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Associations between climate stress and coral reef diversity in the western Indian Ocean

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Abstract

Climatic–oceanographic stress and coral reef diversity were mapped in the western Indian Ocean (WIO) in order to determine if there were associations between high diversity coral reefs and regions with low-to-moderate climate stress. A multivariate stress model developed to estimate environmental exposure to stress, an empirical index of the coral community's susceptibility to stress, and field data on numbers of fish and corals taxa from 197 WIO sites were overlain to evaluate these associations. Exposure to stress was modeled from satellite data based on nine geophysical–biological oceanographic characteristics known to influence coral bleaching (i.e. temperature, light, and current variables). The environmental stress model and the coral community's susceptibility index were moderately correlated ($r = -0.51$) with southern and eastern parts of the WIO identified as areas with low environmental stress and coral communities with greater dominance of bleaching stress-sensitive taxa. Numbers of coral and fish taxa were positive and moderately correlated ($r = 0.47$) but high diversity regions for fish were in the north and west while diversity was highest for corals in central regions from Tanzania to northwestern Madagascar. Combining three and four of these variables into composite maps identified a region from southern Kenya to northern Mozambique across to northern–eastern Madagascar and the Mascarene Islands and the Mozambique–South Africa border as areas where low-moderate environmental exposure overlaps with moderate-high taxonomic diversity. In these areas management efforts aimed at maintaining high-diversity and intact ecosystems are considered least likely to be undermined by climate disturbances in the near term. Reducing additional human disturbances, such as fishing and pollution, in these areas is expected to improve the chances for their persistence. These reefs are considered a high priority for increased local, national, and international management efforts aimed at establishing coral reef refugia for climate change impacts.

Keywords: Africa, biodiversity, climate change, environmental stress, latitudinal patterns, marine protected areas, prioritization, resilience, spatial autocorrelation

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Introduction

Coral reefs are highly diverse and economically important to approximately 100 million people in the tropics, yet their future is being threatened by rapid climate change (Hoegh-Guldberg *et al*., 2007). Identifying and prioritizing management of coral reefs in areas of low climate stress or reefs that are resilient to climate change is a leading rationale for informing the placement and implementation of challenging management interventions, such as no-take or closed areas (Sutherland *et al*., 2009). Severe climate impacts over the past decade have heightened awareness of climate change and the declining health of coral reefs (Bruno *et al*., 2009). In the Indian Ocean, for example, 45% of living coral was killed across the 1998 warm temperature anomaly, although the spatial distribution of this mortality and subsequent recovery was highly variable (Baker *et al*., 2008; Ateweberhan & McClanahan, 2010). The temperature anomaly interacted in a complex way with many physico-chemical, biological, and ecological variables to create heterogeneous responses (McClanahan *et al*., 2007c; Maina *et al*., 2008). This spatial heterogeneity, often associated with large-scale stable oceanographic conditions, indicates the potential for identifying and prioritizing areas where conditions are likely to promote resilience to climate change (McClanahan *et al*., 2008).

In the western Indian Ocean (WIO), efforts to develop tools to prioritize management options for coral reefs have focused on a multivariate environmental stress model, integrative metrics of reef ecology and condition, and social adaptive capacity of human communities in selected locations where all three of these data sources were available (McClanahan *et al*., 2009a).

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Another less explored component of prioritization, frequently the highest priority for conservation biologists interested in conservation through the elimination of local human disturbances (i.e. IUCN categories 1–4), is the identification of biodiversity centers under threat (Myers *et al.*, 2000). Incomplete, coarse resolution and variations in sampling effort have made it challenging to fully describe biodiversity of coral reefs in the Indian Ocean (Sheppard, 1998) and particularly the tropical African coastline (Awad *et al.,* 2002; Barnes & Bell, 2002). A high-diversity area of corals has been reported in the islands south of India (Maldives and Chagos; Sheppard 1998) but the African coastline and southern Indian Ocean were not well sampled, patterns of algae diversity are patchy and complex (Price *et al.,* 2006), and patterns of reef scleractinian or hard corals and fish diversity have been reported only at coarse spatial scales (Veron, 2000; Allen, 2008).

Given the potential detrimental impacts of climate change on the coral reefs in the WIO and elsewhere, there is a need to develop multiple metrics and tools for prioritizing areas for conservation and management at the regional scale. While governments have achieved some success, through a variety of national measures to control detrimental human activities including fisheries closures, there is growing interest and discussion among conservation organizations to address regional-scale priorities and interventions focused on underlying regional patterns of diversity and oceanography. Many efforts at prioritizing coral reef closures are based on identifying reefs with low human impacts or perceived to be close to pristine, but this has lead to the placement of many closures within high environmentally stressed oceanographic conditions (Maina *et al.*, 2008; McClanahan *et al.*, 2009a). Efforts to manage these reefs in their original or pristine condition are expected to become increasingly challenging given the rate of climate change.

