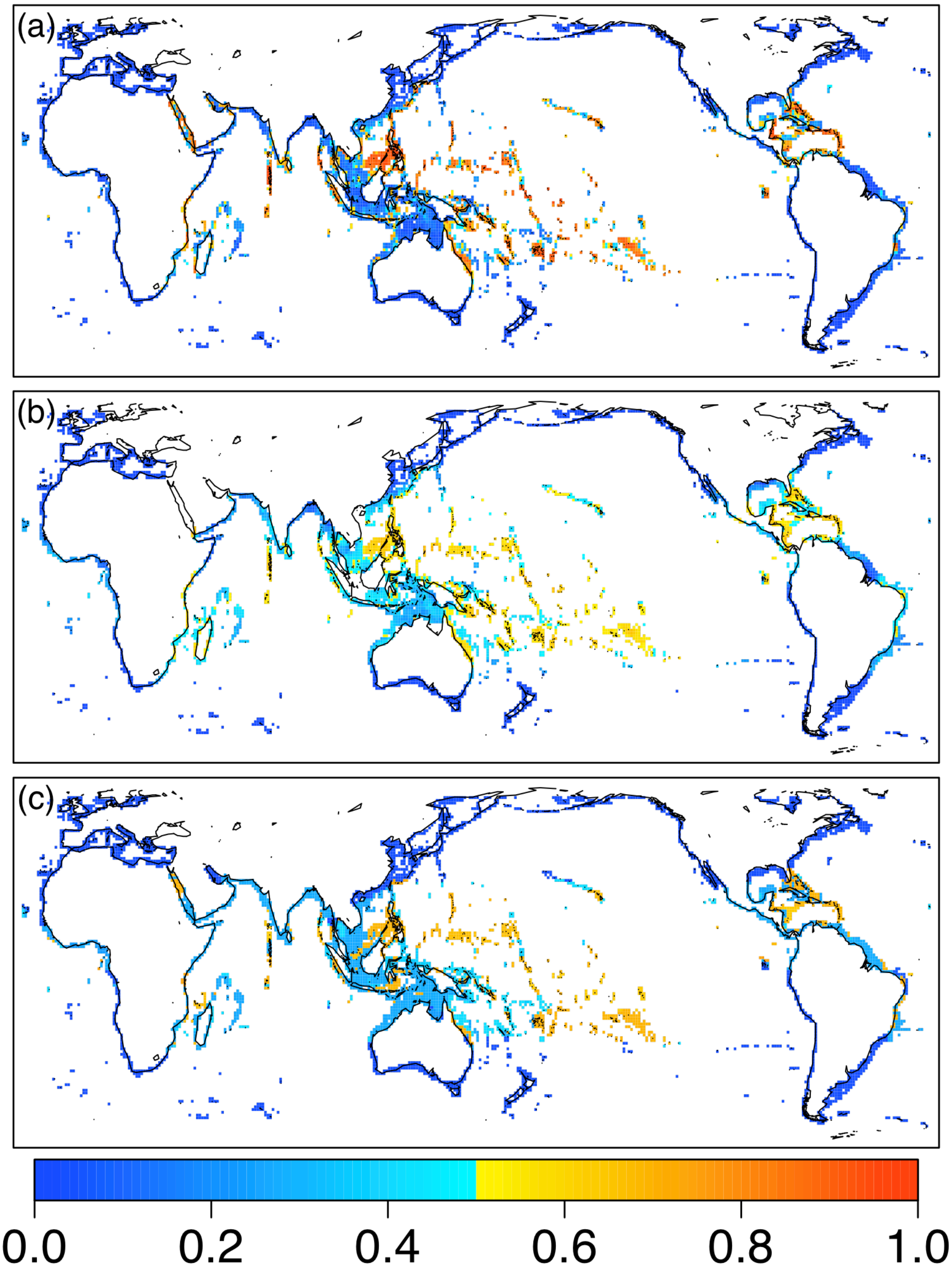

Figure 3.

