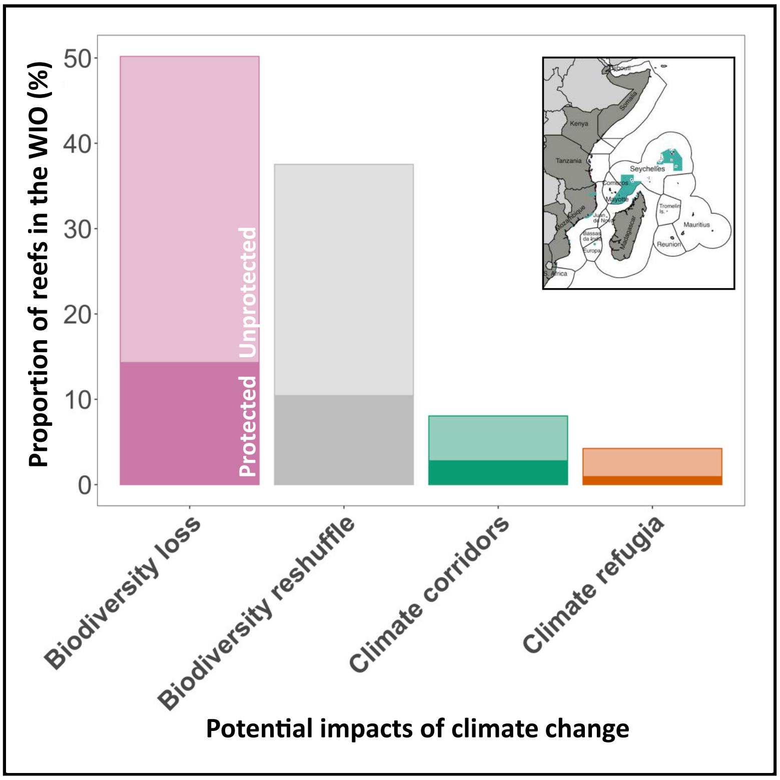
One Earth

Article

Climate change reduces the conservation benefits of tropical coastal ecosystems

Graphical abstract



Highlights

- Climate change threatens 50% of coral reefs in the Western Indian Ocean
- 40% of coral reefs in the WIO might undergo significant biodiversity reshuffling
- About half of the MPAs in the WIO are located in climate risk areas
- Climate refugia are rare, and only a quarter are protected

Authors

Stephanie D'Agata, Joseph M. Maina

Correspondence

stephanie.dagata@gmail.com

In brief

The ocean is vital to human well-being, but climate change is rapidly modifying the marine environment. About half of the 82 marine protected areas in the exclusive economic zones of 12 Western Indian Ocean countries are located in areas that are at risk of biodiversity loss due to climate change. There are only 7% of coral reefs in climate refugia, and only a quarter of them are protected. Conservation plans should anticipate climate risks to maintain biodiversity and socioeconomic benefits.

D'Agata & Maina, 2022, One Earth *5*, 1228–1238
November 18, 2022
https://doi.org/10.1016/j.oneear.2022.10.012

CellPress

CellPress

One Earth

Article

Climate change reduces the conservation benefits of tropical coastal ecosystems

Stephanie D'Agata[1,2,3,4,*] **and Joseph M. Maina**[1]
[1]School of Natural Sciences, Macquarie University, Sydney, NSW, Australia
[2]Marine Programs, Wildlife Conservation Society, Bronx, NY, USA
[3]ENTROPIE (IRD, University of La Reunion, CNRS, University of New Caledonia, Ifremer), La Reunion c/o IUEM, Saint-Denis, Plouzané, France
[4]Lead contact
*Correspondence: stephanie.dagata@gmail.com
https://doi.org/10.1016/j.oneear.2022.10.012

SCIENCE FOR SOCIETY Marine protected areas (MPAs) are a common area-based management tool for coastal ecosystems. They are designed to protect marine and coastal habitats from the effects of human exploitation and support the conservation of biodiversity and preserve services and resources, including food provision. However, whereas MPAs are static with defined boundaries, the species and ecosystems they seek to protect can shift their locations in response to the effects of climate change. Consequently, the conditions and biodiversity within MPAs and the services MPAs seek to preserve can deteriorate over time. The extent to which MPAs are fit for purpose in a warming world remains unclear, and greater understanding is required to guide adaptation efforts. An analysis of the effectiveness of MPAs in the Western Indian Ocean casts doubt on the capacity of MPAs to promote biodiversity persistence and resilience to climate change, with important consequences for society. There is a clear need for innovative climate-smart management strategies, flexible both in time and space, that consider the variability of climate change impacts to safeguard biodiversity regionally.

SUMMARY

Marine protected areas (MPAs) are among the most effective management responses to human environmental impacts. However, their capacity to sustain biodiversity and associated ecosystem services under climate change is uncertain. Understanding how climate shifts impact ecosystem functioning and socioeconomic well-being is vital for biodiversity conservation and adaptation planning. Here, we show that climate change could render the current MPAs network in 12 nations in the Western Indian Ocean ineffective in supporting conservation and socioeconomic outcomes. Approximately half of the coral reefs and MPAs in countries most at risk of food insecurity will likely experience significant biodiversity losses. Only 4% of reefs and 6% of MPAs were located within areas less likely to experience climate shifts. Biodiversity hotspots for coral and reef fish were generally over-represented in the most at-risk areas. Conservation actions planned to anticipate climate risks can help to maintain biodiversity and socioeconomic benefits.

INTRODUCTION

Climate change is rapidly modifying the marine environment, severely impacting economies and ecosystems.[9–11] Consequences at the local scale include the collapse of populations and modified species distributions, leading to changes in community interactions and ecosystem functioning.[9,12–15] Without transformative adaptation in the face of significant climate shifts,[16] how much climate change alters temperature or precipitation, the impacts of these changes on high resource-dependent economies and socio-ecologically sensitive communities will be substantial.[17] While there are estimates of climatic niche trajectories and their consequences for species distributions under climate change,[1] spatially explicit implications for biodiversity conservation and ecosystem health have yet to be assessed. Understanding how projected climate shifts will impact ecosystem functioning and socioeconomic well-being is essential for planning for biodiversity conservation and social adaptation strategies.

Marine Protected Areas (MPAs) are a common area-based management tool for coastal and marine ecosystems,[18] with

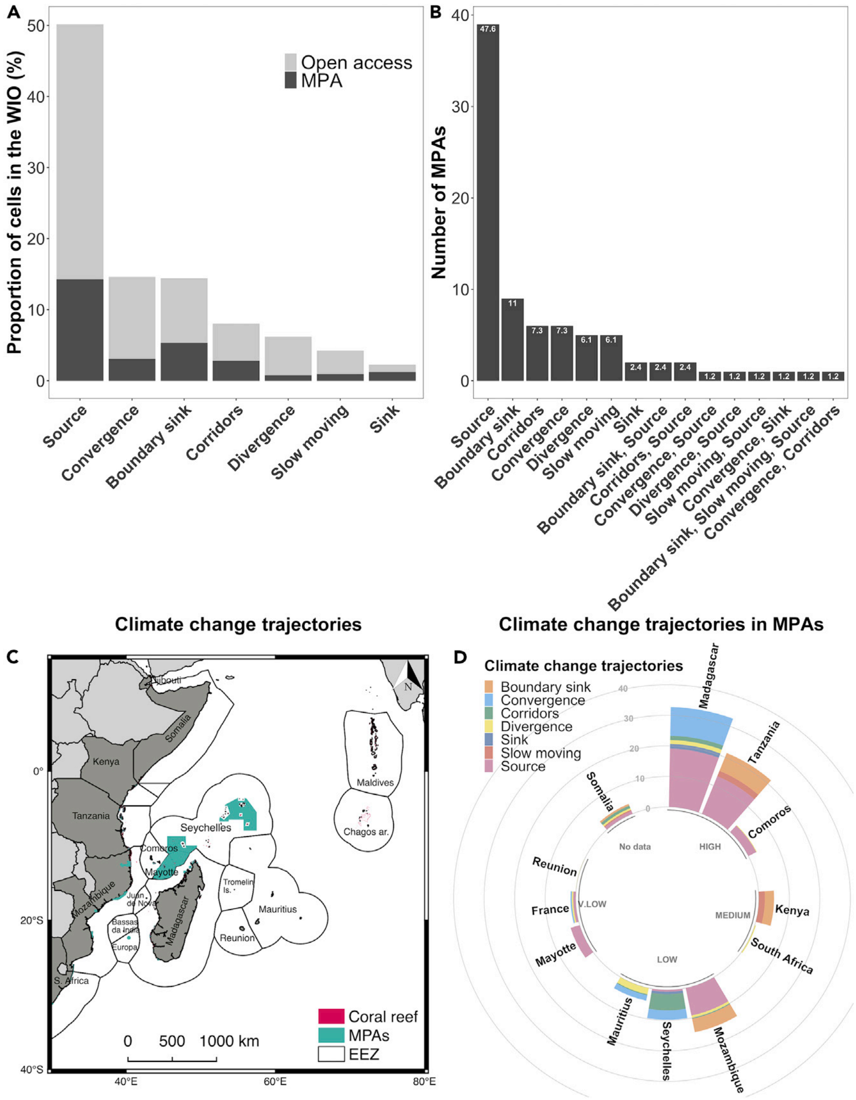


Figure 1. The spatial intersection of climate change trajectories, MPAs, and level of food security levels by country in the WIO

(A and B) Proportion of reefs in each climate change trajectory (protected – dark gray; unprotected – light gray) (A). Number of MPAs with reefs in one or more climate trajectories (B). The proportion of MPAs is indicated for one or more climate change trajectories.

(C) Reef and MPAs location in the WIO.

(D) Reef distribution (%) among WIO nations and their intersection with climate change trajectory (Figure S2). Countries are classified and ordered according to their level of true subsistence (TS)[2] (see experimental procedures): high >80% to very low <10%. The TS level in Somalia is unknown (NA) due to high uncertainties in catch data.[2] Remote inhabited French territory atolls (Juan de Nova Island, Europa Island, Glorioso Islands, Tromelin Island) were combined under “France”; Reunion Island was considered a separate French territory (Table S5). Tanzania and Zanzibar were combined under “Tanzania.”.

overall positive social outcomes.[19] However, MPAs are static in both space and time, while the expected climate change shifts in species distributions[10,20,21] mean present-day biodiversity hotspots may shift. Given ongoing species reorganization under a changing climate,[1,21] many present-day conservation areas may become suboptimal in the future.[22] Unless climate-smart adaptive management approaches are adopted, taking into account climate refugia,[23] future biodiversity hotspots, and exposure to climate change,[24] the biodiversity outcomes of MPAs will be seriously compromised, along with their capacity to support the needs of human communities.[25,26] This is particularly true in low- to middle-income countries where communities are highly dependent on natural resources for their livelihood.[27]

Understanding the future capacity of MPAs to support biodiversity persistence and the associated socioeconomic benefits is therefore vital.[28] However, while MPAs must be adapted based on climate change responses, there is still uncertainty surrounding their management and scheduling.[29] It is imperative to address the knowledge gap surrounding climate change in order to improve anticipatory and dynamic spatial prioritization of conservation areas that maximize long-term conservation goals. The future role of MPAs and their potential to provide benefits can be tested based on projections of potential species shifts[26] and the distribution of biodiversity hotspots.

We focused our study in the Western Indian Ocean (WIO) region (Figure 1C). The WIO comprises small islands and continental states along the WIO boundary. Approximately 30 to 60 million people live on the WIO coasts, with highly resource-dependent coastal communities.[30] Subsistence and artisanal fisheries support livelihoods and are key nutrient and protein sources for more than 85% of fishers.[27,31,32] The WIO is experiencing the fastest changes globally due to climate change.[33] To estimate climate change impacts, we used previously published estimates of marine climate velocity, which represent species climate change trajectory trends. Climate velocity is a vector that describes the speed and direction of isothermal shift through space under climate change.[10,1,20] From an ecological perspective, climate velocity is the speed and direction a species needs to move to maintain its current climate conditions.[10] Climate velocity provides a simple and generic metric of exposure to warming that predicts species' range shifts.[20]

Nine climate change trajectories are expected to occur globally.[1] These are (1) climate sources characterized by novel thermal conditions with mostly trajectories starting (>80%) and no new climate migrants, leading to the overall loss of biodiversity; (2) climate convergence, where more trajectories are terminating than starting; (3) climate divergence, where more trajectories are starting than terminating, both climate convergence and divergence areas have the potential for species reshuffling and new ecological interactions; (4) climate corridors or pathways through which a high percentage of trajectories pass; (5) climate slow-moving areas, and (6) climate non-moving areas, characterized by slow/very slow trajectories and acting as potential climate refugia; (7) climate boundary sinks, where coasts block trajectories; (8) climate sinks, where more trajectories are terminating than starting; and (9) internal sinks.[1] Projected climate sinks have the potential for biodiversity loss unless species adapt to new ecological conditions.[10] Climate sources are characterized by novel warmer conditions and are disconnected from warmer locales where similar conditions previously existed[20]; consequently, there are no communities of organisms from warmer regions to replace those moving out, leading to loss of species richness.[10] Out of the nine climate trajectories documented worldwide, seven are expected to occur in the WIO (source, convergence, divergence, sinks, boundary sinks, corridors, and slow-moving) (Figure S2). With 143 MPAs in the region, most of which are nearshore, approximately 7% of the ocean is protected.[34] Given the high dependence of WIO coastal communities on the marine environment and the rapid adverse changes occurring in the region, we explored potential changes in ecosystem functioning and efficiency of MPAs in supporting multispecies fisheries now and into the future.