The metrics for evaluating reefs proposed here are largely independent of the local current human use patterns, such as fishing, but reflect underlying exposure to stress by oceanographic conditions, coral community susceptibility to stress, and taxonomic diversity. In this paper, we apply a multivariate analysis that uses these metrics to identify management priority areas based on the need for national and regional climate change interventions. Consequently, hard coral and reef fish diversity in the WIO are, for the first time, presented at a regional level for ~200 sites where data were collected by a few experienced observers using similar methods. Metrics of environmental conditions and disturbances, multivariate stress exposure and coral community susceptibility were combined with two measures of taxonomic richness (McClanahan *et al.*, 2007c), to evaluate their interrelationships and possible associations. The purpose was to determine if there were coral reefs that had a combination of low exposure to environmental stress and high biodiversity. This methodology provides a basis for evaluating and prioritizing coral reef management plans based on environments known to minimize the conditions for coral bleaching and to maintain high biodiversity.

Materials and methods

Study area

The WIO is a biogeographic subdivision of the Indian Ocean stretching from the coast of East Africa to the banks of the Mascarene Plateau (Fig. 1). The WIO region has a rich diversity of marine and coastal ecosystems dominated by coral reefs that cover approximately 7000 km^2 (Spalding *et al.,* 2001). The coral reef atolls that form the Maldive Islands are situated in the central Indian Ocean between Minicoy Island and Chagos Archipelago and have reef communities similar to the broader region (Sheppard, 1998) and, therefore, included in this study and referred to as WIO. The coastal and marine ecosystems of the WIO provide food and income for an estimated 30 million people as well as other goods and services of strategic importance to national economies (Berg *et al.,* 2002). These ecosystems are, however, increasingly becoming degraded due to human-induced threats, such as heavy and destructive use, habitat loss, pollution, and rapid climate change (Muthiga *et al.,* 2000).

Data sources and analyses

The evaluation presented here uses measures of environmental stress and taxonomic richness, evaluating each of four variables separately and then combining them into a map based on the normalized layers.

Environmental stress

Multivariate stress model. Environmental stress was based on a multivariate stress model (SM1) calibrated for environmental factors that promote coral bleaching (Maina *et al.,* 2008). The stress model was based on oceanographic factors relevant to environmental exposure, including sea surface temperature (SST) rate of rise, SST variability, SST maximum, ocean current and wind speed and direction, chlorophyll concentrations, photosynthetically available radiation, and ultra-violet light. These factors were weighted and combined in a fuzzy logic system to create a weighted map of environmental stress based on the demonstrated relationships between these variables and coral bleaching. Here, we extracted the environmental stress values for each site where field studies were undertaken.

Coral community susceptibility. Bleaching susceptibility of the coral community was a weighted measure or index of the hard coral community's response to bleaching that often reflected the communities resistance to bleaching, which can