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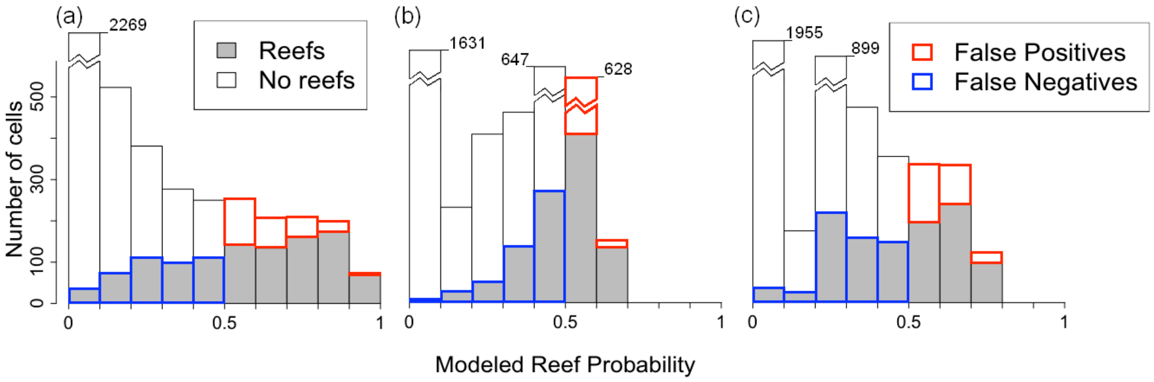

(a)
(b)
(c)
2269
1631
647
628
1955
899
Reefs
No reefs
False Positives
False Negatives
Number of cells
0
100
300
500
0
0.5
1
0
0.5
1
0
0.5
1
Modeled Reef Probability

Figure 4.