We achieve this by retrospective evaluation of overlaps of climate risks, multifaceted biodiversity hotspots for fish and corals—where multifaceted biodiversity comprises multiple functional components linked to ecosystem processes and ecosystem services[35]—and the current spatial arrangement of a regional MPA network. Using climate forecasts and species distribution data for coral and fish, we evaluate the potential for the existing MPA network to protect both present and future multifaceted biodiversity in coral reef ecosystems. We used global distribution range maps of scleractinian coral and fish species to derive three complementary facets of biodiversity: species richness, functional richness,[35] and phylogenetic diversity.[36] Combined, these indicators represent a quasi-complete multifaceted structure and composition dynamics of stony coral and fish ecological communities,[35,37–39] Specifically, we first investigated conservation gaps for coral reefs now and in the future. We tested the hypothesis that biodiversity hotspots are (1) currently protected and (2) located in expected climate refugia. We focused on coral reefs because many human societies in tropical regions worldwide depend heavily on the critical ecosystem goods and services they provide. As coral reef ecosystems degrade, human populations in these regions are at much greater risk.[40] To test the hypothesis, we spatially intersected the present distribution of coral and fish species with management restrictions and the predicted species' climate change categories. Second, we simulated the expected loss of structural complexity, one of the most important characteristics of coral reefs,[41] in places likely to experience significant climate changes. Complex habitats are associated with higher coral reef ecosystem functioning, as well as services such as fisheries[42] and coastal protection through wave energy dissipation.[43] In addition, the loss of architectural complexity may reduce diversity and compromise the productivity of fisheries[42] by, *inter alia*, raising post-settlement mortality among juvenile fish.[44] A decline in architectural complexity will likely have significant ecological and socioeconomic repercussions,[45] especially for fishing-dependent communities. Based on current knowledge of coral species thermal sensitivity,[46] we hypothesized that as climate change occurs, highly climate-sensitive taxa within predicted source areas with novel climate conditions (e.g., *Acropora*) and the least competitive taxa (e.g., *Porites*) within indicated convergent areas will be the first casualties.

Our analysis reveals that approximately half of reefs and MPAs were located in areas most susceptible to climate-mediated biodiversity loss. In addition, hotspots of biodiversity components directly associated with ecosystem processes were found in MPAs that may experience significant biodiversity loss due to climate change. Interestingly, we found that 40% of reefs were in areas that might experience biodiversity reshuffling, with high probability of reef complexity maintenance despite climate change. Those areas might highly benefit from resilience-based management approaches to maximize socio-ecological benefits for dependent populations. Although limited by the moderate spatial resolution of available data, our results highlight the utility of innovative and anticipatory regional-scale climate-smart portfolio management strategies, coupled with adaptive and flexible MPAs. We argue that such an approach is urgently required to address climate change and ensure the sustainability of multispecies fisheries contributions to food and nutrition security.

RESULTS

Marine protected areas and climate change trajectory

Using global coral reef distribution data,[47] we extracted 4,490 ~4 × 4-km grids representing coral reef locations across 12 countries of the UNEP–Nairobi Convention regional sea in WIO (Figure 1C). Overall, 28% of grids (hereafter reefs) were located within 82 MPAs. By 2100, approximately 50% of reefs in the WIO will be under the predicted source trajectory (Figure 1A). The majority of these were found in the Comoros, Madagascar, and Tanzania, where food security is highly dependent on multispecies fisheries (Figure 1D).[2] Furthermore, ~15% of WIO reefs in Madagascar and Seychelles may undergo convergence (Figure 3A and Table 1). Another 15% may experience boundary sinks, mainly in Tanzania, Kenya, and Mozambique (Figure 1D). A smaller percentage (4.2%) of reefs may undergo a slow-moving trajectory, predicted to occur off the Kenyan and Tanzanian coasts (Figure 1D). Overall, 2.2% of coral reefs were in predicted climatic sinks (Figure 1A), and approximately 40% will experience species reshuffle (convergent, divergent, and sink trajectories) (Table 1). Importantly, we found that most MPAs intersected with a single projected climate change trajectory (Figure 1B), and approximately half the protected areas (39 of 82) were located only in predicted climate source areas (Figure 1B). The other six climate change trajectories intersected spatially with 2–9 MPAs (Figure 1B).

Coral and fish biodiversity hotspots in the WIO

The distribution of coral and reef fish biodiversity facets is summarized in Figure S1. The location of biodiversity hotspots for coral and reef fish is presented in Figures S3 and S4. Biodiversity hotspots are defined as areas within the top 10% on each of the three biodiversity metric scores.[48] When considering only the UNEP–Nairobi Convention regional sea countries (n = 12), coral

Table 1. The proportion of reefs in each climate category and management

Climate change trajectories	Fished	MPA	Total
Source	35.9	14.3	50.2
Convergence	11.6	3.1	14.6
Boundary sink	9.1	5.3	14.4
Corridors	5.3	2.8	8.1
Divergence	5.4	0.8	6.2
Slow-moving	3.3	0.9	4.2
Sink	1.0	1.2	2.2
Total	71.5	28.4	100.0

biodiversity hotspots were poorly represented within the current arrangement of protected areas[49] except phylogenetic diversity hotspots. Overall, there was little spatial overlap between coral and fish biodiversity facets in the WIO (Lee index ranged from −0.3 to −0.4, Table S1). The multifaceted coral biodiversity hotspots were in Mayotte in the Mozambique channel (Figure S3).

Coral species richness and phylogenetic diversity had the strongest spatial congruence (Lee = 0.9). Hotspots for the two biodiversity metrics were in northwestern Madagascar and Mayotte–Comoros islands (Figures S3B and S3D, and Table S2). Hotspots of coral functional richness were situated on the northern coast of Mozambique and in the Mayotte–Comoros islands (Figure S3C and Table S2). The fish's multifaceted biodiversity hotspots were located on the Tanzanian coast (Figure S4A). Fish species richness and phylogenetic diversity had the highest spatial congruence (Lee = 0.9), with hotspots on the Tanzanian and Kenyan coasts. Fish functional richness hotspots were located on the southern Tanzanian and Mozambican coasts and the north of Madagascar (Figure S4C and Table S2). Based on estimates of travel time to the nearest market, we evaluated the accessibility of biodiversity hotspots (and, therefore, their exposure to human pressure[50]). Overall, coral and fish biodiversity hotspots were distributed homogeneously along the gradient of travel time to market at an average of between 3 and 5 hours (Figure S5). Hotspots for coral species and phylogenetic richness were located approximately 5 hours from the nearest market, while functional richness hotspots were located at 3 hours (Figure S5C). Hotspots for fish functional richness and phylogenetic diversity were located farther from the closest market (~5 hours) than hotspots for fish species richness (~2 hours) (Figure S5D).

Protecting multifaceted biodiversity hotspots

To evaluate qualitative gaps in coral reef conservation in the WIO, we tested for a spatial intersection between climate change trajectories, MPAs, and the coral and fish multifaceted biodiversity hotspots. We spatially intersected the occurrence of 367 scleractinian coral and 557 reef fish species with MPAs' location and climate change trajectories (Figure S2). We then evaluated the proportion of protected reefs in biodiversity hotspots and in each of the seven climate change trajectories. We assumed that in a balanced conservation portfolio design,[51] protected reefs would have equal representation within each of seven climate change trajectories (i.e., 4% reefs in each climate trajectory [see experimental procedures]). We then used 4% protected reefs as a baseline for estimating the level of representation of protected reefs within each climate change category. We found a strong spatial correlation between species richness and phylogenetic diversity for coral and fish species, whereas functional richness was relatively weakly correlated with species richness and phylogenetic diversity (Table S1). Overall, coral biodiversity was highly represented on protected reefs for each facet separately and the three facets combined in convergence areas (Figures S3A and S3D). Conversely, fish functional and phylogenetic diversity hotspots were less protected than fish species richness (Figure S4B).

Coral biodiversity hotspots (top 10% of each of the three biodiversity metric values[48]) were highly represented in protected reefs within projected convergent areas compared with less diverse reefs (from 20% for functional richness to 28% for species richness) (Figures 2A–2D). The least diverse protected reefs intersected mainly within the predicted source trajectory (Figures 2A–2D). Moreover, coral biodiversity hotspots in predicted slow-moving regions were rare (Figures 2A–2D). Protection arrangements for fish biodiversity were variable depending on the biodiversity metrics. Fish species richness hotspots were highly represented within predicted slow-moving areas (28% reefs), while fish functional richness hotspots were highly represented within predicted divergence areas (28% reefs) (Figures 2A and 2B). Fish phylogenetic diversity hotspots were highly represented within the predicted source trajectory (28% reefs) (Figure 2C). The least diverse protected reefs for fish biodiversity were over-represented within the predicted source and boundary sink areas compared with the predicted slow-moving areas (Figures 2E–2H). There were no combined multifaceted fish biodiversity hotspots (top 10%) (Figure 2H).

Loss of mean assemblage coral complexity

We tested for potential impacts of climate change on coral reefs by simulating changes in functional richness and reef complexity based on predicted climate trajectories (Figure 3A). We used the coral convexity metric as a proxy for coral complexity (Figure 3B).[52] Coral convexity is a continuous morphological trait that captures volume compactness and space within a colony and increases from most complex branching (0) to least complex massive colony shapes (1).[52] As already stated and based on current knowledge of coral species thermal sensitivity,[46] highly climate-sensitive taxa within predicted source areas with novel climate conditions (e.g., *Acropora*) and the least competitive taxa (e.g., *Porites*) within indicated convergent areas will decline first.

Consequently, simulating the source trajectory involved removing coral species that are most sensitive to climate change. Simulating the convergence trajectory involved sequential removal of the least competitive species (see experimental procedures). The loss of coral species from both source and convergence areas induced a faster loss of functional richness than would be expected by chance, particularly after 25% of species were removed from the species pool (Figure 3A). However, the impact of species loss on the assemblage average coral convexity diverged between the two scenarios. In future source areas, the average coral convexity of coral assemblage increased faster than would be expected by chance while