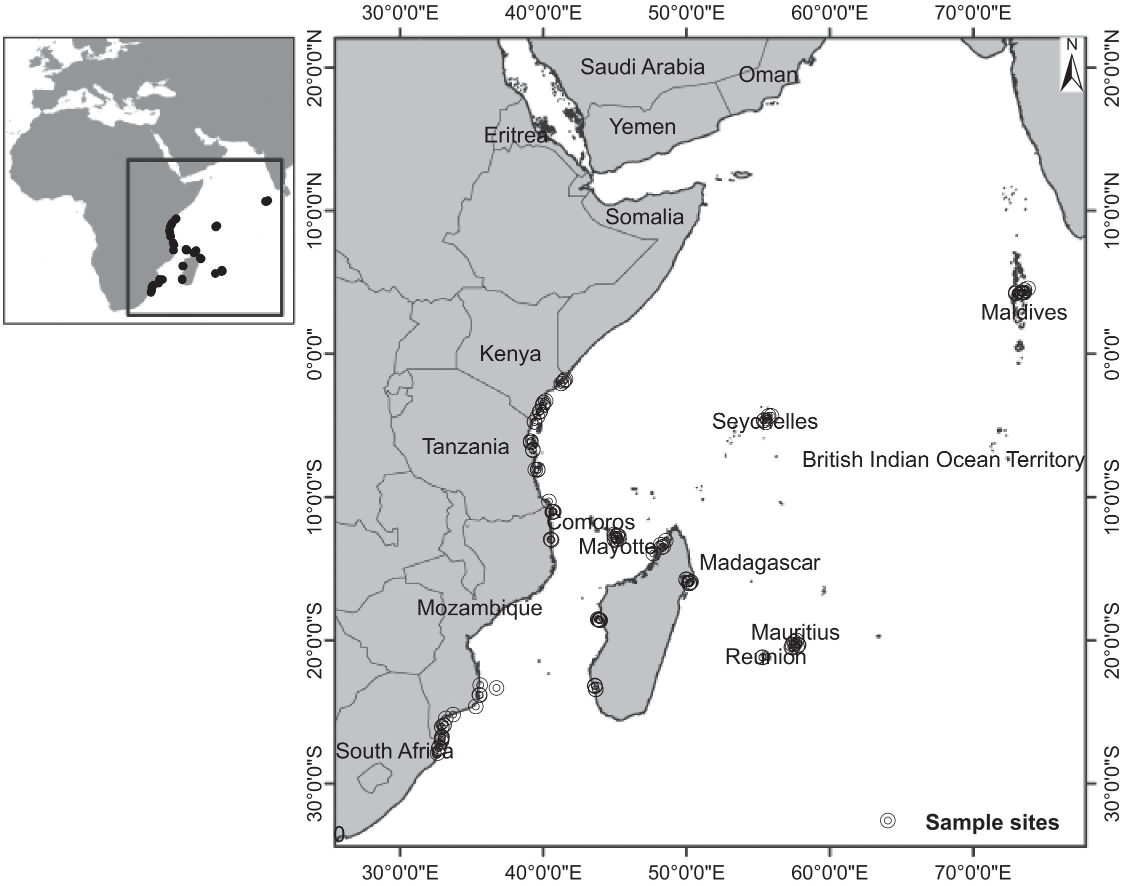

Fig. 1 Map of the study area showing field sampling locations.

be influenced by the history of coral bleaching-induced mortality but also other disturbances and recovery from those disturbances (McClanahan *et al.*, 2007b, c). Coral community susceptibility is calculated as the coral taxon's relative abundance multiplied by its bleaching index and summed for all taxa (McClanahan *et al.*, 2007c). The bleaching index is a scaled response to bleaching for each taxon based on the intensity of bleaching during warm-water anomalies and was derived from a large database of $>45\,000$ observations of corals collected throughout the WIO (McClanahan *et al.*, 2007c). Higher coral community susceptibility indices are typically dominated by bleaching sensitive taxa such as *Acropora* and *Montipora*. Susceptibility can also be influenced by other disturbances and the changes in coral communities that occur after the disturbance. Nevertheless, because most of the studies were undertaken <10 years after the major bleaching disturbance of 1998, the recovery effect on the coral taxa composition is likely to be small relative to the impact. Additionally, the coral community is expected to represent the history of disturbance as reflected in the remnant and emerging coral taxa. For example, coral cover can recover well after a disturbance but the composition of the community still reflects the past disturbance because of the disturbance favors bleaching-resilient taxa (McClanahan, 2008).

Biodiversity metrics

Biodiversity is a broad concept covering different aspects of a community, including evenness, genetic and taxonomic diversity, and species richness (Merck *et al.*, 2009). Here we used the numbers of coral and fish taxa as our metric of biodiversity. Data were based on field studies that included belt-transect surveys of common coral reef fish (McClanahan, 1994) and visual evaluations of coral communities using a previously described search method (McClanahan *et al.*, 2007c). Fish biomass was sampled at 128 and coral communities at 197 sites × time replicates, between 1991 and 2009 (Fig. 1).

Numbers of coral taxa. Coral taxonomic richness was based on the number of coral taxa observed during 40-min search intervals where this bleaching data were collected (McClanahan *et al.*, 2007c). The observer haphazardly swam with closed eyes and, after a haphazard number of fin strokes, opened their eyes and identified all hard corals in a 2 m diameter area directly beneath the observer. Coral identification categories included all standard genera for the region with the exception that the genus *Porites* was separated into three taxa – branching, massive, and *Synarea* (Veron, 2000).

Numbers of fish taxa. Fish taxonomic richness was based on the number of species observed per 500 m^2 among nine sampled coral reef families (Acanthuridae, Balistidae, Chaetodontidae, Diodontidae, Labridae, Monocanthidae, Pomacanthidae, Pomacentridae, and Scaridae) using the species descriptions of Lieske & Meyers (1994). Species richness used average numbers of species per 500 m^2 based on two to three transects per site. Fish taxonomic richness data display a saturation curve relationship where numbers of species is reduced below a biomass of $\sim 500\,kg\,ha^{-1}$ (McClanahan, 2007), which is expected to be an effect of fishing. To eliminate the confounding effect of fishing and focus on the underlying expected biogeographic diversity patterns, sites with fish biomass $<500\,kg\,ha^{-1}$ were eliminated from the final fish diversity GIS layer. Nevertheless, the analyses with these data included are presented for correlation analyses and maps were produced and examined but not presented.

Data analyses and mapping

The data sources were first evaluated by pairwise correlation analyses to determine their degree of interrelatedness. Fish diversity analyses included pairwise comparisons for all sites and for sites with biomass $>500\,kg\,ha^{-1}$. Relationships of these variables with latitude were evaluated by testing a variety of realistic model equations using the dynamic smoothing module in SIGMAPLOT (http://www.sigmaplot.com). The best-fit functions were selected on the basis of the r^2 associated with the linear, quadratic, and sigmoid functions.

Maps of each layer, environmental stress, coral community susceptibility, numbers of coral and fish taxa, were developed from the above data. Analyses of spatial distributions in ecology are often influenced by spatial autocorrelation, such that the higher the similarity the closer the samples, which comes from either the shared forcing of environmental variables (exogenous) or from dispersal, competition, and other ecological factors (endogenous) (Bahn & McGill, 2007). Consequently, spatial autocorrelations were examined for the numbers of fish and coral taxa shape files prior to interpolation of this point data and surface filtering.

