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CONTRIBUTED PAPER

Testing for concordance between predicted species richness, past prioritization, and marine protected area designations in the western Indian Ocean

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Abstract

Scientific advances in environmental data coverage and machine learning algorithms have improved the ability to make large-scale predictions where data are missing. These advances allowed us to develop a spatially resolved proxy for predicting numbers of tropical nearshore marine taxa. A diverse marine environmental spatial database was used to model numbers of taxa from ~1000 field sites, and the predictions were applied to all 7039 6.25-km^2 reef cells in 9 ecoregions and 11 nations of the western Indian Ocean. Our proxy for total numbers of taxa was based on the positive correlation ($r^2 = 0.24$) of numbers of taxa of hard corals and 5 highly diverse reef fish families. Environmental relationships indicated that the number of fish species was largely influenced by biomass, nearness to people, governance, connectivity, and productivity and that coral taxa were influenced mostly by physicochemical environmental variability. At spatial delineations of province, ecoregion, nation, and strength of spatial clustering, we compared areas of conservation priority based on our total species proxy with those identified in 3 previous priority-setting reports and with the protected area database. Our method identified 119 locations that fit 3 numbers of taxa (hard coral, fish, and their combination) and 4 spatial delineations (nation, ecoregion, province, and reef clustering) criteria. Previous publications on priority setting identified 91 priority locations of which 6 were identified by all reports. We identified 12 locations that fit our 12 criteria and corresponded with 3 previously identified locations, 65 that aligned

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with at least 1 past report, and 28 that were new locations. Only 34% of the 208 marine protected areas in this province overlapped with identified locations with high numbers of predicted taxa. Differences occurred because past priorities were frequently based on unquantified perceptions of remoteness and preselected priority taxa. Our environment–species proxy and modeling approach can be considered among other important criteria for making conservation decisions.

INTRODUCTION

Large-scale evaluations of biodiversity often fail to articulate fine-scale spatial variability due to limited, biased, and variable sampling relative to the numbers of taxa and the area of coverage (Molinos et al., 2016; Selig et al., 2014). Priority biodiversity areas may, therefore, often reflect biases in sampling efforts rather than local realized taxonomic diversity (Table 1). Therefore, identifying priority areas for biodiversity conservation can be influenced by limits set by sampling rather than actual patterns of biodiversity. For example, large-scale taxonomic diversity maps of corals often reflect the patchy and incomplete nature of species occurrence sampling (Kusumoto et al., 2020). Yet, these distributions of biodiversity and associated maps often play important roles in where conservation resources are distributed and the quantity of those resources (Beger et al., 2015). We devised an environment–number-of-taxa machine learning model (boosted regression tree [BRT]) to address sampling and species selectivity limitations that are common among poorly sampled locations. We also refined the spatial resolution relative to past efforts to assist in the current movement toward smaller scale governance and protected areas in poor tropical countries.

Past efforts to prioritize conservation spending have relied on coarse-scale data, a limited number of focal species, and underlying sampling biases. A common method to estimate numbers of taxa has been to first use species presence–absence information and a limited number of environmental variables to establish species' niches, distribution polygons, and cumulative overlapping species distributions (Table 1). Second, the cumulative frequency of species sampled in a spatial delineation is used to estimate numbers of taxa but often at coarse scales, such as an ecoregion or subregion. Finally, consultant and expert-based opinions are frequently used to guide conservation spending decisions.

In the western Indian Ocean (WIO), previous identification of priority conservation locations has frequently been influenced by the existence of large-bodied and space-requiring species (mammals, turtles, seabirds), remoteness, or nesting locations (EAME, 2004; Everett & van der Elst, 2015; Obura et al., 2012). These approaches do not address smaller scales and more complex taxa and environmental subtidal niche and associated distribution patterns. Past methods have frequently provided planners with coarse biodiversity distribution maps, which are often weakly predictive of local population metrics,

such as numbers of taxa (Kusumoto et al., 2020; Lee-Yaw et al., 2022). We believe modern biodiversity and conservation spending on priority mapping needs to better account for species' niches, or their required environment and habitats, the area required to support viable populations, and the scale of threats and conservation spending (Pilowsky et al., 2022). To begin this process, we evaluated the potential overlap between consultancy-based and protected area-designated locations with the first provincial environment–numbers of taxa model. The comparison allowed us to test the efficacy of past prioritization exercises and determine whether current marine protected areas (MPAs) overlap with locations with high numbers of taxa. Thus, we asked whether these coarse-scale or umbrella species approaches work to include the most taxa-diverse sites (Branton & Richardson, 2011).