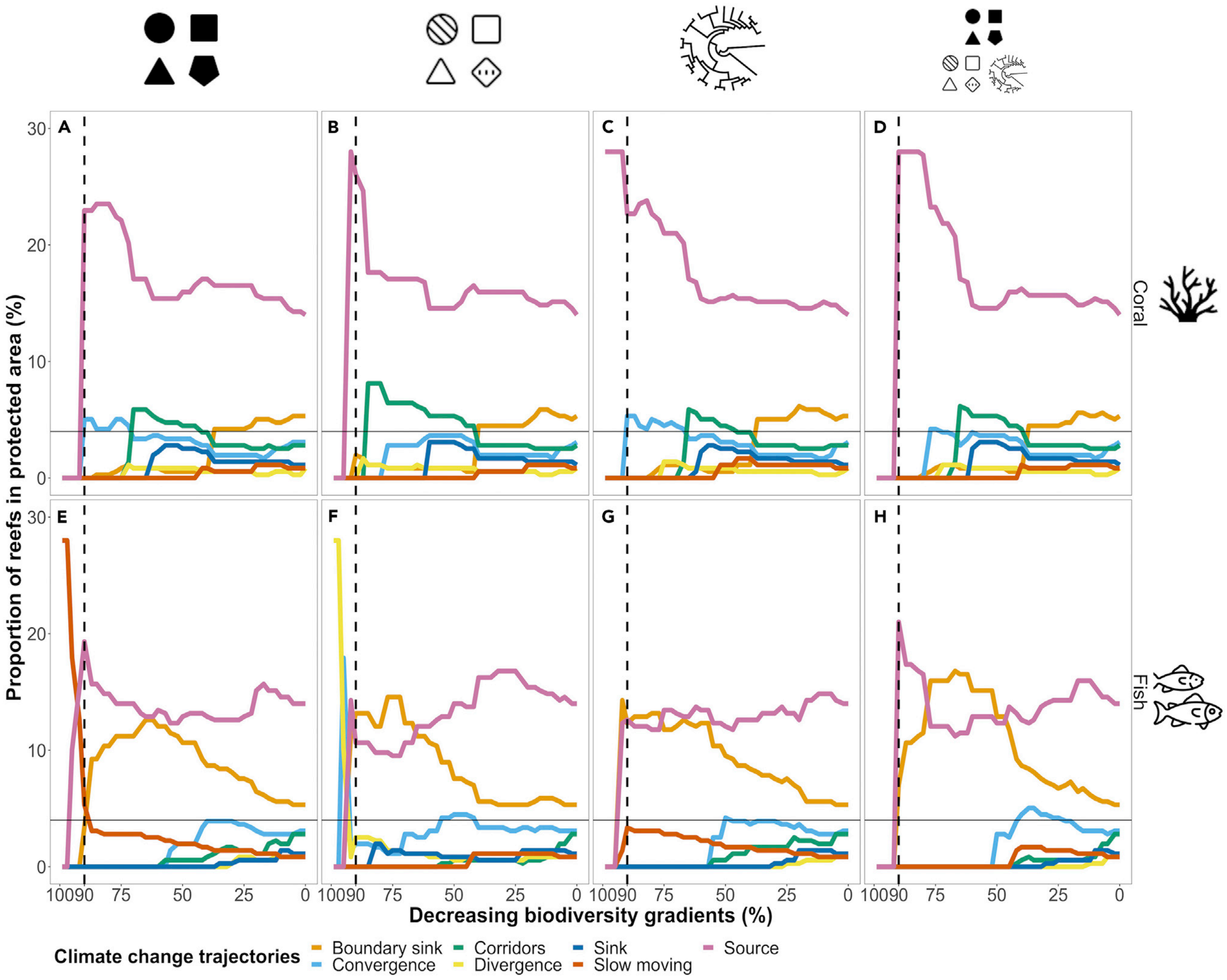


Figure 2. Proportion of protected reefs within each of the seven climate trajectory zones along the coral and the fish biodiversity gradients and for each biodiversity component

Proportion of protected reefs for total species richness (S) (A and E), functional richness (FRic) (B and F), phylogenetic diversity (PD) (C and G), and all three components of multifaceted biodiversity together (D and H) for corals (top: A–D) and reef fish (bottom: D–G) for the seven climate change categories estimated for each percentile. For each biodiversity component and taxa, we ranked the 4,490 reefs from most (left side of the x axis) to least diverse (right side of x axis) and estimated the cumulative proportion of protected reefs for each percentile. The dashed vertical line indicates the 90th percentile. The black horizontal line indicates that the balanced percentage of reefs in MPAs in each category is 4% (see experimental procedures). If MPAs were equally located in each of the seven climate change categories, proportions of protected reefs located over and under the 4% reference value (see experimental procedures) would reveal the over/under-representation of reefs located in MPA for a particular climate change trajectory.

remaining lower than expected by chance in climate convergence areas (Figure 3B).

DISCUSSION

In this study, we explored changes in ecosystem functioning and the effectiveness of MPAs in supporting multispecies food fisheries in the WIO under climate change. We showed that climate change might render the current MPA network in 12 WIO nations a food insecurity hotspot, ineffective in supporting biodiversity conservation and food security outcomes. With less than 4% of reefs within climate refugia and only a quarter under management, the current spatial arrangement of the MPA network in the WIO may not be strategically located to conserve the most diverse and functional reefs now or in the future, casting doubt on the capacity of the current MPA network to promote biodiversity persistence and resilience to climate change in the WIO.

Marine protected areas can effectively improve fisheries yield while safeguarding biodiversity, carbon stocks, and other ecosystem services.[18,19] However, climate change is threatening the capacity of MPAs to deliver successful biodiversity conservation outcomes. There is mounting evidence of species redistribution as the climate warms, which is expected to cause profound rearrangement of ecological communities in exposed reefs and to alter species interactions, particularly for scleractinian coral species.[53,54] Under climate change, we found that

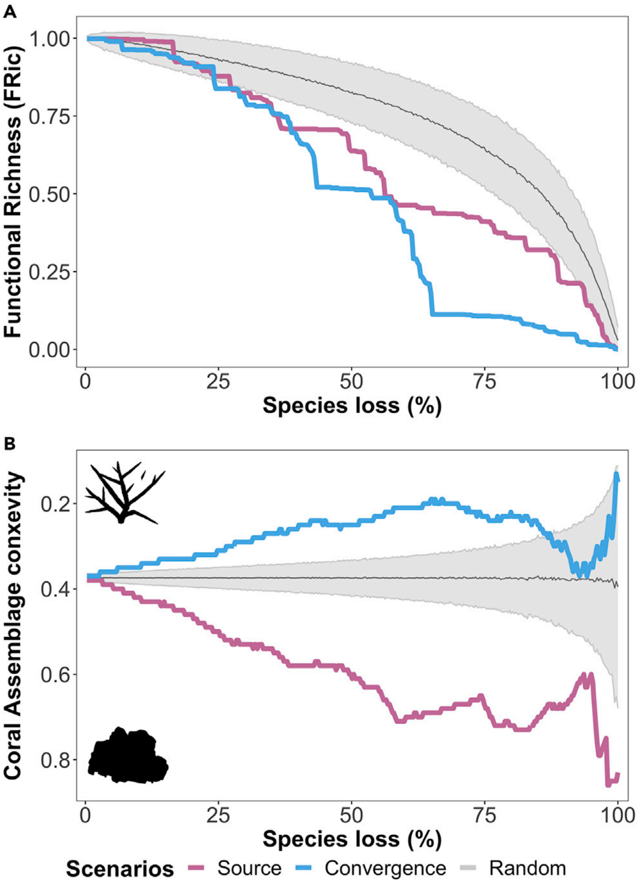


Figure 3. The projected loss of scleractinian coral functional richness and mean coral convexity with the loss of species richness

(A) Potential coral functional richness in the source (pink line) and convergence (blue line) areas based on relative species sensitivity to climate change and (B) associated average convexity of coral assemblage in the source (red line) and convergent (black line) areas. In source areas, the species most sensitive to climate change were removed first, and in convergence areas, the least competitive species were extracted first (Table S5). The random scenario involved randomly selecting scleractinian coral species 999 times along the species extinction gradient. The light blue line is the mean functional richness (A), coral convexity (B), and the upper and lower limit is the 95% predictive interval. Coral convexity is a continuous morphological trait that captures volume compactness and space within a colony and increases from branching (most complex, 0) to massive colony shapes (least complex, 1) (Table S4). The y axis of the coral convexity plot (B) has been reversed.

half of the protected reefs in the WIO are likely to experience significant biodiversity loss in sources. With species potentially escaping warming conditions and with no replacement species from warmer areas, the capacity of MPAs in the WIO to sustain associated ecosystem services may be undermined.[25,55,56] Unfortunately, the nations most dependent on coastal resources for food security are among those most exposed to these changes, highlighting the need for adaptive management to sustain livelihoods under future climate stress.[57] Furthermore, management strategies designed to increase resilience in source areas[58] may be rendered less effective in preventing biodiversity loss. Instead, actions aimed at increasing ecological resilience in convergent, divergent, and sink areas (~40% of reefs), as well as in climate refugia, reducing non-climate stressors such as overfishing and pollution, and ensuring connectivity[59] between the most resilient reefs should be prioritized to minimize socio-ecological risks. In addition, protecting climate corridors is critical in order to maintain safe pathways for species migrating toward more suitable conditions. Our findings provide compelling evidence that innovative and anticipatory regional-scale climate-smart portfolio management strategies, coupled with both spatially and temporally adaptive and flexible MPAs, should be considered to reduce the risk of climate change impacts on coastal ecosystems and livelihoods. To achieve this, predicting responses and reorganization of species assemblages under climate change and conservation impacts across space and time are needed to inform decisions on area-based conservation measures.[55,60]

The primary MPA goals of supporting biodiversity and fisheries outcomes are underpinned by the effective management of reefs with the highest biodiversity values, among other considerations.[61] However, a portfolio of less biodiverse yet strategically located reefs can serve as seedling cradles, supporting connectivity among reefs[62] and promoting the recovery of degraded reefs.[63] To maximize the conservation benefits of MPAs now and into the future, strategic planning of locations is therefore critical. Protecting functionally and phylogenetically diverse reefs located in climate refugia and less diverse reefs that are not subject to biodiversity loss in the future, can buffer MPA networks against ongoing climate change and uncertainties. We found that only coral biodiversity hotspots are adequately protected within the current MPA network, particularly phylogenetic diversity but not fish taxa (except species richness). Despite the need for a tradeoff between ecological and socioeconomic considerations, especially in highly resource-dependent regions, the results suggest a lack of adequate biodiversity consideration in the current MPA design in the WIO. When we spatially intersected biodiversity hotspots with climate trajectories, only fish species richness hotspots were located in both climate refugia and MPAs. Yet fish functional richness and phylogenetic diversity hotspots are in average less accessible from major human settlements and so could be protected with lower socioeconomic cost while offering potential high ecological benefits.

Overall, hotspots of biodiversity components directly associated with ecosystem processes (e.g., functional richness and phylogenetic diversity) were found in MPAs that may experience significant biodiversity loss (source trajectories) and biodiversity reshuffle (e.g., convergent and divergent trajectories) due to climate change. Taken together, the findings demonstrate that the current spatial arrangement of the MPA network in the WIO may not conserve the most diverse and functional reefs in the future, particularly for fish, and hence might not promote biodiversity persistence and resilience to climate change. The variable patterns among biodiversity facets and limited overlapping between taxa reinforce the need for a multifaceted and multitaxon approach to biodiversity conservation that can identify and prioritize taxa-specific hotspots of key biodiversity components. In addition, long-term multidimensional and multitaxon biodiversity monitoring is essential to capture the expected changes experienced by coastal ecosystems. This will inform climate change adaptations to minimize the risk of adverse conservation outcomes and sustain ecosystem services.

Reef complexity is a crucial ecosystem function linked to coral cover and the identity of dominant species, and their associated morphological and functional traits.[52,64] Coral complexity depends largely on coral community assemblage. As found in previous studies,[65] extinction of the least tolerant coral species may lead to an excessive loss of coral functional richness and increased associated assemblage convexity (and hence a decrease in complexity) of the coral reefs most exposed to climate change stress. This is mainly due to the loss of branching fast-growing *Acropora* spp., which are highly susceptible to environmental disturbance.[9,66–68]. The branching coral taxa are also the primary carbonate source on most reefs and provide micro-scale complexity and habitat for diverse reef organisms.[46] On the other hand, slow-growing massive corals (e.g., *Porites* spp.) tend to resist stress and cope better with environmental disturbance. However, their growth morphology provides lower habitat complexity (i.e., higher convexity).[8,69]

Importantly, our results suggest that areas likely to experience species reshuffle (e.g., convergent trajectory) may maintain coral complexity and the associated ecosystem functions and fisheries productivity[56,70] due to *Acropora*'s competitive characteristics. Therefore, there is an opportunity to safeguard a key ecosystem function for a significant proportion (40%) of coral reefs in the WIO. These areas might benefit from management measures to reduce other stressors and minimize cumulative impacts on reefs (e.g., MPAs, reduced runoff, etc.) to increase ecological resilience. As climate change impacts transcend national jurisdictions, coordination of conservation and adaptation actions across local, national, regional, and global scales is critical.[71]

Increasing the climate change adaptive capacity of both institutions and households will require transformational adaptation,[72] including more adaptive, participatory, and collaborative forms of governance and a combination of autonomous and government-led efforts.[73] In addition, in view of the uncertainties in climate change impacts on ecological communities and associated fisheries,[74–76] it is crucial to monitor small-scale ecological changes to track climate change impacts through the involvement of local fishing communities. Providing local fishing communities with the tools to monitor and observe their territories can assist in reconnecting people to their lands and revitalize stewardship and cultural practices[77] while providing valuable information on ecological changes. It can also promote social learning and visibility of changes, essential attributes for adaptive responses to climate change.[78]

Climate change will have adverse impacts on coastal tropical ecosystems and associated fisheries, resulting in a decrease in fisheries productivity as well as other, less studied consequences, such as novel species interactions and reorganization of communities.[74,75] These impacts are already manifesting in shifts in marine species' distribution patterns, disrupting fisheries and fishing communities and threatening food security.[73] The WIO countries most vulnerable to climate change also have the greatest vulnerability to food insecurity, particularly Madagascar, Tanzania, and Comoros. The moderate spatial resolution of the climate models used in this study limits the effectiveness of the predictions at smaller spatial scales. Also, climatic variables, such as temperature, can be more heterogeneous over space than our analyses represent. Since no single analysis can capture all ecological risks link to climate change, further work is needed to ground truth ecological changes. In addition, biodiversity data were derived from different sources and therefore featured different time and spatial resolutions. Spatial and temporal aggregation and eventual integration can increase errors from a mismatch in the spatial and temporal correlations.[79] Local-scale studies incorporating socioeconomic aspects may be needed for small-scale evaluation of socio-ecological dynamics and the impact of climate change, including the adaptive capacity of local fishing communities. Likewise, in evaluating exposure to future climate change, the study does not consider the potential for adaptation; this remains a potential area for model improvement. The study focused on MPAs with variable levels of protection and did not include Locally Marine Managed Areas (LMMAs) and Other Effective Area-Based Conservation Measures (OECMs). Evidence of the role of LMMAs and OECMs in biodiversity conservation is growing.[80,81] Future studies should specifically investigate the effectiveness of MPAs considering their actual level of protection,[82] as well as the effectiveness of alternative conservation tools in sustaining ecosystem services under climate change.