At all spatial scales, most ecological phenomena display spatial patchiness or gradients (Legendre, 1993). Given a set of features and associated attributes, Moran's Index evaluates whether the pattern expressed is clustered, dispersed, or random. Moran's Index value near + 1.0 indicates clustering while an index value near −1.0 indicates dispersion (Burrough & McDonnell, 2005). Moran's Indices for coral community susceptibility and the numbers of fish and coral taxa were 0.40, 0.13, and 0.28, respectively, indicating that for these layers, there was less than a 1% likelihood that the clustered patterns resulted from chance. Consequently, point data for coral site susceptibility and numbers of coral and fish taxa were interpolated over the spatial extent of the study area (~4°N–26°S; 33–74°E) using the inverse distance weighting (IDW) method (Burrough & McDonnell, 2005). The IDW method determines a cell's value based on a linearly weighted combination of the sampled points. The weight was a function of the inverse distance and the surface being interpolated and a likely reflection of the change in the variable in space (Watson & Phillip, 1985). Cell size for the output raster maps were set to 0.5 of a degree (55.5 km) and the search radius set to a fixed distance of 1° (111 km). These settings gave more significance to nearer than to distant points.

Interpolated maps were standardized using a left trapezoidal function given by a single sloping line increasing from 0 (high stress or low biodiversity) and peaked at 1 (low stress and high biodiversity). Outputs of the multivariate stress model (SM1described in Maina et al., 2008) extracted for each site were reversed, such that 0 represented high stress and 1 represented low stress, in order to scale in the direction of the positive attributes (high diversity and community susceptibility) of the other variables.

The standardized layers were synthesized in two steps: the coral and fish diversity measures were integrated using the algebraic sum equation [Eqn (1)] to obtain a layer representing biodiversity based on coral and fish taxonomic diversity.

$$\text{Biodiversity layer} = \text{Coral} + \text{Fish} - \text{Fish} \times \text{Coral} \qquad (1)$$

This equation aggregates two data layers and insures that a pixel value in the output layer is higher than in either layer individually while maintaining the map values between 0 and 1 (Islam & Metternicht, 2005). The reversed environmental stress layers and coral community susceptibility were also averaged as above to obtain a layer representing positive environmental conditions or low stress and high susceptibility. Finally, the composite environment–biodiversity layer was computed as the average of these two composite layers. This final layer integrates the four layers, such that high values represent areas of low environmental stress and high numbers of taxa giving equal weight to all layers. A final map, based on the highest site replication, focused on coral–stress relationships by removing the fish diversity layer.

Results

Pairwise comparisons indicated that a number of the variables were statistically significantly correlated but not strongly (Table 1). The multivariate stress model was most strongly and negatively correlated to the coral community susceptibility ($r = -0.51$) and coral community susceptibility was negatively correlated to number of coral taxa ($r = -0.40$). The stress model was positively correlated to numbers of fish species for sites having a fish biomass $>500\,kg\,ha^{-1}$ ($r = 0.36$), for all sites irrespective of biomass ($r = 0.25$), and also with the number of coral taxa ($r = 0.35$). Numbers of fish and coral taxa were positively correlated for sites where fish biomass was $>500\,kg\,ha^{-1}$ ($r = 0.47$) and all sites ($r = 0.40$).

Scatter-plots of the four variables with latitude indicate a high density of field data along this geographic gradient and statistically significant relationships with latitude (Fig. 2). Both the multivariate stress and coral community susceptibility indices had moderately strong relationships with latitude (both $r^2 = 0.56$), with the stress index decreasing and the coral community susceptibility increasing towards southern latitudes. Estimates of stress and the coral susceptibility were

Table 1 Pairwise correlation of the site attributes

Variable	Pairwise comparisons × variable	Correlation r	Sample size, n	Significance, $P<$
Number of coral taxa	Coral community susceptibility	−0.40	197	0.001
Multivariate stress model	Coral community susceptibility	−0.51	182	0.001
Multivariate stress model	Number of coral taxa	0.35	182	0.001
Multivariate stress model	Number of fish taxa (when biomass $>500\,\mathrm{kg\,ha^{-1}}$)	0.36	104	0.001
Number of fish taxa (when biomass $>500\,\mathrm{kg\,ha^{-1}}$)	Coral community susceptibility	−0.08	59	ns
Number of fish taxa (when biomass $>500\,\mathrm{kg\,ha^{-1}}$)	Number of coral taxa	0.47	59	0.001
Multivariate stress model	Numbers of fish taxa for all sites and times	0.25	176	0.007
Number of fish taxa for all sites and times	Number of coral taxa	0.40	93	0.001
Number of fish taxa	Coral community susceptibility	−0.14	93	ns

Numbers of fish species is tested for all sites and for only the sites with biomass $>500\,\mathrm{kg\,ha^{-1}}$.