The relevance of biodiversity conservation to ecosystem services, such as fisheries and shoreline protection, should benefit from a focus on more common, small-bodied, and ecosystem-service-providing species. Moreover, refining biodiversity predictions to smaller spatial scales can provide more actionable and economically appropriate goals (McClanahan, 2023). Therefore, we developed a proxy and model for numbers of subtidal tropical marine taxa, mapped this proxy at 6.25 km² in the WIO, and compared it with the above consultancy and protected area designations found in the World Database of Protected Areas (WDPA) (https://www.protectedplanet.net/en/thematic-areas/wdpa?tab=WDPA). We asked whether and how the outcomes of the environment–taxa predictions of the numbers of taxa would correspond with past recommendations and current MPA designations.

METHODS

We sought to improve understanding of finer spatial and taxonomic scales of variability in the tropical WIO. We developed a status quo empirical model to predict number of taxa observed in field data with their relationships to numerous environmental, demographic, and management variables. The environmental variables compiled for all 7039 ~6.25-km² cells were then used to predict numbers of taxa in the mapped coral reef cells (Figure 1). We then used the analyses to identify high-biodiversity locations at 4 spatial scales, namely, provincial, ecoregional, national, and spatial clustering scales. Spatial clus-

TABLE 1 Compilation of published studies that evaluated the spatial distribution of biodiversity in the western Indian Ocean region.

Taxonomic group	Geographic scope	Methods	Environmental influences	Human influences	Identified priority locations	Weaknesses	Citation
Coral	Global	Species occurrence, rarefaction, sampling completeness, variable scales	Temperature and depth	None	Western Indian Ocean including Red Sea, Coral Triangle, northern Australia	Low spatial replication or completeness; coarse spatial priority location resolution shown to affect patterns	Kusumoto et al., 2020
Coral	Indian Ocean	Species lists, rarefaction, and modeling	Temperature, reef area, geography	None	Western Australia, central Indian Ocean Islands, southern India, Mozambique Channel, East Africa, southern Red Sea, and Gulf of Aden	Low spatial replication or completeness; coarse spatial priority location resolution	Ateweberhan et al., 2018
Coral	Western and central Indian Ocean	Alpha and beta diversity	Temperature variability	None	Kenya–Tanzania border, Tanzania–Mozambique border, NW Madagascar–Mayotte	Low spatial replication or completeness; coarse spatial priority location resolution	Ateweberhan & McClanahan, 2016
Coral	Western and central Indian Ocean	Coral species presence/absence	None	None	Mozambique Channel	Low spatial replication or completeness; coarse spatial priority location resolution	Obura et al., 2012
Coral	Western Indian Ocean	Numbers of taxa and low environmental stress	Bleaching stress	None	Kenya–Tanzania border, Tanzania–Mozambique border, NW Madagascar	Low spatial replication or completeness; coarse spatial priority location resolution	McClanahan et al., 2011
Fish	Western Indian Ocean	Numbers of reef species and residuals from management and habitat	Benthic cover	Fisheries management	African coastline in Mozambique Channel	Low spatial replication or completeness; coarse spatial priority location resolution	McClanahan, 2015
Mammals	Global	Habitat for marine mammals to reduce vulnerability	Expert panel	Expert panel	Maldives, Seychelles, northern Kenya, western and northern Madagascar, Mascarene Islands	Assumptions of overlapping polygons and coarse resolution	Tetley et al., 2022
Marine turtles	Western Indian Ocean	Nesting locations of species	None	None	Rufiji–Mafia, northern Madagascar to southern Kenya, Samangaliso Wetlands	Assumptions of overlapping polygons and coarse resolution	Van de Geer et al., 2022
Sharks	Global	Top 5% of richness	None	None	Western Pacific, southern Mozambique, and South Africa	Low spatial replication or completeness; coarse spatial priority location resolution	Lucifora et al., 2011
Diverse set of marine species	Western and central Indian Ocean and Red Sea	Evaluated and threatened species	Expert panel	Human influences	Red Sea and southern India	Low spatial replication or completeness; coarse spatial priority location resolution	Bullock et al., 2021
Diverse set of marine species	Global	Species distributions and polygon overlaps	None	None	Coral Triangle	Assumptions of overlapping polygons and coarse resolution	Jenkins & van Houtan, 2016

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TABLE 1 (Continued)

Taxonomic group	Geographic scope	Methods	Environmental influences	Human influences	Identified priority locations	Weaknesses	Citation
Diverse set of marine species	Global	Richness, rarity, distribution polygon overlaps, and 10% area threshold	None	Low and high human populations	Coral Triangle, Madagascar	Assumptions of overlapping polygons and coarse resolution	Selig et al., 2014
Diverse set of marine species	Global	Richness and endemism	None	None	Coral Triangle, southern India, South Africa, Red Sea, Mascarene Islands	Low spatial replication or completeness; coarse spatial priority location resolution	Roberts et al., 2002
Mangroves	Global	Species distributions and polygon overlaps	None	None	Central Indo-West Pacific	Assumptions of overlapping polygons and coarse resolution	Spalding, 2010
Seagrass	Global	Species distributions and polygon overlaps	None	None	Tropical Indo-Pacific (East Africa, south Asia, and tropical Australia to the eastern Pacific)	Assumptions of overlapping polygons and coarse resolution	Short et al., 2007

Note: Terms applied in a Google Scholar search in 2022: *Africa, western Indian Ocean, species distribution, diversity, richness*, and so forth.

tering identified neighborhoods of dense numbers of taxa, referred to as *biodiversity hotspots*.