The findings highlight the need for flexible coastal biodiversity management approaches for biodiversity conservation and sustainable fisheries, tailored to local contexts but regionally coherent, coupled with adaptive management to achieve transformational change for local fishing communities. Reef conservation and management efforts must strive for sustained ecosystem services, and MPAs should encompass a range of reefs along the spectrum of vulnerability, impacts, and climate futures. Effective management requires anticipatory, innovative, and climate-smart portfolio management strategies, flexible both in time and space and shaped by the international collaboration to implement successful policies at the regional scale. This study also highlights the need for social adaptation of highly dependent local fishing communities, which will be the first to experience the detrimental consequences of biodiversity loss. Fine-scale multidimensional and multitaxon biodiversity monitoring will be essential to capturing the expected changes in coastal ecosystems in the WIO and identifying future biodiversity hotspots to best inform effective climate change adaptation actions to minimize adverse conservation outcomes.

EXPERIMENTAL PROCEDURES

Resource availability

Lead contact

Further information and requests for resources and reagents should be directed to and will be fulfilled by the lead contact, Stephanie D'Agata (stephanie.dagata@gmail.com).

Materials availability

This study did not generate new unique materials.

Data and code availability

Scleractinian coral and fish species distribution data are publicly available from the International Union for Conservation of Nature (IUCN) redlist (www.iucnredlist.org). Coral reef distributions are publicly available from the World Resources Institute (datasets.wri.org). MPA data are publicly available from the World Database on Protected Areas database (http://protectedplanet.net/). Worldwide climate change trajectories data can be obtained from Burrow et al.[1] Country True Subsistence (TS) index data can be obtained from Taylor et al.[2] Molecular phylogeny for scleractinian coral can be obtained from Huang and Roy (2015).[3] Molecular phylogeny for fish species can be obtained from Mazel et al.[4] Scleractinian coral species functional traits can be obtained from Madin et al.[5] and McWilliam et al.[6] Fish species functional traits can be obtained from Mouillot et al.[7] Coral mean convexity and standard deviation for each coral growth form can be obtained from Zawada et al.[8] All original code has been deposited at Zenodo: https://doi.org/10.5281/zenodo.7308504. The code is also openly available at https://github.com/StephDag/OneEarth_2022_Climate_MPAs_WIO. Any additional information required for reanalyzing the data reported in this paper is available from the lead contact upon request.

Spatial data

Coral and fish occurrence data

We selected 367 scleractinian coral (shallow habitat species) and 557 fish species, for which global range maps were downloaded from http://www.iucnredlist.org/technical-documents/spatial-data. We focused on scleractinian coral species since this taxa is the primary carbonate source on most reefs, providing complexity and habitat for diverse organisms while being highly sensitive to climate change.[46]

We estimated species richness of different species groupings as the sum of the species co-occurring by overlapping distribution maps at fine-scale resolution (0.04 × 0.04° grid cell, i.e., approximately 4 km at this latitude).

We collected spatial information on coral reefs distribution (500 m resolution) from the World Resources Institute (https://datasets.wri.org/dataset/tropical-coral-reefs-of-the-world-500-m-resolution-grid). We collected spatial information on MPAs in the Nairobi Convention countries in the WIO from the World Database on Protected Areas database (http://protectedplanet.net/). We recorded 4,490 coral reef cells (0.04 × 0.04°) in the WIO across 12 countries. Of these, 28% were within MPAs.

Climate change trajectories

We extracted climate change categories from Burrows et al.[1] (Figure S2). Climate change categories were extracted at each centroid of the 0.04° × 0.04° coral reef raster to match biodiversity resolution.

If the MPA system was balanced across the climate change trajectories, the distribution of the seven climate change categories in protected reef cells (28% in total) would be uniform (i.e., 28% divided by 7 = 4%). Thus, proportions of protected cells located over and under the 4% threshold revealed over- and under-representation, respectively, of cells found in protected areas or hotspots of fishing pressure.

Phylogenetic and functional traits data

Phylogenetic diversity

We used a dated molecular phylogeny for scleractinian coral[3] and fish species[4] to estimate phylogenetic diversity based on the Faith index[83] for 358 (97% species pool) scleractinian coral species (supplemental information) and 353 (63% species pool) fish species for which phylogenetic information was available.

We estimated the phylogenetic diversity of scleractinian coral and fish assemblages in each grid cell (0.04° × 0.04° resolution).

These calculations were carried out using R version 4.0.2 software (R Development Core Team 2020) and Picante and Ape packages.

Functional traits diversity

We characterized scleractinian coral species (n = 367) using seven functional traits selected for their functional importance: (1) growth rate, (2) skeletal density, (3) corallite width, (4) maximum colony size, (5) colony height, (6) interstitial space size, and (7) surface-area-to-volume ratio.[5,6]

The growth rate was coded using five categories: 0–5, 5–10, 10–25, 25–50, and 50–200 mm/y^{-1}. Skeletal density was coded using five categories: 0–1.2, 1.2–1.5, 1.5–1.8, 1.8–2.1, and 2.1–3 g/cm^3. Corallite width was coded using five categories: 0–1.5, 1.5–6, 6–12, 12–25, and 25–100 mm. Maximum colony size was coded using five categories: 0–50, 50–100, 100–200, 200–400, and 400–2,000 cm. Colony height, interstitial space size, and surface-area-to-volume ratio were assigned to species based on their morphological types and a simplified model of coral geometry from 1 to 5.[5,6]

We characterized fish species using six functional traits linked to diet and feeding behavior[35]: (1) maximum size, (2) diet, (3) mobility, (4) position over the reef, (5) activity, and (6) gregariousness. Fish size was coded using six ordered categories: 0–7, 7.1–15, 15.1–30, 30.1–50, 50.1–80, and >80 cm. Mobility was coded using three ordered categories: sedentary (including territorial species), mobile within a reef, and mobile between reefs. The activity period was coded using three ordered types: diurnal, both diurnal and nocturnal, and nocturnal. Schooling was coded using five ordered categories: solitary, pairing, or living in small (3–20 individuals), medium (20–50 individuals), or large (>50 individuals) groups. Vertical position in the water column was coded using three ordered categories: benthic, benthopelagic, and pelagic. Diet was characterized based on main items consumed by each species, which resulted in seven trophic categories: herbivorous–detritivorous (i.e., fish feeding on turf or filamentous algae and/or undefined organic material); macroalgal herbivorous (feeding on large fleshy algae and/or seagrass); invertivorous targeting sessile invertebrates (feeding on corals, sponges, and ascidians); invertivorous targeting mobile invertebrate (feeding on benthic species such as crustaceans); planktivorous (feeding on small organisms in the water column); piscivorous (feeding on fish and cephalopods); and omnivorous (fish for which both vegetal and animal material are important in their diet).

Pairwise functional distances between species were computed using the Gower distance, allowing mixing different variables while giving them equal weight.[84] A principal-coordinates analysis was then performed using this functional distance matrix, and the first four principal axes were retained to build a multidimensional functional space.[85,86]

We estimated functional richness for each scleractinian coral and fish assemblage independently in each coral reef pixel as the volume inside the convex hull occupied by species of the assemblage. Functional richness was computed using the presence/absence data only. It represents the breadth of trait ranges in the community and can be considered a proxy for the diversity of roles, and is linked to community assembly and ecosystem processes.[35]

Simulating coral functional and phylogenetic diversity and coral convexity in source and convergent areas

We measured the functional and phylogenetic diversity from the global pool of scleractinian coral species (367 species).

Coral mean convexity and standard deviation for each coral growth form were extracted from Zawada et al.[52] (Table S3). Briefly, coral convexity is a continuous morphological trait that captures volume compactness and amount of space within a colony, reflecting a continuous gradient from branching to massive colony shapes as convexity increases. Therefore, convexity can simultaneously explore how coral morphology affects reef ecology across multiple coral species and growth forms. The convexity of the pool of coral species was computed as the weighted average of coral convexity.

The extinction of scleractinian coral species was simulated by removing them from the global pool and calculating the diversity index and global convexity of the remaining collection of species. The order of the simulated extinctions varied between source and convergence areas since traits will not be selected the same way (Table S4). For the source category, the most vulnerable species to increase temperature were extirpated first, followed by a generalist, weedy, and, last, stress-tolerant species.[46] We assumed the opposite scenario in convergence areas, in which competitive species will have a potentially higher capacity to colonize than stress-tolerant species.[46] Sensitivity to increase temperature was missing for 95 species. We fitted a random forest to predict sensitivity class to increase temperature (independent variable) for the missing species with (1) growth rate, (2) skeletal density, (3) corallite width, (4) maximum colony size, (5) colony height, (6) interstitial space size, and (7) surface-area-to-volume ratio and (8) growth form as the independent variables.

We fitted the model on 90% of the dataset and tested the model with the remaining 10%. The model accuracy was 82%. We then predicted the species sensitivity to increase the temperature for the 95 species for which we did not have sufficient information.

To evaluate whether the diversity and global convexity changes for each scenario were significantly different from random, we constructed 999 random scenarios in which species were removed randomly from the global pool. We used the mean and 95% prediction interval for graphical representation.

These calculations were carried out using R version 4.0.2 software (R Development Core Team 2020) and the packages Picante, Ape, randomForest, and FD.

Country subsistence index

Fisheries within each country in the WIO were classified based on the TS index, representing the percentage of true subsistence fishers that rely on catch only for food. True subsistence fishers do not sell any portion of their catch, making their level of dependence on a healthy ocean the highest as they do not generate money from this activity.[2] Countries were classified based on the level of true subsistence (Table S5): high >80%; medium >50% and <80%; low >10% and <50%; and very low <10%. The TS level in Somalia is unknown (NA) due to high levels of uncertainty in catch data.[2]

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.oneear.2022.10.012.

ACKNOWLEDGMENTS

We thank the Environmental and Earth Science department of the Macquarie University for support. This work was also supported by the Wildlife Conservation Society. Funding for S.D. was provided by the Laboratory of Excellence "Corail" (LIVELIHOOD project, grant EPHE IRD PD A02020), France. We thank the IUCN and World Resources Institute for data collection, dissemination, and guidance on data use. The authors thank two anonymous reviewers and Anthony J. Richardson for invaluable feedback and suggestions that have strengthened this paper.

AUTHOR CONTRIBUTIONS

Conceptualization, S.D. and J.M.M.; Methodology, S.D.; Formal analysis, S.D.; Writing – Original Draft, S.D. Writing – Review & Editing, S.D. and J.M.M.; Visualization, S.D.; Supervision, S.D. and J.M.M.; Funding Acquisition, J.M.M.

DECLARATION OF INTERESTS

The authors declare no competing interests.