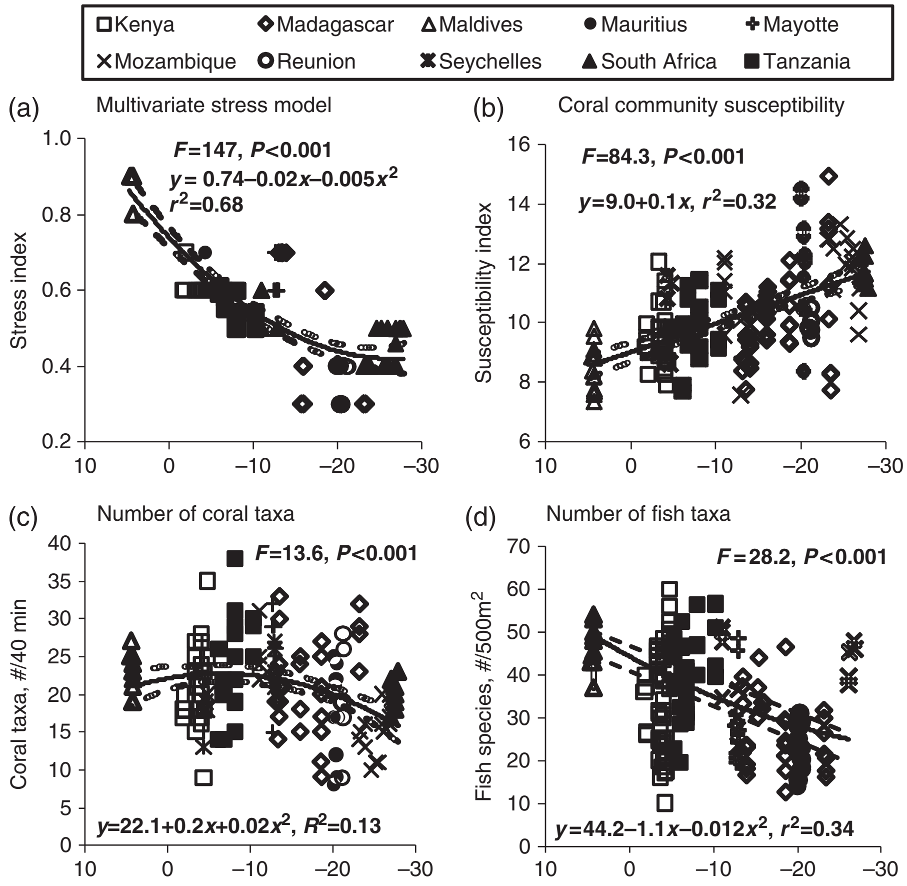

Fig. 2 Scatter plots of studied variables with latitude for (a) the multivariate stress model predictions for field sites, (b) the coral communities susceptibility to bleaching, and numbers of (c) hard corals and (d) coral reef fishes. Best-fit models were based on negative values being used for southern latitudes. Dotted lines represent 95% confidence level.

more spatially heterogeneous between 10 and 30°S. The stress model values were lowest and leveled at about 15°S. Numbers of coral taxa were richest at intermediate latitudes between 5 and 10°S but showed considerable scatter and the weakest fit with latitude ($r^2 = 0.36$). Number of fish species had moderately strong relationships with latitude ($r^2 = 0.58$), with richer sites in the north.

Interpolated maps for the four variables and various composites showed both dispersed and areas of concentration in the region (Figs 3 and 4). The reversed multivariate stress model indicates that stress is lowest (i.e. >0.6) in the south of Mozambique and Madagascar and extends north up the eastern coast of Madagascar into the southern Seychelles, moderate (<0.6 and >0.4) for most of the east African coast, and highest (<0.4) in the north over the Maldives (Fig. 3a). The African coastline from southern Kenya had interspersions of moderately stressful areas. Coral community susceptibility generally increased towards the south with a few spots of high susceptibility on the Tanzanian–Mozambique border, northeast Madagascar, and the Seychelles (Fig. 3b). Taxonomic richness was patchier with high numbers of coral taxa concentrated from southern Kenya down to northern Mozambique, across to the Comoros and northwestern Madagascar, and a separate high concentration in the Maldives. Numbers of fish species also exhibited a series of high values in the Maldives, southern Kenya to northern Mozambique, and the Mozambique–South African border.

A composite map of the multivariate stress and community susceptibility variables identified the southern WIO region as low stress with some moderate stress regions along the Tanzanian–Mozambique border and a few very high stress areas in northern Kenya, northern Seychelles, northwestern Madagascar, and the Maldives (Fig. 3e). The map combining numbers of coral and fish taxa identified high numbers of reef taxa from southern Kenya to northern Mozambique and across to northwest Madagascar, a site on the Mozambique–South African border, and the Maldives (Fig. 3f). A composite of the four variables produced a tongue-shaped concentration of low stress/high diversity from southern Kenya to northern Mozambique and across to northern Madagascar and the western Mauritius, with the Comoros not sampled (Fig. 4a). There was also a low-stress/high-diversity area near the Mozambique–South African border. The composite map with the numbers of fish taxa excluded had the highest site replication, produced the broadest view of the region, and indicates the importance of the Tanzania–Mozambique border east to the Mascarene Islands as a low-stress/high-diversity area for corals (Fig. 4b).