Several scientific advances have allowed finer scale predictions and maps of marine biodiversity (Kuhn & Johnson, 2013; Pilowsky et al., 2022). These include moderate resolution ($\sim$6.25 km^2) but large-scale mapping of coral reefs, global satellite coverage of environmental variables and proxies (<10-km steps), and predictive statistical algorithms. Specifically, we used a BRT algorithm, which can handle large amounts of data and many predictor variables and combines decisions from a sequence of base models to make predictions. Prior analyses indicated that BRT models are often effective at handling nonlinear relationships, account for missing values in covariates and interactions between predictors, and have high predictive performance (Elith et al., 2008). Combing the BRT algorithm with environment and taxa data should improve predictions of numbers of taxa compared with traditional rarefaction or cumulative taxa techniques (McClanahan et al., 2024).

Study region

A digital coral reef map established the distribution of coral reefs (https://data.unep-wcmc.org/datasets/1) (Table 1; Appendix S1) (Burke et al., 2011). Specifically, we used the WIO map and 9 ecoregions, namely, the Northern Monsoon Current Coast, East African Coral Coast, Seychelles, Cargados Carajos and Tromelin Island, Mascarene Islands, Southeast Madagascar, Western and Northern Madagascar, Bight of Sofala and Swamp Coast, and Delagoa. The WIO faunal province also includes 11 national governance jurisdictions. Madagascar, Tanzania, and Mozambique combined contained 43% of the 7039 total reef cells for the province (Appendix S2).

Environmental data sources

We compiled 70 spatially complete environmental data layers derived from satellite and shipboard measurements (Appendix S3). Oceanographic data included potential ecological drivers, such as photosynthetic active radiation (PAR), pH, calcite and dissolved oxygen concentrations, diffusion attenuation, salinity, net primary productivity, chlorophyll-a variables, phytoplankton carbon, and wave height among other derivatives (Tyberghein et al., 2012; Yeager et al., 2017). We calculated several long-term sea surface temperature (SST) or thermal stress metrics, including SST mean, median, range, standard deviation (SD), skewness, kurtosis, and rate of rise taken from National Ocean and Atmospheric Administration CoralTemp 5-km resolution daily SST observations database collected from 1985 to 2020 (https://coralreefwatch.noaa.gov/product/5km/index_5km_sst.php) (Liu et al., 2014). Cumulative degree-heating weeks (DHW) was calculated from the same data set as the sum of the maximum annual DHW for all years from 1985 to 2020. We included several composite thermal and water quality stress metrics, such as the global stress model and composite nutrient concentrations (Andrello et al., 2022; Maina et al.,
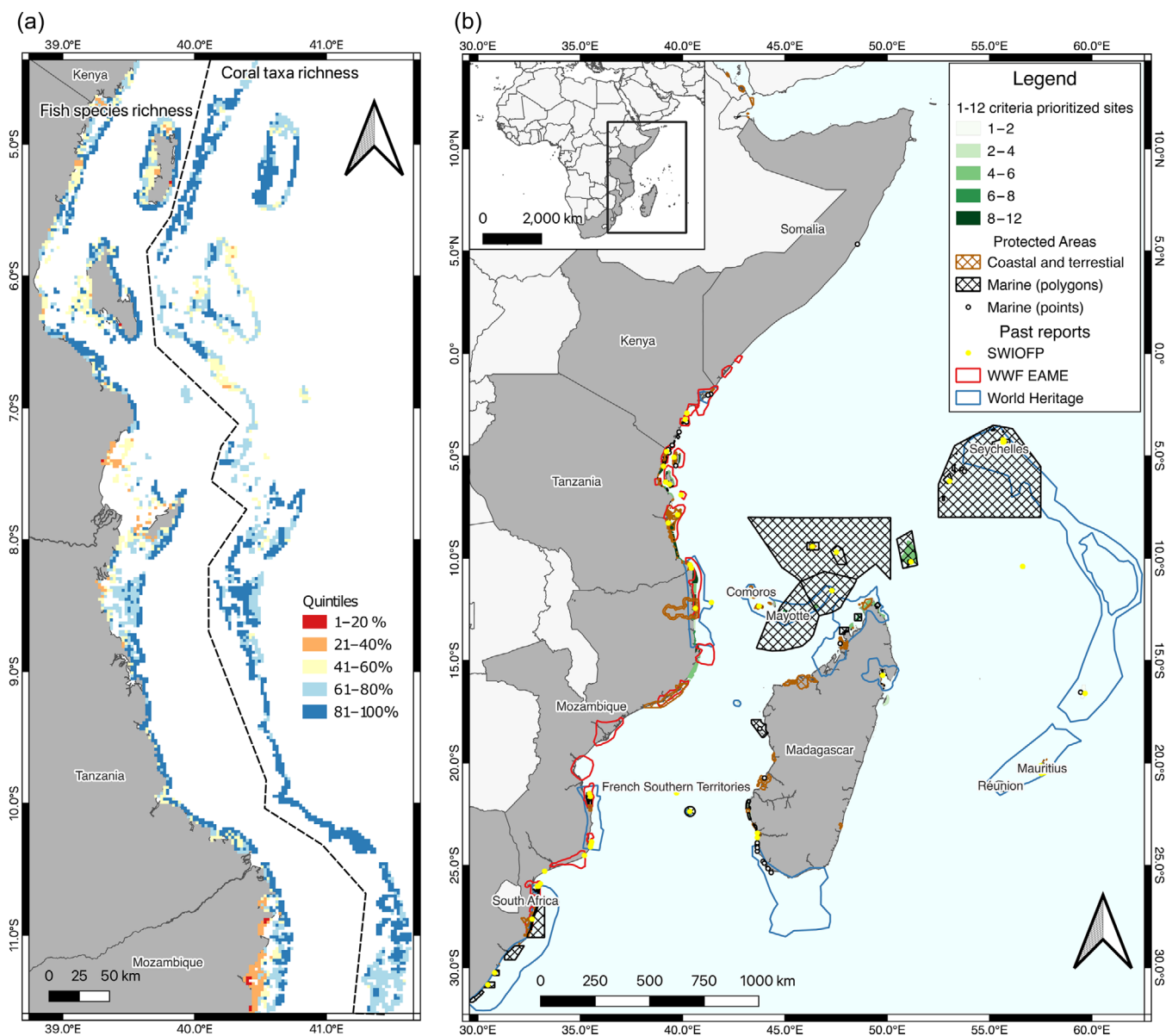
FIGURE 1 (a) Locations of sites with a large number of fish and coral taxa from southern Kenya to northern Mozambique (individual reef cells and their number of taxa quintiles shown) and (b) provincial study area with the 119 areas of high conservation priority identified based on the 12-point environment–number of taxa predictive models, 3 past recommendations of priority location reports (SWIOFP, Southwest Indian Ocean Fisheries Programme; protected areas taken from the World Bank World Database of Protected Areas). The model of the relationship between the environment and the number of taxa scales locations by number of criteria met for the 3 taxa groupings and 4 spatial delineations (Table 3). More highly resolved maps at the country level are provided in Appendix S7.