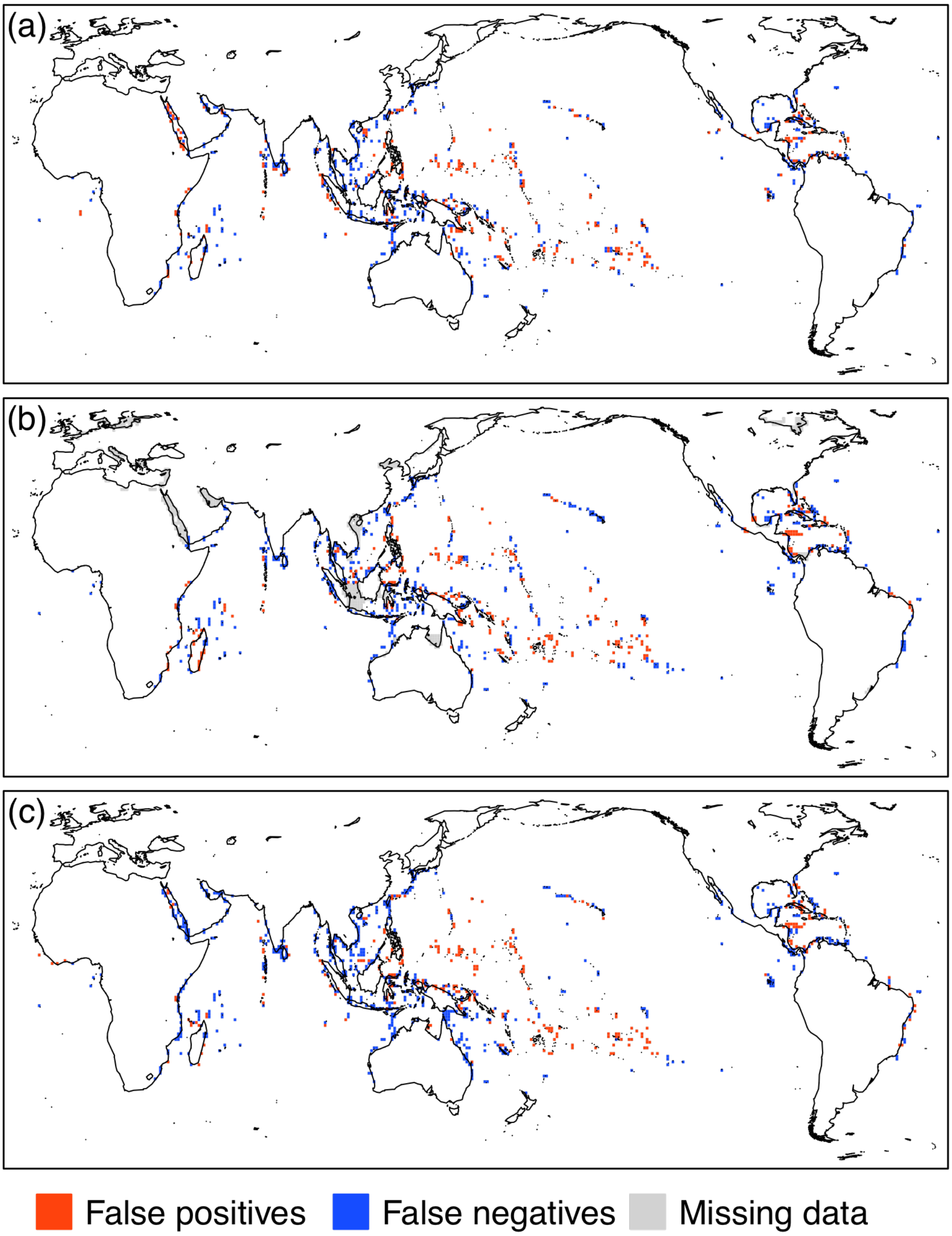
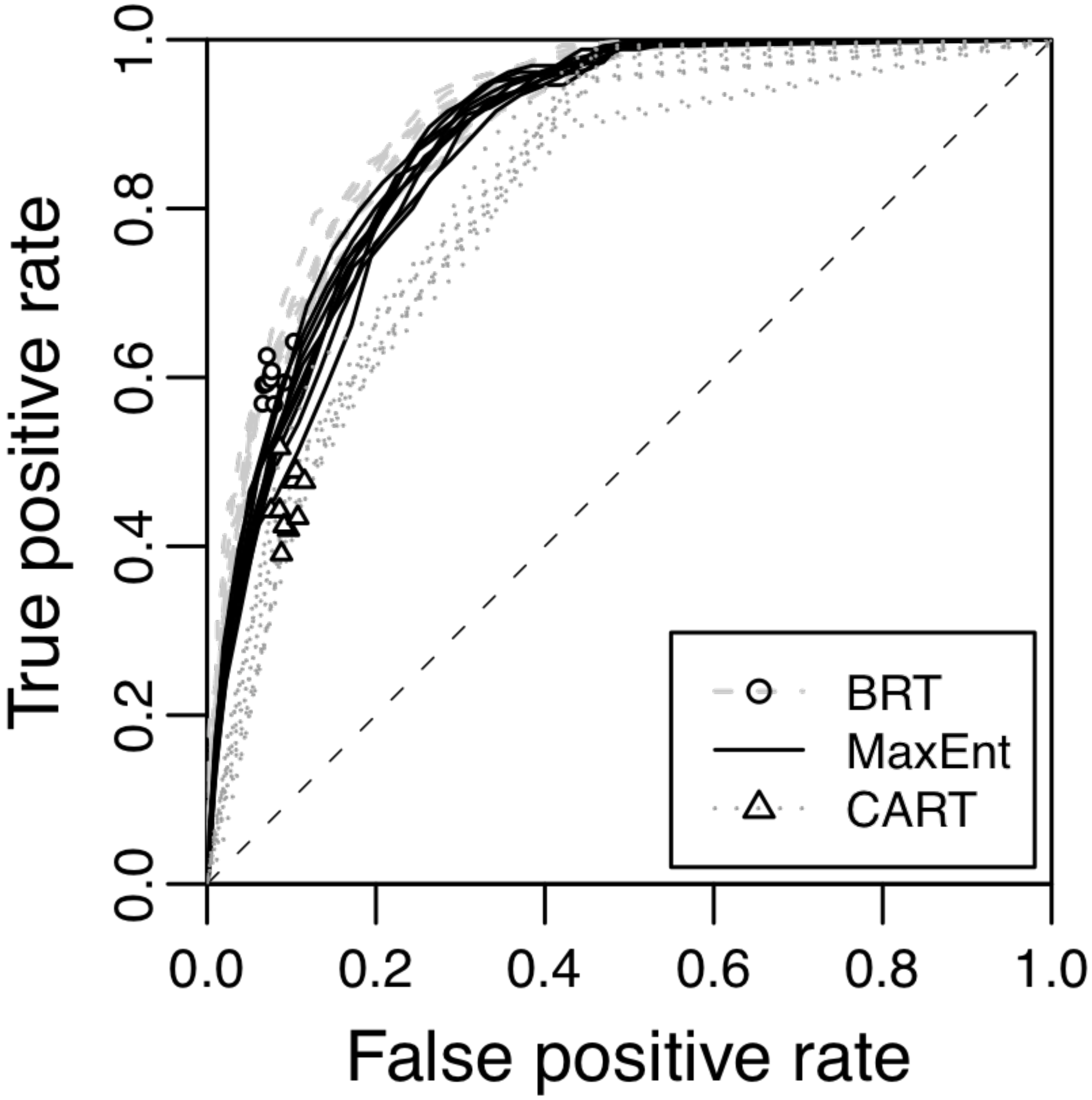


Figure 5.


True positive rate
False positive rate
0.0
0.2
0.4
0.6
0.8
1.0
0.0
0.2
0.4
0.6
0.8
1.0
BRT
MaxEnt
CART