Discussion

The investigation explored the potential for high-biodiversity areas to be associated with low environmental exposure to climate change in the WIO. Whereas high-biodiversity areas with high local human threats are considered a priority for conservation planning and reducing threats (Myers *et al.*, 2000), climate change impacts are not locally manageable. Therefore, prioritization is focused on identifying areas with low exposure to climate threats and managing to reduce local human impacts (West & Salm, 2003). Managing and reducing local threats is expected to reduce the cumulative disturbances and insure their full potential as climate refugia (Glynn, 2000; Riegl & Piller, 2003). The study here indicates some potential refugia within the WIO but also weak and often conflicting associations between measures of environmental stress and diversity. This makes it difficult to clearly identify locations that have all the attributes of high numbers of taxa for different threatened species assemblages and low environmental stress, which is a common problem for coral reef taxa (Hughes *et al.*, 2002; Beger *et al.*, 2007). For example, the stress index and the numbers of coral and fish taxa were weakly positively correlated and, consequently, it is the outliers to this positive relationship that will have the desired attributes of low stress and high diversity.

The multivariate stress model and the coral community susceptibility metrics were moderately correlated and both measures suggest broad-scale patterns of bleaching stress and mortality with the lowest environmental stress and highest community susceptibility values in the southern part of the WIO. In contrast, diversity measures suggest more fish diversity in the north and coral diversity at intermediate southern latitudes. The impacts of climate change on corals will have indirect negative effects on coral reef fish, particularly coral-dependent and small-bodied species (Graham *et al.*, 2008). Consequently, because of their susceptibility, these two groups are appropriate taxa for prioritizing climate change disturbances. Regardless, these taxonomic groups were weakly correlated in space and different biogeographic processes probably influenced the distributions of species richness.

The study identifies the region from southern Kenya to northern Mozambique across to Madagascar and the Mascarene Islands as a regional priority area for conservation based on the overlap in environmental stress and biodiversity measures. This is particularly true if climate change disturbances and local impacts, such as fishing and pollution, have the greatest impact on corals (West & Salm, 2003). Environmental stress ranges from low to moderate but there is evidence for resistance and recovery from climate disturbances in the areas with moderate stress (McClanahan *et al.*, 2007a, 2009c). There are also more limited priority areas in the southern region of Mozambique and more sampling is needed to determine the extent of this potential priority area. Many of these southern sites, including reefs in the Mascarene Islands and southern Madagascar have