2011). Finally, we used estimates of larval dynamics, including measures of connectivity, net flow, indegree, outdegree, and retention, for each reef cell (Fontoura et al., 2022).

The geographic variables we evaluated included ecoregion, nation, wilderness (>4 h travel time from a human population), travel distance to people, shore, and ports, and market gravity or the number of people living on the shore or in cities as divided by the square of the distance or travel time (Maire et al., 2016). We assigned cells to 4 fisheries management categories, including unrestricted fishing (42% of cells), restricted fishing (42%), low-compliance closures (14%), and high-compliance closures (2%). We based management classifications on infor-

mation in published literature, the experience of the observers, and discussions with knowledgeable observers (McClanahan et al., 2015).

Coral data collection

We sampled corals in haphazardly located quadrats while snorkeling or scuba diving and maintaining a near-constant recorded depth (Appendix S4). Quadrats were visually estimated or measured as ~2 m², and all corals >5 cm in ~15–20 replicates were identified to taxa and counted (McClanahan,

Ateweberhan, et al., 2007). Thus, we estimated the total number of taxa in ~40 m^2. We identified taxa to the genus, but we classified *Porites* as massive, branching, or *Porites rus* and *Galaxea* as either *G. astreata* or *G. fascicularis*. These growth forms represent different life histories and ecologies important to distinguish in this province. We sampled 1001 well-distributed sites and recorded 67 taxa (Appendix S4). Sixteen observers contributed to the database, but 3 observers sampled 939 of the 1001 sites and had nonsignificant differences between them. We also recorded the habitat type of sites as reef edge, reef crest, reef flat, or reef lagoon.