Received: September 27, 2021
Revised: August 3, 2022
Accepted: October 25, 2022
Published: November 18, 2022

REFERENCES

1. Burrows, M.T., Schoeman, D.S., Richardson, A.J., Molinos, J.G., Hoffmann, A., Buckley, L.B., Moore, P.J., Brown, C.J., Bruno, J.F., Duarte, C.M., et al. (2014). Geographical limits to species-range shifts are suggested by climate velocity. Nature *507*, 492–495. https://doi.org/10.1038/nature12976.
2. Taylor, S.F.W., Roberts, M.J., Milligan, B., and Ncwadi, R. (2019). Measurement and implications of marine food security in the Western Indian Ocean: an impending crisis? Food Secur. *11*, 1395–1415. https://doi.org/10.1007/s12571-019-00971-6.
3. Huang, D., and Roy, K. (2015). The future of evolutionary diversity in reef corals. Philos. Trans. R. Soc. Lond. B Biol. Sci. *370*, 20140010. https://doi.org/10.1098/rstb.2014.0010.
4. Mazel, F., Pennell, M.W., Cadotte, M.W., Diaz, S., Dalla Riva, G.V., Grenyer, R., Leprieur, F., Mooers, A.O., Mouillot, D., Tucker, C.M., and Pearse, W.D. (2018). Prioritizing phylogenetic diversity captures functional diversity unreliably. Nat. Commun. *9*, 2888. https://doi.org/10.1038/s41467-018-05126-3.
5. Madin, J.S., Anderson, K.D., Andreasen, M.H., Bridge, T.C.L., Cairns, S.D., Connolly, S.R., Darling, E.S., Diaz, M., Falster, D.S., Franklin, E.C., et al. (2016). The Coral Trait Database, a curated database of trait information for coral species from the global oceans. Sci. Data *3*, 160017. https://doi.org/10.1038/sdata.2016.17.
6. McWilliam, M., Hoogenboom, M.O., Baird, A.H., Kuo, C.-Y., Madin, J.S., and Hughes, T.P. (2018). Biogeographical disparity in the functional diversity and redundancy of corals. Proc. Natl. Acad. Sci. USA. *115*, 3084–3089. https://doi.org/10.1073/pnas.1716643115.
7. Mouillot, D., Villéger, S., Parravicini, V., Kulbicki, M., Arias-González, J.E., Bender, M., Chabanet, P., Floeter, S.R., Friedlander, A., Vigliola, L., and Bellwood, D.R. (2014). Functional over-redundancy and high functional vulnerability in global fish faunas on tropical reefs. Proc. Natl. Acad. Sci. USA. *111*, 13757–13762. https://doi.org/10.1073/pnas.1317625111.
8. Zawada, K.J.A., Madin, J.S., Baird, A.H., Bridge, T.C.L., and Dornelas, M. (2019). Morphological traits can track coral reef responses to the Anthropocene. Funct. Ecol. *33*, 962–975. https://doi.org/10.1111/1365-2435.13358.
9. Hughes, T.P., Kerry, J.T., Baird, A.H., Connolly, S.R., Dietzel, A., Eakin, C.M., Heron, S.F., Hoey, A.S., Hoogenboom, M.O., Liu, G., et al. (2018). Global warming transforms coral reef assemblages. Nature *556*, 492–496. https://doi.org/10.1038/s41586-018-0041-2.
10. Brito-Morales, I., García Molinos, J., Schoeman, D.S., Burrows, M.T., Poloczanska, E.S., Brown, C.J., Ferrier, S., Harwood, T.D., Klein, C.J., McDonald-Madden, E., et al. (2018). Climate velocity can inform conservation in a warming world. Trends Ecol. Evol. *33*, 441–457. https://doi.org/10.1016/j.tree.2018.03.009.
11. Lenoir, J., Bertrand, R., Comte, L., Bourgeaud, L., Hattab, T., Murienne, J., and Grenouillet, G. (2020). Species better track climate warming in the oceans than on land. Nat. Ecol. Evol. *4*, 1044–1059. https://doi.org/10.1038/s41559-020-1198-2.
12. Rilov, G., Fraschetti, S., Gissi, E., Pipitone, C., Badalamenti, F., Tamburello, L., Menini, E., Goriup, P., Mazaris, A.D., Garrabou, J., et al. (2020). A fast-moving target: achieving marine conservation goals under shifting climate and policies. Ecol. Appl. *30*, e02009. https://doi.org/10.1002/eap.2009.
13. D'Amen, M., and Azzurro, E. (2020). Lessepsian fish invasion in Mediterranean marine protected areas: a risk assessment under climate change scenarios. ICES J. Mar. Sci. *77*, 388–397. https://doi.org/10.1093/icesjms/fsz207.
14. Pessarrodona, A., Foggo, A., and Smale, D.A. (2019). Can ecosystem functioning be maintained despite climate-driven shifts in species composition? Insights from novel marine forests. J. Ecol. *107*, 91–104. https://doi.org/10.1111/1365-2745.13053.
15. Vergés, A., McCosker, E., Mayer-Pinto, M., Coleman, M.A., Wernberg, T., Ainsworth, T., and Steinberg, P.D. (2019). Tropicalisation of temperate reefs: implications for ecosystem functions and management actions. Funct. Ecol. *33*, 1000–1013. https://doi.org/10.1111/1365-2435.13310.
16. Fedele, G., Donatti, C.I., Harvey, C.A., Hannah, L., and Hole, D.G. (2019). Transformative adaptation to climate change for sustainable social-ecological systems. Environ. Sci. Pol. *101*, 116–125. https://doi.org/10.1016/j.envsci.2019.07.001.
17. Eddy, T.D., Lam, V.W., Reygondeau, G., Cisneros-Montemayor, A.M., Greer, K., Palomares, M.L.D., Bruno, J.F., Ota, Y., and Cheung, W.W. (2021). Global decline in capacity of coral reefs to provide ecosystem services. One Earth *4*, 1278–1285. https://doi.org/10.1016/j.oneear.2021.08.016.
18. Sala, E., Mayorga, J., Bradley, D., Cabral, R.B., Atwood, T.B., Auber, A., Cheung, W., Costello, C., Ferretti, F., Friedlander, A.M., et al. (2021). Protecting the global ocean for biodiversity, food and climate. Nature *592*, 397–402. https://doi.org/10.1038/s41586-021-03371-z.
19. Ban, N.C., Gurney, G.G., Marshall, N.A., Whitney, C.K., Mills, M., Gelcich, S., Bennett, N.J., Meehan, M.C., Butler, C., Ban, S., et al. (2019). Well-being outcomes of marine protected areas. Nat. Sustain. *2*, 524–532. https://doi.org/10.1038/s41893-019-0306-2.
20. Brito-Morales, I., Schoeman, D.S., Molinos, J.G., Burrows, M.T., Klein, C.J., Arafeh-Dalmau, N., Kaschner, K., Garilao, C., Kesner-Reyes, K., and Richardson, A.J. (2020). Climate velocity reveals increasing exposure of deep-ocean biodiversity to future warming. Nat. Clim. Chang. *10*, 576–581. https://doi.org/10.1038/s41558-020-0773-5.
21. Pinsky, M.L., Worm, B., Fogarty, M.J., Sarmiento, J.L., and Levin, S.A. (2013). Marine taxa track local climate velocities. Science *341*, 1239–1242. https://doi.org/10.1126/science.1239352.

22. Alagador, D., Cerdeira, J.O., and Araújo, M.B. (2014). Shifting protected areas: scheduling spatial priorities under climate change. J. Appl. Ecol. *51*, 703–713. https://doi.org/10.1111/1365-2664.12230.

23. Arafeh-Dalmau, N., Brito-Morales, I., Schoeman, D.S., Possingham, H.P., Klein, C.J., and Richardson, A.J. (2021). Incorporating climate velocity into the design of climate-smart networks of marine protected areas. Methods Ecol. Evol. *12*, 1969–1983. https://doi.org/10.1111/2041-210X.13675.

24. Tittensor, D.P., Novaglio, C., Harrison, C.S., Heneghan, R.F., Barrier, N., Bianchi, D., Bopp, L., Bryndum-Buchholz, A., Britten, G.L., Büchner, M., et al. (2021). Next-generation ensemble projections reveal higher climate risks for marine ecosystems. Nat. Clim. Chang. *11*, 973–981. https://doi.org/10.1038/s41558-021-01173-9.

25. Bruno, J.F., Bates, A.E., Cacciapaglia, C., Pike, E.P., Amstrup, S.C., van Hooidonk, R., Henson, S.A., and Aronson, R.B. (2018). Climate change threatens the world's marine protected areas. Nat. Clim. Chang. *8*, 499–503. https://doi.org/10.1038/s41558-018-0149-2.

26. Melbourne-Thomas, J., Audzijonyte, A., Brasier, M.J., Cresswell, K.A., Fogarty, H.E., Haward, M., Hobday, A.J., Hunt, H.L., Ling, S.D., McCormack, P.C., et al. (2021). Poleward bound: adapting to climate-driven species redistribution. Rev. Fish Biol. Fish. *32*, 231–251. https://doi.org/10.1007/s11160-021-09641-3.

27. Golden, C.D., Allison, E.H., Cheung, W.W.L., Dey, M.M., Halpern, B.S., McCauley, D.J., Smith, M., Vaitla, B., Zeller, D., and Myers, S.S. (2016). Nutrition: fall in fish catch threatens human health. Nature *534*, 317–320. https://doi.org/10.1038/534317a.

28. Woodhead, A.J., Hicks, C.C., Norström, A.V., Williams, G.J., and Graham, N.A.J. (2019). Coral reef ecosystem services in the Anthropocene. Funct. Ecol. *33*, 1023–1034. https://doi.org/10.1111/1365-2435.13331.

29. Doukas, H., and Nikas, A. (2020). Decision support models in climate policy. Eur. J. Oper. Res. *280*, 1–24. https://doi.org/10.1016/j.ejor.2019.01.017.

30. UNEP-Nairobi Convention; WIOMSA (2015). The Regional State of the Coast Report: Western Indian Ocean. https://wedocs.unep.org/20.500.11822/9668.

31. Barnes-Mauthe, M., Arita, S., Allen, S.D., Gray, S.A., and Leung, P. (2013). The influence of ethnic diversity on social network structure in a common-pool resource system: implications for collaborative management. Ecol. Soc. *18*, art23.

32. Béné, C. (2006). Small-scale Fisheries: Assessing Their Contribution to Rural Livelihoods in Developing Countries*Vol. 1008* (Rome, Italy: Food and Agriculture Organization of the United Nations).

33. IPCC (2018). Global Warming of 1.5°C. In An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty, V. Masson-Delmotte, P. Zhai, H.-O. Pörtner, D. Roberts, J. Skea, and P.R. Shukla, et al., eds. (Cambridge University Press). https://doi.org/10.1017/9781009157940.

34. UNEP-Nairobi Convention; WIOMSA (2021). Western Indian Ocean Marine Protected Areas Outlook: Towards Achievement of the Global Biodiversity Framework Targets (UNEP and WIOMSA), p. 298. https://www.wiomsa.org/publications/western-indian-ocean-wio-marine-protected-areas-outlook/.

35. Mouillot, D., Graham, N.A.J., Villéger, S., Mason, N.W.H., and Bellwood, D.R. (2013). A functional approach reveals community responses to disturbances. Trends Ecol. Evol. *28*, 167–177. https://doi.org/10.1016/j.tree.2012.10.004.

36. Allen, B., Kon, M., and Bar-Yam, Y. (2009). A new phylogenetic diversity measure generalizing the shannon index and its application to phyllostomid bats. Am. Nat. *174*, 236–243. https://doi.org/10.1086/600101.

37. Bellwood, D.R., Streit, R.P., Brandl, S.J., and Tebbett, S.B. (2019). The meaning of the term 'function' in ecology: a coral reef perspective. Funct. Ecol. *33*, 948–961. https://doi.org/10.1111/1365-2435.13265.

38. Duffy, J.E., Lefcheck, J.S., Stuart-Smith, R.D., Navarrete, S.A., and Edgar, G.J. (2016). Biodiversity enhances reef fish biomass and resistance to climate change. Proc. Natl. Acad. Sci. USA. *113*, 6230–6235. https://doi.org/10.1073/pnas.1524465113.

39. Maherali, H., and Klironomos, J.N. (2007). Influence of phylogeny on fungal community assembly and ecosystem functioning. Science (New York, N.Y.) *316*, 1746–1748. https://doi.org/10.1126/science.1143082.

40. Kittinger, J.N., Finkbeiner, E.M., Ban, N.C., Broad, K., Carr, M.H., Cinner, J.E., Gelcich, S., Cornwell, M.L., Koehn, J.Z., Basurto, X., et al. (2013). Emerging frontiers in social-ecological systems research for sustainability of small-scale fisheries. Curr. Opin. Environ. Sustain. *5*, 352–357. https://doi.org/10.1016/j.cosust.2013.06.008.

41. Graham, N.A.J., and Nash, K.L. (2012). The importance of structural complexity in coral reef ecosystems. Coral Reefs *32*, 315–326. https://doi.org/10.1007/s00338-012-0984-y.

42. Rogers, A., Blanchard, J.L., and Mumby, P.J. (2014). Vulnerability of coral reef fisheries to a loss of structural complexity. Curr. Biol. *24*, 1000–1005. https://doi.org/10.1016/j.cub.2014.03.026.

43. Ferrario, F., Beck, M.W., Storlazzi, C.D., Micheli, F., Shepard, C.C., and Airoldi, L. (2014). The effectiveness of coral reefs for coastal hazard risk reduction and adaptation. Nat. Commun. *5*, 3794. https://doi.org/10.1038/ncomms4794.

44. Fontoura, L., Zawada, K.J.A., D'Agata, S., Álvarez-Noriega, M., Baird, A.H., Boutros, N., Dornelas, M., Luiz, O.J., Madin, J.S., Maina, J.M., et al. (2020). Climate-driven shift in coral morphological structure predicts decline of juvenile reef fishes. Glob. Chang. Biol. *26*, 557–567. https://doi.org/10.1111/gcb.14911.