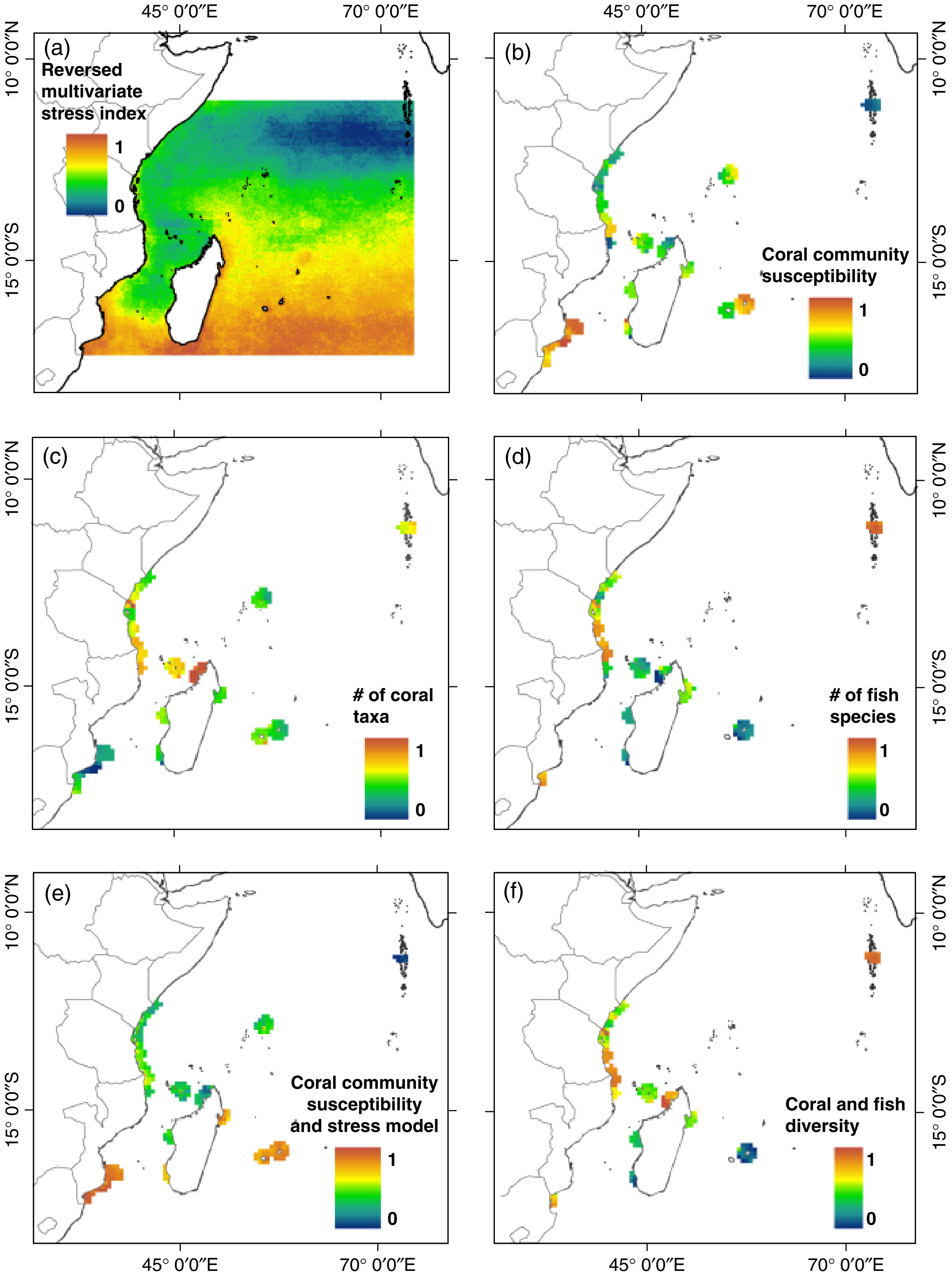

Fig. 3 Map of interpolated and standardized surfaces scaled from 0 (low) to 1 (high) for (a) reversed multivariate stress model (SM1, adopted from Maina *et al.*, 2008) where 0 is the highest and 1 the lowest stress, (b) the coral community susceptibility to bleaching and taxonomic richness of (c) hard corals, and (d) coral reef fishes. Composite maps include the (e) multivariate stress and coral community susceptibility and (f) coral reef fishes and hard corals taxonomic richness combined.