Fish data collection

We counted fish in designated areas with either repeated circular methods (154 m^2) or belt transects of 100, 250, and 500 m^2 according to the methods selected by the investigators. Each observer's methods are described in their foundational papers (Chabanet et al., 2016; Friedlander et al., 2012; Graham et al., 2020; McClanahan, 1994). Three of us were single individual observers (A.F., N.G., and T.M.), whereas 2 were small groups that shared the same methods and leaders (H.B. and P.C.). We pooled or averaged adjacent replicates such that the final units were number of species per ~ 250, 300, 462, and 500 m^2. We evaluated the observer method and sampling area effects by including them in the BRT solutions and setting them to a constant via partial effects methods when making modeling predictions (see below). We extracted the number of species for the 5 selected families known to be good proxies for total fish diversity (Acanthuridae, Chaetodontidae, Labridae: Scarinae, Pomacanthidae, and Pomacentridae) (Allen & Werner, 2002). We estimated total biomass as the summed weights of the individual species or families based on length estimates and known length–weight relationships. We sampled 313 species in the 5 families among 1201 transect sites in the WIO province. Coral and fish transect sampling were largely done in the same locations, and differences in total sample sizes occurred when one of the 2 censuses were not completed.

Variable selection

The total number of species in all reef cells was based on the relationship between the environment and the number of taxa (environment–number-of-taxa model) based on separate coral and fish field data sources, units, and models (Appendices S3 & S4). Therefore, the following procedures were developed to find the most predictive environmental variables for each taxon. First, we used standard variable choice procedures and evaluated Spearman rank collinearity between predictor variables (Appendix S5). Following recommendations for reducing collinearity, variables that had a correlation coefficient ≥0.7 were further examined for potential elimination (Dormann et al., 2013). Thereafter, multicollinearity was investigated using variance inflation factors (VIFs), with a VIF acceptance cutoff of <5. If after these 2 processes, a potentially eliminated

variable had prior good evidence from the scientific literature of being causative, it was not eliminated but used to create an alternative model, referred to as models 1 and 2, as advised by Araujo and New (2007). Common SST metrics are a good example of the problem of strong correlations and the potential problems of eliminating variables that potentially have important causative relationships. Temperature variation metrics are measures of chronic and acute stress (i.e., SD, skewness, and kurtosis), which are highly but not linearly correlated with mean temperature, and frequentlycorrelated with biodiversity (Chaudhary et al., 2021; McClanahan, 2020a). In the final predictive mapping, we used the averages of the 2 models and weighted the predictions by the R^2 of the individual models. Decisions and the variables included in the 2 models are in Appendix S3. By this process, we reduced the number of potential environmental variables ($n = 70$) to 35 for corals and 37 for fish to be included in the next variable selection and strength step, or the BRT model building.

Modeling the number of taxa predictions

We used the BRT models to look for associations between the environmental data and the empirical number of fish and coral taxa field data. Users are required to input 5 hyperparameters that control its performance and complexity. These include number of trees, minimum number of observations in tree node, learning rate (determines the contribution of each tree to the expanding model), tree complexity (allows for variable interactions), and bagging fraction (i.e., random proportion of training data used). We evaluated the predictive performance of 400 possible models with varying combinations of the hyperparameters: minimum number of observations in node (5, 8, 10, 15), learning rate (0.001, 0.01, 0.1, 0.3), tree complexity (range 1–5 by 1), and bag fraction (0.5–0.75 by 0.05). The hyperparameter combination that produced the smallest Poisson deviance and produced >1000 trees was used to fit subsequent numbers of fish species and coral taxa BRTs (i.e., number of trees = 5000, learning rate = 0.01, tree complexity = 3, minimum observations in node = 8, bag fraction = 0.5). A 10-fold cross-validation was conducted to determine the optimal number of trees needed to minimize deviance and maximize predictive performance.

Model performance

We evaluated model performances by splitting the data into a 70% training set and a 30% testing set to calculate the R^2 and root mean square error (RMSE) for training and testing data sources (Kuhn & Johnson, 2013). We further validated the models with the full data set and applied 5 times repeated 10-fold cross-validation to calculate performance metrics. The 10-fold cross-validation created 10 subsets of the data and randomly selected 90% of each subset for model training and 10% for testing. In repeated 10-fold cross-validation, the process was repeated 5 times, thus model performance was evaluated based

on 50 random subsets of the data. We then calculated performance metrics for each subset and averaged them to give a single metric (Kuhn & Johnson, 2013). The BRT models had similar R^2 and RMSE between training and testing with a 70 to 30 split and the repeated 10-fold cross-validation procedures (Appendix S6).

The influence of the number of predictors used in the model was also investigated through recursive feature elimination (analogous to backward selection) of the final models and a 10-fold cross-validation (Kuhn & Johnson, 2013; Miller, 2002). For each model, we plotted the RMSE profile, which showed the number of predictors with the minimum RMSE within 1 SE of the minimum RMSE (Breiman et al., 1984). We retained models with the full set of preselected predictors with collinear variables removed because BRT models have embedded methods of variable selection that minimize the influence of noninformative predictors (Elith et al., 2008). The BRT model fitting and performance evaluation used the caret 6.0-93 and gbm package 2.1.8 in the *R* statistical programming language (Greenwell et al., 2020; Kuhn, 2015; R Core Team, 2021). We further evaluated model spatial autocorrelation in the raw numbers of fish and coral taxa and the BRT model residuals via a Moran's *I* test (Moran, 1950) with the ape package in R (Paradis & Schliep, 2019). The raw numbers of taxa values for both fish and corals showed evidence of positive spatial autocorrelation, which was not detected in the model residuals. We used pdp package 0.8.1 to create partial dependence plots to present associational relationships between each strong predictor and numbers of taxa (Greenwell, 2017).