45. Pratchett, M.S., Bay, L.K., Gehrke, P.C., Koehn, J.D., Osborne, K., Pressey, R.L., Sweatman, H.P.a., and Wachenfeld, D. (2011). Contribution of climate change to degradation and loss of critical fish habitats in Australian marine and freshwater environments. Mar. Freshw. Res. *62*, 1062. https://doi.org/10.1071/MF10303.

46. Darling, E.S., McClanahan, T.R., Maina, J., Gurney, G.G., Graham, N.A.J., Januchowski-Hartley, F., Cinner, J.E., Mora, C., Hicks, C.C., Maire, E., et al. (2019). Social–environmental drivers inform strategic management of coral reefs in the Anthropocene. Nat. Ecol. Evol. *3*, 1341–1350. https://doi.org/10.1038/s41559-019-0953-8.

47. UNEP-WCMC; WorldFish Centre; WRI; TNC (2021). Global Distribution of Warm-Water Coral Reefs, Compiled from Multiple Sources Including the Millennium Coral Reef Mapping Project (UN Environment World Conservation Monitoring Centre). Version 4.1. Includes contributions from IMaRS-USF and IRD (2005), IMaRS-USF (2005) and Spalding et al. (2001). https://doi.org/10.34892/t2wk-5t34.

48. Myers, N., Mittermeier, R. a, Mittermeier, C.G., da Fonseca, G.A., and Kent, J. (2000). Biodiversity hotspots for conservation priorities. Nature *403*, 853–858. https://doi.org/10.1038/35002501.

49. Obura, D. (2012). The diversity and biogeography of western Indian ocean reef-building corals. PLoS One *7*, e45013. https://doi.org/10.1371/journal.pone.0045013.

50. Maire, E., Cinner, J., Velez, L., Huchery, C., Mora, C., Dagata, S., Vigliola, L., Wantiez, L., Kulbicki, M., and Mouillot, D. (2016). How accessible are coral reefs to people? A global assessment based on travel time. Ecol. Lett. *19*, 351–360. https://doi.org/10.1111/ele.12577.

51. Mallory, M.L., and Ando, A.W. (2014). Implementing efficient conservation portfolio design. Resour. Energy Econ. *38*, 1–18. https://doi.org/10.1016/j.reseneeco.2014.05.001.

52. Zawada, K.J.A., Dornelas, M., and Madin, J.S. (2019). Quantifying coral morphology. Coral Reefs *38*, 1281–1292. https://doi.org/10.1007/s00338-019-01842-4.

53. Robinson, J.P.W., Wilson, S.K., Robinson, J., Gerry, C., Lucas, J., Assan, C., Govinden, R., Jennings, S., and Graham, N.A.J. (2019). Productive instability of coral reef fisheries after climate-driven regime shifts. Nat. Ecol. Evol. *3*, 183–190. https://doi.org/10.1038/s41559-018-0715-z.

54. O'Hara, C.C., Frazier, M., and Halpern, B.S. (2021). At-risk marine biodiversity faces extensive, expanding, and intensifying human impacts. Science *372*, 84–87. https://doi.org/10.1126/science.abe6731.

55. Graham, N.A.J., Robinson, J.P.W., Smith, S.E., Govinden, R., Gendron, G., and Wilson, S.K. (2020). Changing role of coral reef marine reserves in a warming climate. Nat. Commun. *11*, 2000. https://doi.org/10.1038/s41467-020-15863-z.

56. Morais, R.A., Depczynski, M., Fulton, C., Marnane, M., Narvaez, P., Huertas, V., Brandl, S.J., and Bellwood, D.R. (2020). Severe coral loss shifts energetic dynamics on a coral reef. Funct. Ecol. *34*, 1507–1518. https://doi.org/10.1111/1365-2435.13568.

57. D'Agata, S., Darling, E.S., Gurney, G.G., McClanahan, T.R., Muthiga, N.A., Rabearisoa, A., and Maina, J.M. (2020). Multiscale determinants of social adaptive capacity in small-scale fishing communities. Environ. Sci. Pol. *108*, 56–66. https://doi.org/10.1016/j.envsci.2020.03.006.

58. Wilson, K.L., Tittensor, D.P., Worm, B., and Lotze, H.K. (2020). Incorporating climate change adaptation into marine protected area planning. Glob. Chang. Biol. *26*, 3251–3267. https://doi.org/10.1111/gcb.15094.

59. Fontoura, L., D'Agata, S., Gamoyo, M., Barneche, D.R., Luiz, O.J., Madin, E.M.P., Eggertsen, L., and Maina, J.M. (2022). Protecting connectivity promotes successful biodiversity and fisheries conservation. Science *375*, 336–340. https://doi.org/10.1126/science.abg4351.

60. Makino, A., Klein, C.J., Possingham, H.P., Yamano, H., Yara, Y., Ariga, T., Matsuhasi, K., and Beger, M. (2015). The effect of applying alternate IPCC climate scenarios to marine reserve design for range changing species. Conservation Letters *8*, 320–328. https://doi.org/10.1111/conl.12147.

61. Roberts, C.M., O'Leary, B.C., McCauley, D.J., Cury, P.M., Duarte, C.M., Lubchenco, J., Pauly, D., Sáenz-Arroyo, A., Sumaila, U.R., Wilson, R.W., et al. (2017). Marine reserves can mitigate and promote adaptation to climate change. Proc. Natl. Acad. Sci. USA. *114*, 6167–6175. https://doi.org/10.1073/pnas.1701262114.

62. Harrison, H.B., Bode, M., Williamson, D.H., Berumen, M.L., and Jones, G.P. (2020). A connectivity portfolio effect stabilizes marine reserve performance. Proc. Natl. Acad. Sci. USA. *117*, 25595–25600. https://doi.org/10.1073/pnas.1920580117.

63. Abelson, A., Nelson, P.A., Edgar, G.J., Shashar, N., Reed, D.C., Belmaker, J., Krause, G., Beck, M.W., Brokovich, E., France, R., and Gaines, S.D. (2016). Expanding marine protected areas to include degraded coral reefs. Conserv. Biol. *30*, 1182–1191. https://doi.org/10.1111/cobi.12722.

64. Alvarez-Filip, L., Gill, J.a., Dulvy, N.K., Perry, a.L., Watkinson, a.R., and Côté, I.M. (2011). Drivers of region-wide declines in architectural complexity on Caribbean reefs. Coral Reefs *30*, 1051–1060. https://doi.org/10.1007/s00338-011-0795-6.

65. McClanahan, T.R., Darling, E.S., Maina, J.M., Muthiga, N.A., 'agata, S.D., Jupiter, S.D., Arthur, R., Wilson, S.K., Mangubhai, S., Nand, Y., et al. (2019). Temperature patterns and mechanisms influencing coral bleaching during the 2016 El Niño. Nat. Clim. Chang. *9*, 845–851. https://doi.org/10.1038/s41558-019-0576-8.

66. Darling, E.S., McClanahan, T.R., and Côté, I.M. (2013). Life histories predict coral community disassembly under multiple stressors. Glob. Chang. Biol. *19*, 1930–1940. https://doi.org/10.1111/gcb.12191.

67. Perry, C.T., Murphy, G.N., Graham, N.A.J., Wilson, S.K., Januchowski-Hartley, F.A., and East, H.K. (2015). Remote coral reefs can sustain high growth potential and may match future sea-level trends. Sci. Rep. *5*, 18289. https://doi.org/10.1038/srep18289.

68. Pratchett, M.S., Anderson, K.D., Hoogenboom, M.O., Widman, E., Baird, A.H., Pandol, J.M., et al. (2015). Spatial, temporal and taxonomic variation in coral growth—implications for the structure and function of coral reef ecosystems. In Oceanography and Marine Biology: An Annual Review, *53* (CRC Press), pp. 215–295.

69. Carricart-Ganivet, J.P., Cabanillas-Terán, N., Cruz-Ortega, I., and Blanchon, P. (2012). Sensitivity of calcification to thermal stress varies among genera of massive reef-building corals. PLoS One *7*, e32859. https://doi.org/10.1371/journal.pone.0032859.

70. Ainsworth, C.H., and Mumby, P.J. (2014). Coral-algal phase shifts alter fish communities and reduce fisheries production. Glob. Chang. Biol. *21*, 165–172. https://doi.org/10.1111/gcb.12667.

71. Mason, N., Ward, M., Watson, J.E.M., Venter, O., and Runting, R.K. (2020). Global opportunities and challenges for transboundary conservation. Nat. Ecol. Evol. *4*, 694–701. https://doi.org/10.1038/s41559-020-1160-3.

72. Berrang-Ford, L., Siders, A.R., Lesnikowski, A., Fischer, A.P., Callaghan, M.W., Haddaway, N.R., Mach, K.J., Araos, M., Shah, M.A.R., Wannewitz, M., et al. (2021). A systematic global stocktake of evidence on human adaptation to climate change. Nat. Clim. Chang. *11*, 989–1000. https://doi.org/10.1038/s41558-021-01170-y.

73. Ojea, E., Lester, S.E., and Salgueiro-Otero, D. (2020). Adaptation of fishing communities to climate-driven shifts in target species. One Earth *2*, 544–556. https://doi.org/10.1016/j.oneear.2020.05.012.

74. Lam, V.W.Y., Allison, E.H., Bell, J.D., Blythe, J., Cheung, W.W.L., Frölicher, T.L., Gasalla, M.A., and Sumaila, U.R. (2020). Climate change, tropical fisheries and prospects for sustainable development. Nat. Rev. Earth Environ. *1*, 440–454. https://doi.org/10.1038/s43017-020-0071-9.

75. Gaines, S.D., Costello, C., Owashi, B., Mangin, T., Bone, J., Molinos, J.G., Burden, M., Dennis, H., Halpern, B.S., Kappel, C.V., et al. (2018). Improved fisheries management could offset many negative effects of climate change. Sci. Adv. *4*, eaao1378. https://doi.org/10.1126/sciadv.aao1378.

76. D'Agata, S. (2022). Ecosystems services at risk. Nat. Clim. Chang. *12*, 13–14. https://doi.org/10.1038/s41558-021-01256-7.

77. Claudet, J. (2021). The seven domains of action for a sustainable ocean. Cell *184*, 1426–1429. https://doi.org/10.1016/j.cell.2021.01.055.

78. Gianelli, I., Ortega, L., Pittman, J., Vasconcellos, M., and Defeo, O. (2021). Harnessing scientific and local knowledge to face climate change in small-scale fisheries. Global Environ. Change *68*, 102253. https://doi.org/10.1016/j.gloenvcha.2021.102253.

79. Burrough, P.A. (2001). GIS and geostatistics: essential partners for spatial analysis. Environ. Ecol. Stat. *8*, 361–377. https://doi.org/10.1023/A:1012734519752.

80. Dudley, N., Jonas, H., Nelson, F., Parrish, J., Pyhälä, A., Stolton, S., and Watson, J.E. (2018). The essential role of other effective area-based conservation measures in achieving big bold conservation targets. Global Ecology and Conservation *15*, e00424. https://doi.org/10.1016/j.gecco.2018.e00424.

81. Diz, D., Johnson, D., Riddell, M., Rees, S., Battle, J., Gjerde, K., Hennige, S., and Roberts, J.M. (2018). Mainstreaming marine biodiversity into the SDGs: the role of other effective area-based conservation measures (SDG 14.5). Mar. Pol. *93*, 251–261. https://doi.org/10.1016/j.marpol.2017.08.019.

82. Claudet, J., Loiseau, C., Sostres, M., and Zupan, M. (2020). Underprotected marine protected areas in a global biodiversity hotspot. One Earth *2*, 380–384. https://doi.org/10.1016/j.oneear.2020.03.008.

83. Faith, D.P. (1992). Conservation evaluation and phylogenetic diversity. Biol. Conserv. *61*, 1–10. https://doi.org/10.1016/0006-3207(92)91201-3.

84. Gower, J.C. (1971). A general coefficient of similarity and some of its properties. Biometrics *27*, 857–874. https://doi.org/10.2307/2528823.

85. Maire, E., Grenouillet, G., Brosse, S., and Villéger, S. (2015). How many dimensions are needed to accurately assess functional diversity? A pragmatic approach for assessing the quality of functional spaces. Global Ecol. Biogeogr. *24*, 728–740. https://doi.org/10.1111/geb.12299.

86. Villéger, S., Mason, N.W.H., and Mouillot, D. (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology *89*, 2290–2301. https://doi.org/10.1890/07-1206.1.