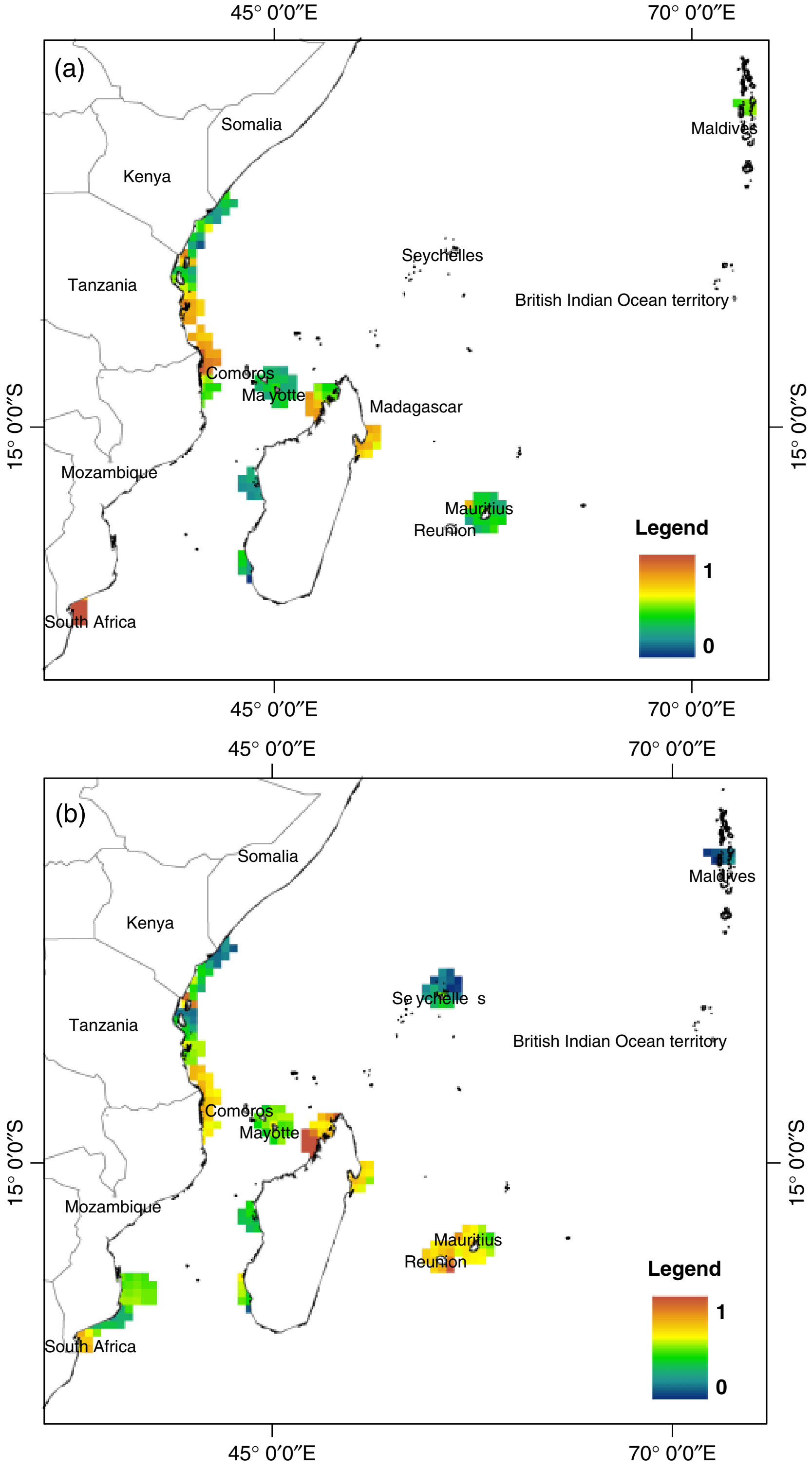

Fig. 4 Composite map based on (a) all four variables of environmental stress model, coral community susceptibility and numbers of coral and fish taxa and (b) based on the three variables of environmental stress, coral community susceptibility and numbers of hard coral taxa.

experienced considerable human and environmental disturbances, which is probably one of the main reasons for the low number of fishes found in field surveys (McClanahan *et al.*, 2005, 2009b). In fact, the reefs in southern Madagascar are in poor ecological condition and whether the cause is heavy fishing, environmental disturbances, or their interaction is not well understood (McClanahan *et al.*, 2009b). In contrast, northern South Africa and southern Mozambique appear to have fewer human impacts and to be in better ecological condition despite some mostly low and nonlethal bleaching events (Schleyer *et al.*, 2008; Ruiz Sebastian *et al.*, 2009).

It should be appreciated that because our methods did not evaluate reefs based on fish biomass and other measures of human use, the priority selection may frequently differ from more traditional prioritization methods where undisturbed ecosystems are given higher priority for protected areas status (McClanahan *et al.*, 2009a). This is most clear when examining islands, such as Mauritius and Reunion, which have low fish biomass and heavy human use (McClanahan *et al.*, 2009a; unpublished results). Nevertheless, based on our criteria, rapid climate change is predicted to have the least effects on these coral reefs and their ecology can be maintained if local human disturbances can be reduced. Further investigation is needed to determine if climate change will alter the oceanography and environmental exposure presented here, which is based on historical data and not the predicted conditions in the future.

Predicting species distribution patterns over large-scales are often constrained by incomplete sampling and can lead to problems associated with coarse resolution. The variety of statistical techniques used for habitat distribution modeling is growing along with the need to analyze these spatial data. Most of these techniques are niche-based models and include ordinary multiple regression and its generalized form (GLM), neural networks, ordination and classification methods, Bayesian models, locally weighted approaches, environmental envelopes or even combinations of these models (Guisan & Zimmermann, 2000). Spatial autocorrelation influences coefficients and inferences from statistical results and the suitability of these models are only as good as the predictor variable data (Betts *et al.*, 2009).

Despite the extensive and uniform field sampling, there are some insufficiently sampled areas including a number of the southern Seychelles islands and much of the central coastline of Mozambique and portions of the Tanzanian, Madagascar, and Mozambique Channel areas. Given the absence of these data, we used and presented conservative interpolation methods and maps that did not extrapolate over long distances. The underpinning concept of most interpolation techniques is spatial autocorrelation and pure interpolation techniques often outperform niche-based models (Bahn & McGill, 2007). Where explanatory variables are present, a hybrid of geo-statistics and niche-based models is recommended (Hengl *et al.*, 2009). Given the modest to strong patterns seen in the data with geography, it is likely that our methods were reasonable at predicting spatial patterns. Nonetheless, there is a constant need to update data, maps, and priority areas as field data accumulates and spatial dispersion and environmental stress/diversity relationships become well understood.

The region is exposed to numerous local human use and threats, particularly widespread fishing but also agricultural and, to a lesser extent, urban runoff. The most common recommendation to reduce climate change impacts is to reduce additional human disturbances through restrictions on fishing and improved watershed and waste management (Hughes *et al.*, 2007; Cinner *et al.*, 2009). Marine resource management has increasingly depended on marine protected areas but few of these were selected based on a their potential as climate refugia, despite it's emerging threat (Hoegh-Guldberg *et al.*, 2007; Wells *et al.*, 2007). Coastal people in the WIO have a high dependency on marine natural resources, a high poverty level, and low institutional capacity to address adverse changes in the environment (Muthiga *et al.*, 2000). These social-ecological conditions create challenges to applying strict protection to these resources and may often require a more graded approach to restrictions (McClanahan *et al.*, 2008). This study provides a basis for understanding the biophysical-climate impact-based priorities and can be used to match appropriate management, based on the costs, social adaptive capacity, and willingness to adopt restrictions. These factors and the willingness of national and international bodies to collaborate and support the appropriate restrictions, alleviate detrimental social consequences, and increase social adaptations to the consequences of these restrictions can help build a sustainable strategy for climate change in the region. Countries planning to meet their commitments under various regional and international conventions will also find the results useful for identifying future focus areas.

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Supporting Information

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

Appendix S1. Summary of the countries and study sites where fish and coral field surveys were undertaken.