The model above was then used to model numbers of taxa in mapped cells without empirical data. This procedure required making comparisons for which some key local variables were held constant, namely, depth, observer, observer methods, and fish biomass. Preferably, these held-constant variables should represent a maximum value or a point above a saturation response, such as the most efficient or experienced observer and the depth and biomass containing the most taxa. Holding them constant allowed direct comparisons of the environmental factors that could influence the number of taxa in the 6.25-km^2 cells. These would be variation in water temperature, light, and chemical properties of the water among other factors. Thus, the prediction is the expected number of taxa under the influence of environmental factors in the absence of confounding local factors in the data, such as depth and fishing intensity. Therefore, we examined the taxa relationships for peak or saturation points with biomass and depth. Numbers of fish taxa associations with biomass saturated at ∼500 kg/ha and 10-m depth (McClanahan, 2022). Numbers of coral taxa also peaked or saturated at 10 m. Therefore, for the partial effect predictions for each cell, we held fish biomass constant at 600 kg/ha and depth at 10 m. To minimize the observer and method effect, we chose the transect area with the most replicates held constant, which was 500 m^2, and the observer with the most observations per country. One observer did most of the fish sampling in most countries (*n* = 613), and 2 observers with nonsignificant differences did most of the coral sampling (*n* = 771). Therefore, we based most predictions in most countries on these 2 observers'

partial effects except in the smaller samples of Reunion and South Africa, where these 2 observers did not collect data.

Mapping biodiversity hotspots

We used the BRT model predictions to model numbers of taxa in all 7039 6.25-km^2 reef cells. The resultant numbers of taxa predictions for both models used averages weighted by their R^2 values to create an ensemble prediction for numbers of fish species and coral taxa in each reef cell. We mapped the ensemble predictions of the full WIO provincial data in quintiles and identified cells with the top 20% of values (80–100% quintile) for fish and corals, which we considered biodiversity hotspots. We combined numbers of fish species and coral taxa ensemble predictions by calculating their z scores and averaging each reef cell's value to create a biodiversity proxy. Additionally, we mapped the combined biodiversity proxy in quintiles to identify the top 20% positive z scores. The above procedure was conducted at the WIO provincial-, ecoregional-, and national-scale delineations.

Further, we conducted an optimized hotspot analysis in ArcGIS 10.3 on the ensemble numbers of fish species and coral taxa predictions at the scale of the WIO province (ESRI, 2022). We used the Getis–Ord Gi* statistic for hotspot analysis to identify the location of statistically significant spatial clusters of high (hotspots) and low values (coldspots) in a defined neighborhood distance (Ord & Getis, 1995). The Gi* statistic for each reef cell is essentially a z score, and statistical significance is established by comparing the local sum of the reef cell and its defined neighbors proportionally with the sum of all reef cells. If the difference of the local sum to the expected local sum is too large to be the result of random chance, then a statistically significant z score is established (ESRI, 2022). A high positive z score with a between-cell neighborhood with $p < 0.10$ indicated a hotspot (spatial clustering of high values), whereas a low negative z score and low p indicated a coldspot (spatial clustering of low values). A score near zero indicated a lack of spatial clustering. The resulting p values were corrected for false discovery rates that can arise from spatial dependency and multiple testing (Ord & Getis, 2001). We used the optimized hotspot analysis and relied on several strategies to determine the optimum parameter settings for the analysis based on the data provided, such as the neighborhood distance for clustering. The ensemble predictions were evaluated for peak incremental spatial autocorrelation, and no peaks were found in numbers of fish and coral taxa predictions. Therefore, the average distance to 30 nearest neighbors was used to establish the neighborhood distance for the analysis (∼25.5 km).

Prioritizing locations

We mapped the locations of past WIO provincial MPA prioritization reports and WDPA borders to compare them with our locations identified for their high numbers of taxa. A location was defined here as a cluster of reef cells between 2 human

settlements or geographic points on an internet (Google) map. We used settlement names that were recognizable to nationals and generally evenly spaced on Google maps. Our site selection criteria were based on the 3 taxa criteria, which were the individual cells' number of fish and coral taxa and their combined biodiversity proxy (z scores). Locations were delineated to determine the location of the top 20% number of taxa locations at 4 scales, which included the province, ecoregion, and nation and the reef clustering criteria. Thus, combining the 3 taxa and 4 spatial delineation scales produced a maximum ranking of 12, which allowed all locations to be ranked from 0 to 12.