One Earth, Volume *5*

Supplemental information

Climate change reduces the conservation benefits of tropical coastal ecosystems

Stephanie D'Agata and Joseph M. Maina

Supplemental information

Supplemental figures

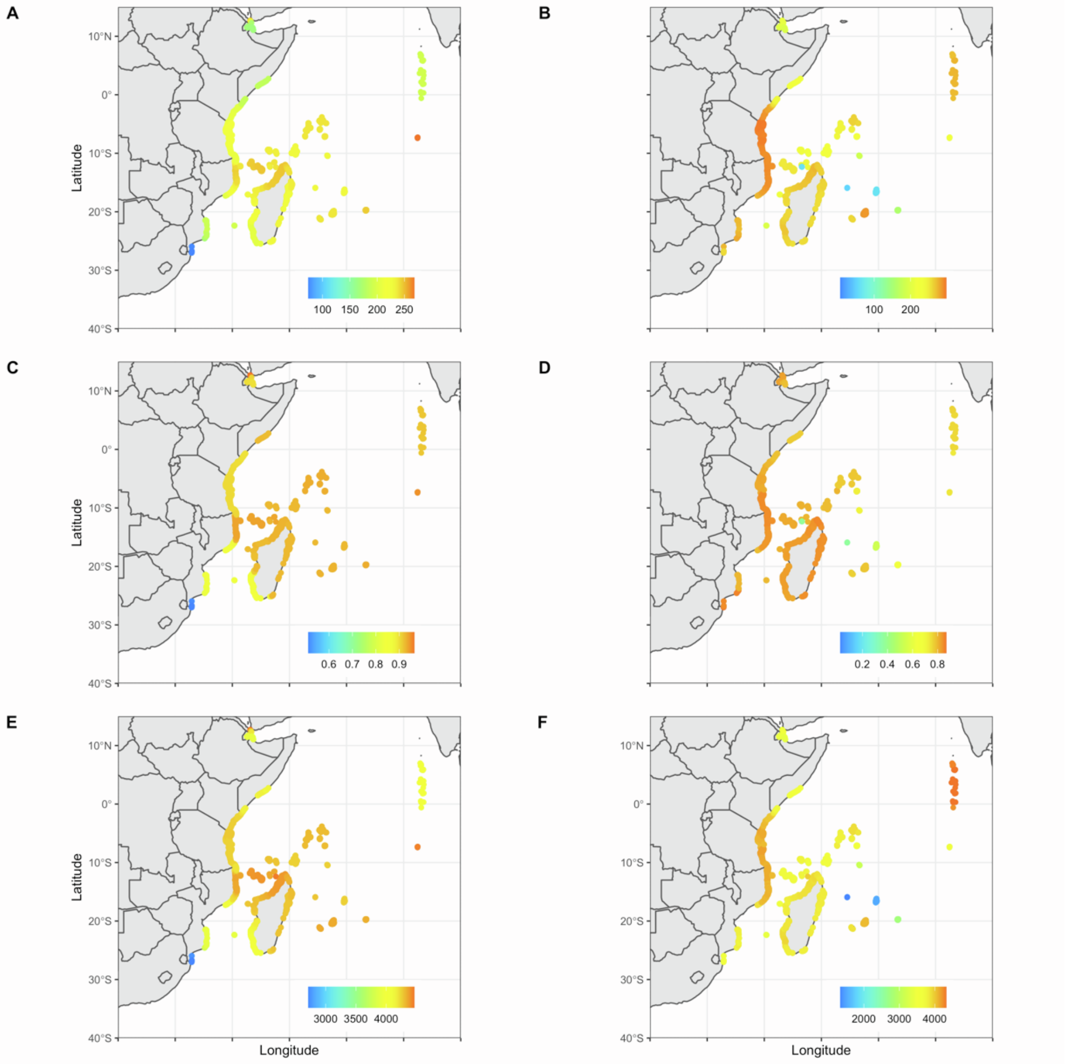


Figure S1. Spatial distribution of three biodiversity components of coral (left) and fish (right) cross a 4x4km grid; species richness (A-Coral, B-Fish), functional richness (C-Coral, D-fish) and the amount of phylogenetic history (phylogenetic diversity (E-Coral, F-Fish)), related to Figure 2.

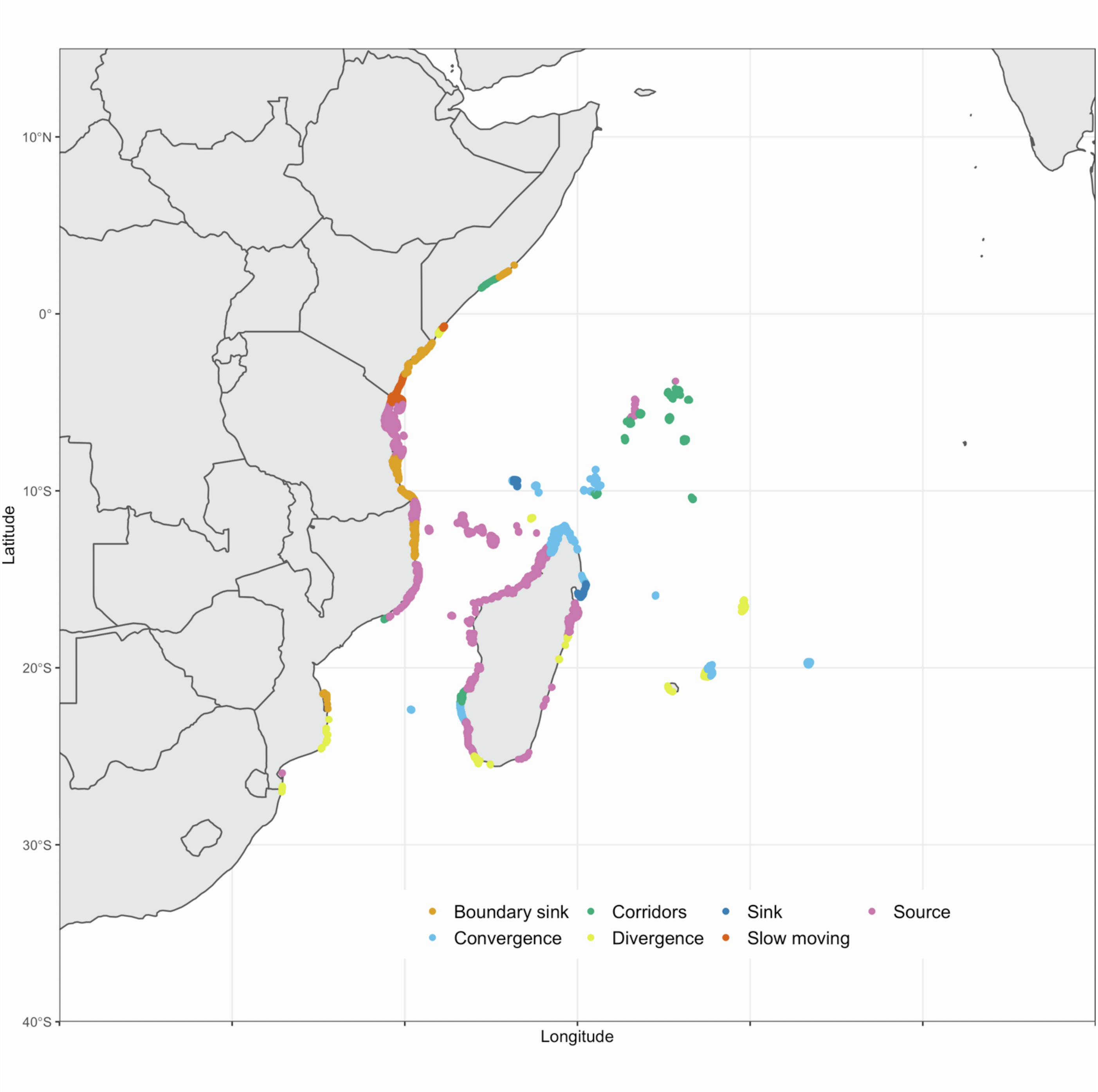


Figure S2. Climate change trajectories spatial distribution, related to Figure 1 and 2

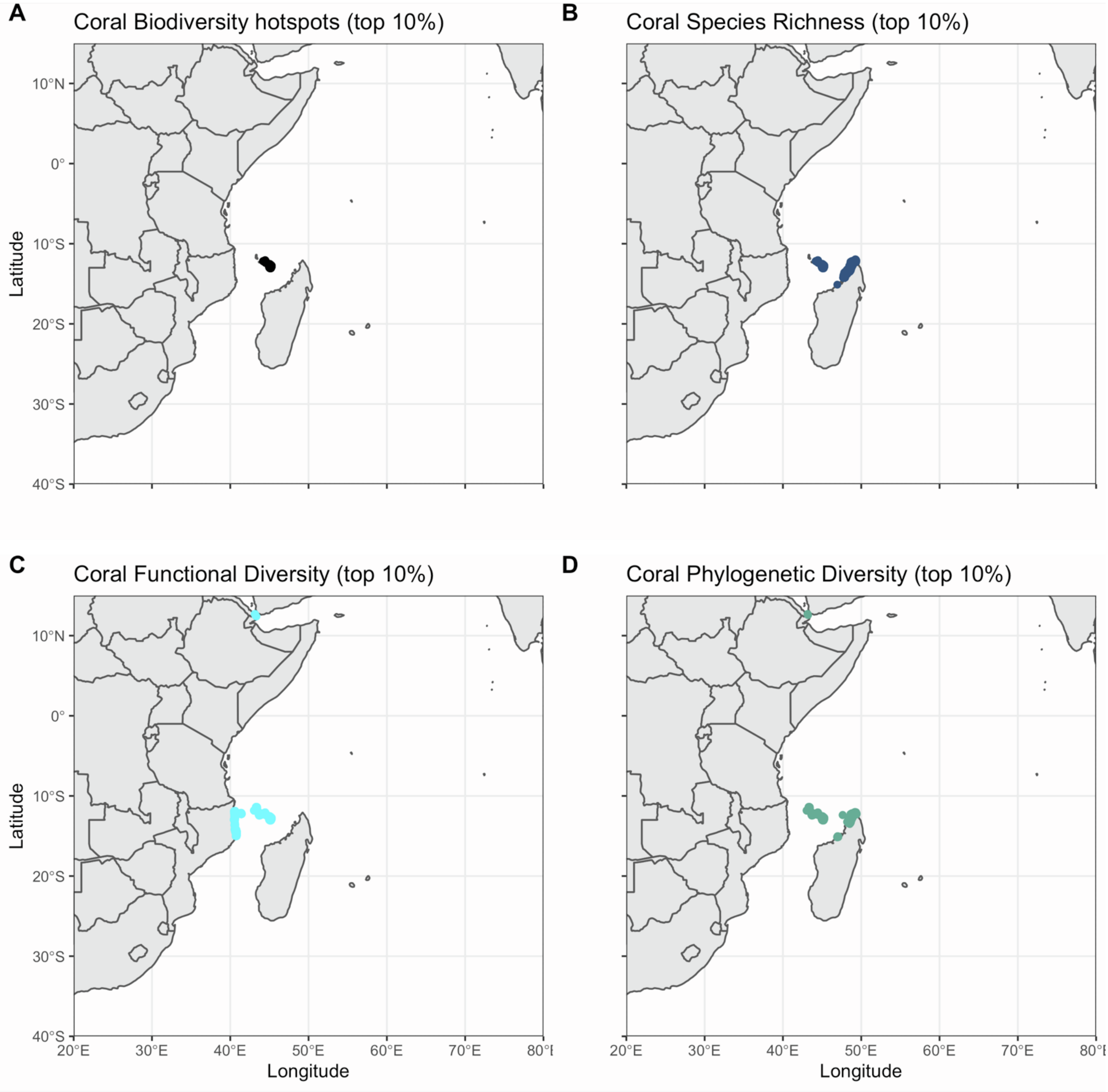


Figure S3. Biodiversity hotspots of Scleractinia coral species, related to Figure 2
Diversity hotspots of scleractinia coral of a) all overlapping biodiversity facets for the three biodiversity components, b) species richness, c) functional richness and d) phylogenetic diversity.

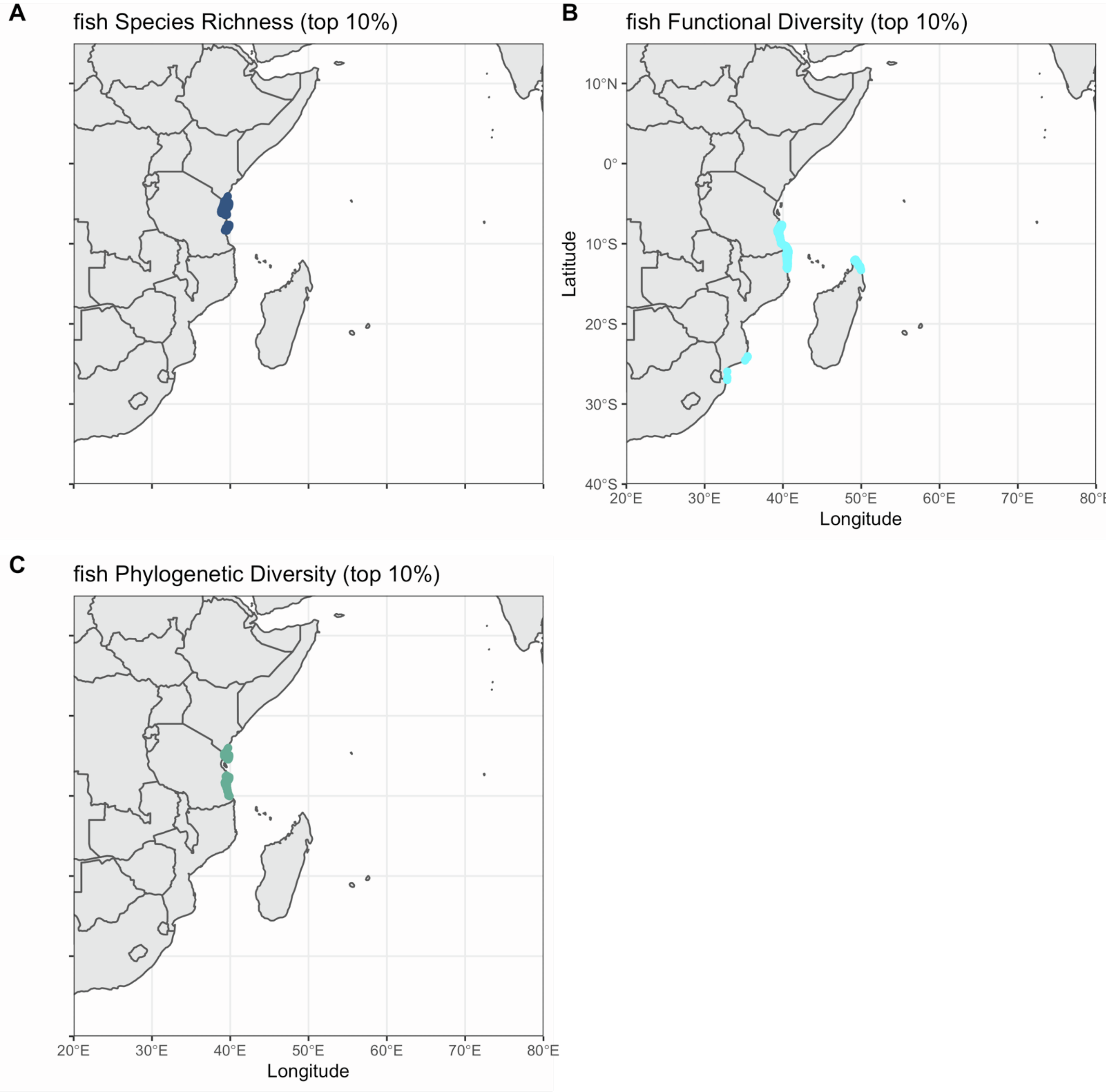


Figure S4. Biodiversity hotspots of coral reef fish, related to Figure 2
Diversity hotspots of coral reef fish of a) all overlapping biodiversity facets for the three biodiversity components, b) species richness, c) functional richness and d) phylogenetic diversity.

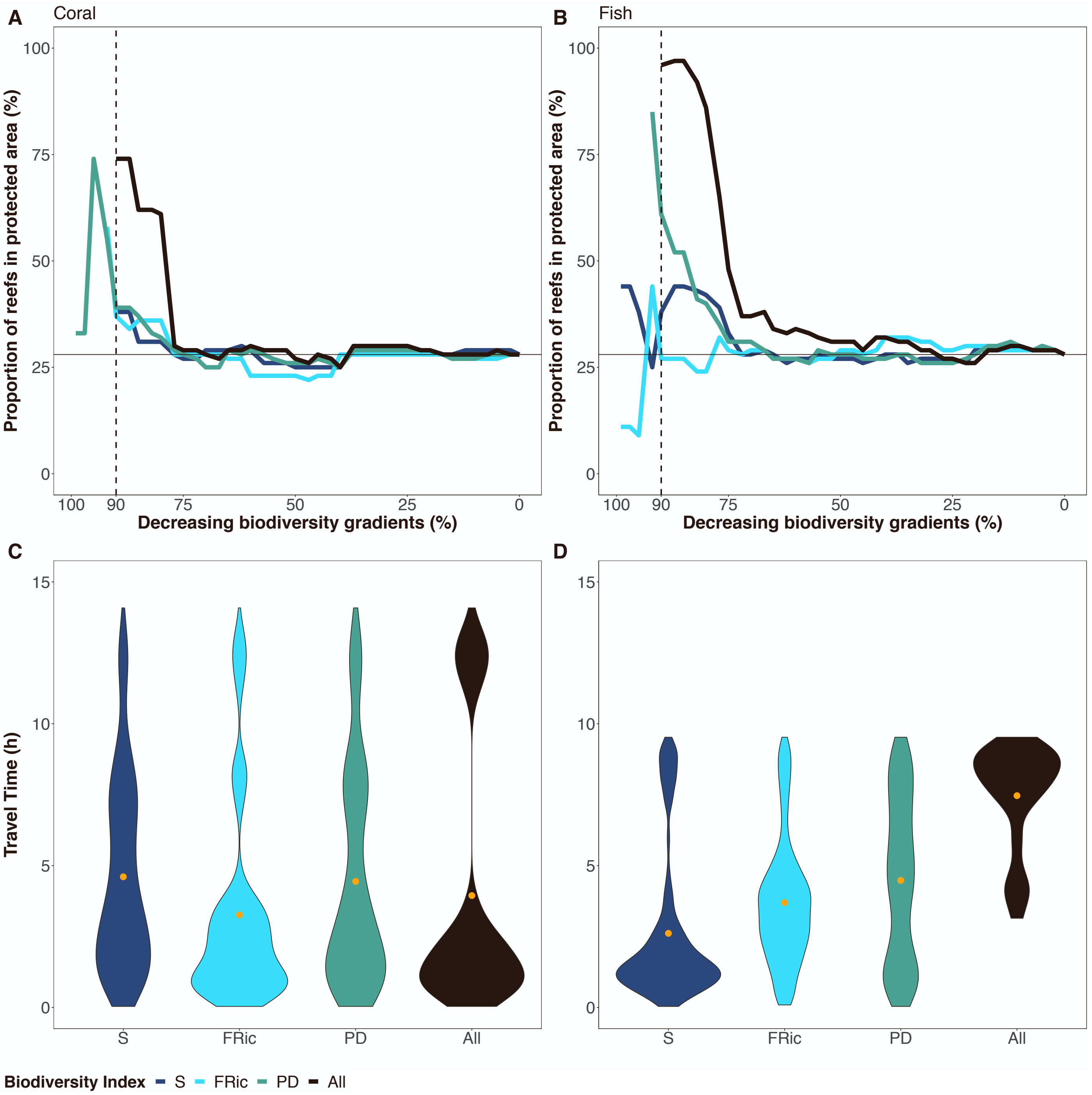


Figure S5. Proportional biodiversity components and accessibility of biodiversity hotspots for coral (left) and reef fish species (right) in Marine Protected Areas (MPAs) for each biodiversity component, related to Figure 2.

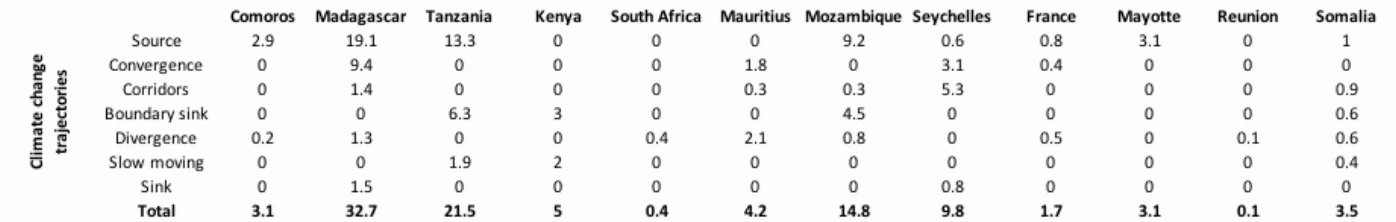
Cumulative proportion of total species richness (S), Functional Richness (FRic), phylogenetic diversity (PD) and all three components of multifaceted biodiversity together (All) for corals (a) and reef fish (b) along the decreasing biodiversity gradient. For each biodiversity component, we ranked the 4490 reefs from the most to the least diverse. Along with this decreasing diversity gradient (x-axis, expressed as a percentage), we calculated the cumulative percentage of protected reefs (y-axis). The black horizontal line indicates that the expected percentage of reefs in MPAs in this study is 28% (see Methods). If MPAs were equally located in each protected reefs, proportions of protected reefs located over and under the 28% reference value would reveal over-under-representation of reefs located in MPA. The violin plot (c,d) compare the biodiversity hotspots (top 10%) accessibility in travel time from the main market (in hour) for each biodiversity component and each taxa. The orange dot is the average travel time.

Supplemental Tables

Table S1. Lee spatial correlation between biodiversity components for scleractinian coral and fish, related to Figure 2. Bottom values (dark grey) are spatial correlations between scleractinian coral biodiversity components. Top values (light grey) are spatial correlations between fish biodiversity components, and central values are correlations between scleractinian coral and fish biodiversity components. Spatial biodiversity distribution for coral and fish are presented in Figure S1. S: species richness; FRic: functional richness; PD: phylogenetic diversity.

	S	FRic	PD
S	−0.3	0.7	0.9
FRic	0.6	−0.3	0.3
PD	0.9	0.7	−0.4

Table S2. Proportion of reef cells at 4x4km resolution in each country of the Nairobi convention, and in each climate change trajectories, related to Figure 1.



		Comoros	Madagascar	Tanzania	Kenya	South Africa	Mauritius	Mozambique	Seychelles	France	Mayotte	Reunion	Somalia
Climate change trajectories	Source	2.9	19.1	13.3	0	0	0	9.2	0.6	0.8	3.1	0	1
	Convergence	0	9.4	0	0	0	1.8	0	3.1	0.4	0	0	0
	Corridors	0	1.4	0	0	0	0.3	0.3	5.3	0	0	0	0.9
	Boundary sink	0	0	6.3	3	0	0	4.5	0	0	0	0	0.6
	Divergence	0.2	1.3	0	0	0.4	2.1	0.8	0	0.5	0	0.1	0.6
	Slow moving	0	0	1.9	2	0	0	0	0	0	0	0	0.4
	Sink	0	1.5	0	0	0	0	0	0.8	0	0	0	0
	Total	**3.1**	**32.7**	**21.5**	**5**	**0.4**	**4.2**	**14.8**	**9.8**	**1.7**	**3.1**	**0.1**	**3.5**

Table S3. Mean and standard deviation coral convexity[1] by growth form, related to Figure 3.

Growth form	Mean convexity	SD convexity
massive	0.86	0.002
submassive	0.88	0.11
digitate	0.69	0.009
arborescent	0.31	0.005
laminar	0.45	0.007
corymbose	0.37	0.003
tabular	0.55	0.01
encrusting	1	0
solitary	1	0

Table S4. Scenario of species removal in source and convergence climate change trajectories, related to Figure 3.

Sensitivity	# species	Source	Convergent
Competitive	134	1	4
Generalist	64	2	3
Weedy	12	3	2
Stress-tolerant	156	4	1

Table S5. True subsistence index[2] for each country, related to Figure 1.

EEZ	Territory	True Subsitance Index	True Subistence Category
Tanzania	Tanzania	0.89	HIGH
Madagascar	Madagascar	0.8	
Comoros	Comoro Islands	0.73	
Kenya	Kenya	0.58	MEDIUM
South Africa	South Africa	0.42	MEDIUM
Mauritius	Mauritius	0.12	LOW
Mozambique	Mozambique	0.14	LOW
Seychelles	Seychelles	0.17	LOW
France	Glorioso Islands	-	VERY lOW
	Ile Europa	-	
	Ile Tromelin	-	
	Juan de Nova Island	-	
	Mayotte	-	
	Reunion	-	
Somalia	Somalia	-	NA

Supplemental references

1. Zawada, K.J.A., Dornelas, M., and Madin, J.S. (2019). Quantifying coral morphology. Coral Reefs *38*, 1281–1292. 10.1007/s00338-019-01842-4.

2. Taylor, S.F.W., Roberts, M.J., Milligan, B., and Ncwadi, R. (2019). Measurement and implications of marine food security in the Western Indian Ocean: an impending crisis? Food Sec. *11*, 1395–1415. 10.1007/s12571-019-00971-6.