We then compared our rankings with locations identified in 3 past prioritization plans undertaken in the WIO province. The East African Marine Ecoregion, World Heritage Report for the WIO Province, and the Southwest Indian Ocean Fisheries Programme (SWIOFP) reports identified 12, 14, and 59 priority locations, respectively. We either split or combined them to make their sizes directly comparable with the same spatial scale or resolution of our locations. We then compared the matches in spatial overlap between our locations with high number of species and the 3 reports delineated at the above 4 spatial scales. The number of coastal and marine protected areas in the province and each nation were determined from WDPA database and evaluated for overlap with our final 119 selections that fit at least 1 of the 12 number of taxa and spatial criteria.

RESULTS

Empirical relationships

Numbers of coral and fish taxa were moderately and positively correlated for the empirical site and the modeled data ($r^2 = 0.24$ and $r^2 = 0.25$, respectively) (Figure 2). Differences in the intercept and slope of the empirical (slope = 0.74) and modeled data (slope = 0.65) indicated variability between the empirical and modeled data. Modeled numbers of fishes started with more but accumulated taxa somewhat slower than the coral taxa for the modeled relative to field sites.

Empirical BRT models

The BRT evaluations indicated the top predictive variables for the number of fish species were biomass, travel time to nearest population, indegree connectivity, median SST, observer and method, larval retention, country, and ocean primary productivity (Figure 3a). Both model options picked biomass as the top variable, explaining 27% of the variance for model 1 and 35% in model 2. An example of differences in the ensemble model variable selection methods can be seen with the outcomes of the highly correlated variables of travel time to nearest population and gravity to nearest population. We used travel time in model 1, and it had the second highest influence of 14.4%, whereas gravity was used in model 2 and had a lesser influence of 3.8%. In model 1, median SST, net primary productivity, DHW, and SST kurtosis were more modest

predictive variables, with 3–5% relative influences. Median SST was strongly correlated with SST skewness, which we included in model 2, but it was weaker and not among the top 12 variables. Larval indegree connectivity and larval retention were positive and saturating for numbers of taxa in both models; relative importance was 3–5.5%. Observer and country effects were included in both models and had similar relative influences that ranged from 3.7% to 5.3% for both models. The countries of Tanzania, Mozambique, and the France—Eparses Islands were legal jurisdictions with the highest numbers of species. Number of fish species increased with biomass, travel times to people, incoming and retention of larvae, and excess heat, but the best-fit relationships indicated saturating effects. Responses were more unimodal for median SST, net primary productivity, light attenuation, and SST kurtosis.

Evaluations of numbers of coral taxa indicated the importance of observers and methods with a relative importance of 15% in both models (Figure 3b). Sixteen observers were compared, whereas 77% of the sampling was done by 2 observers with small nonsignificant differences. Thereafter, depth, SST skewness, excess heat, the climate stress model, and SST kurtosis all had relative influences of >5%. The SST skewness was retained in model 2 and was stronger than the SST median in model 1. Cumulative excess heat and the climate stress model were negatively correlated and both were the fourth- and sixth-ranked variables, respectively. When evaluated separately, they had relative influences of 6–7%. Numbers of coral taxa peaked at 20–30 DHW in model 1 and increased nearly linearly with climate stress in model 2. Current velocity and the composite nutrient delivery index were positively correlated, and velocity was retained in model 2 and was stronger than the nutrient metric used in model 1. Numbers of coral taxa were high for low current velocity and declined as wave energy, salinity, and dissolved oxygen increased. In model 2, the rate of rise in SST was more sinusoidal for both models; it was stable up to 0.015°C before it declined. Country as a variable displayed differences between models, notably for Mozambique, Seychelles, France—Mayotte, and Mauritius. The highest numbers of taxa were predicted for Tanzania and declined south to South Africa, Reunion, Madagascar, France—Eparses Islands, Kenya, Comoros, Mozambique, Mauritius, and Seychelles. Thus, the number of coral taxa increased with depth, centralized SSTs, and the climate stress model, which is a multivariate metric that reflects thermal radiation (light, UV, temperature, etc.). Numbers of coral taxa declined as warm water skewness, excess heat, waves, current velocity, dissolved oxygen, and salinity increased.

Richness and hotspot locations

A cell-based map of the richest taxa region in Tanzania and surroundings indicated high numbers of taxa in the top 2 quintiles in most reefs of East African Coral Coast ecoregion (Figure 1a). Comparing our identified locations at all 4 scales with past reports showed the large areas and wide coverage of some past prioritization recommendations, differences in the spatial reso-

(a)

$y = 20.6 + 0.743\,x,\ r^2 = 0.24,\ p < 0.001,\ n = 254$

(b)

$y = 21.8 + 0.65\,x,\ r^2 = 0.25,\ p < 0.001,\ n = 7039$
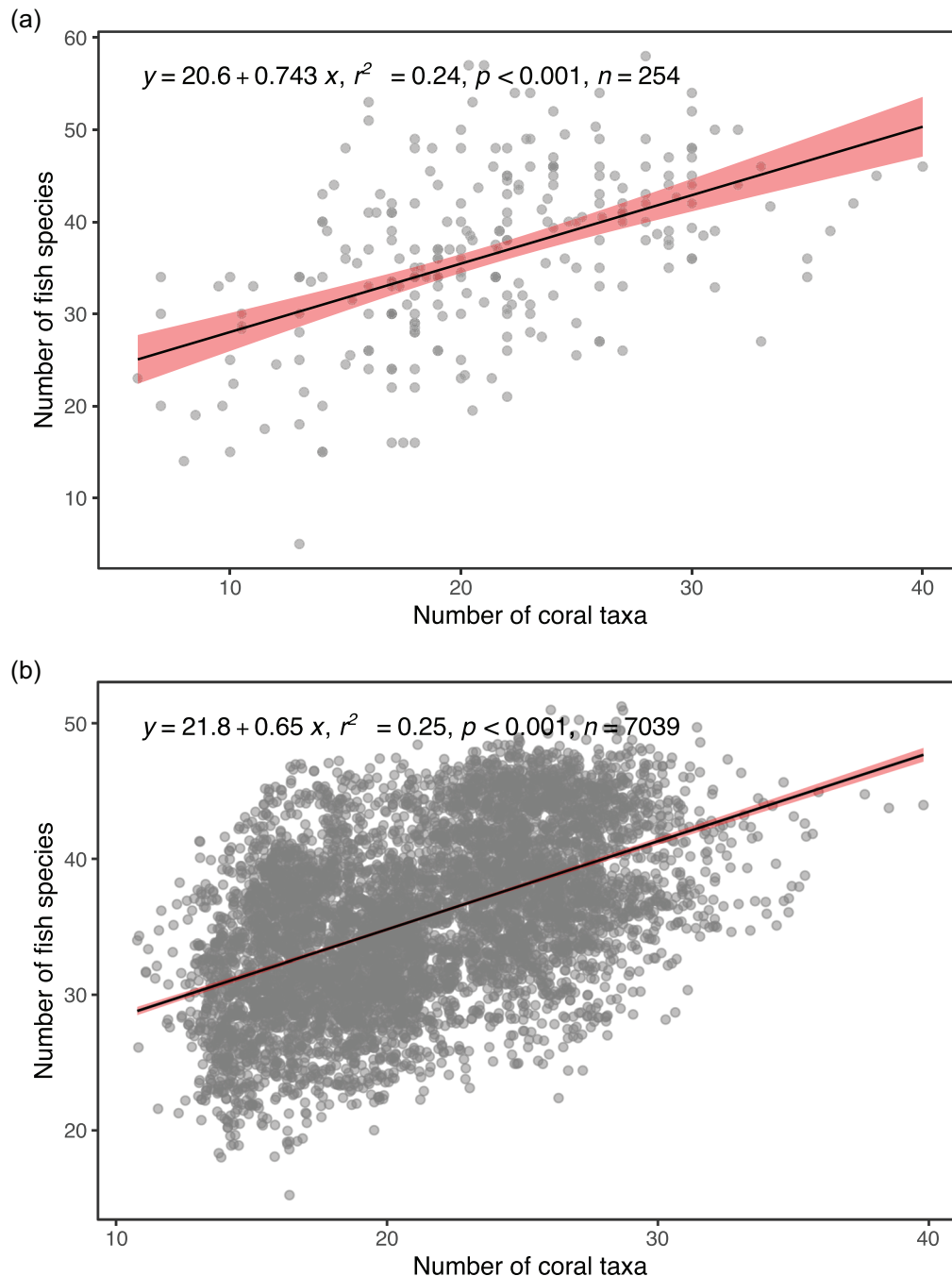
FIGURE 2 Relationship between coral and fish taxa for (a) empirical and (b) modeled data (specific cells and best-fit lines with 95% confidence intervals shown).

lution of the priority location predictions, and, when comparing studies, often differences in identified locations (Figure 1b). Finer scale maps of numbers of taxa z scores at the provincial, ecoregional, and national and clustering delineations are in Appendix S7a. The provincial delineation identified the African continent from northern Mozambique to southern Kenya. However, Kenya had a few top quintile taxa reefs further north in Watamu Marine National Park. Some exceptions were among some nearshore and high-water retention area, such as

the bay in northern Pemba, leeward of Unguja (Zanzibar), the nearshore islands north and south of Dar es Salaam, and the northern Bight of Sofala in northern Mozambique (Figure 1a; Appendix S8). Other top quintile sites extended from northern Mozambique offshore to the Lazarus Bank, Comoros, and Mayotte islands. The islands off northwestern Madagascar, such as Mitsio Island and north to Diego Suarez, were largely in the second highest quintile. The farthest off-continent islands of Seychelles in the north and Reunion toward the south and much
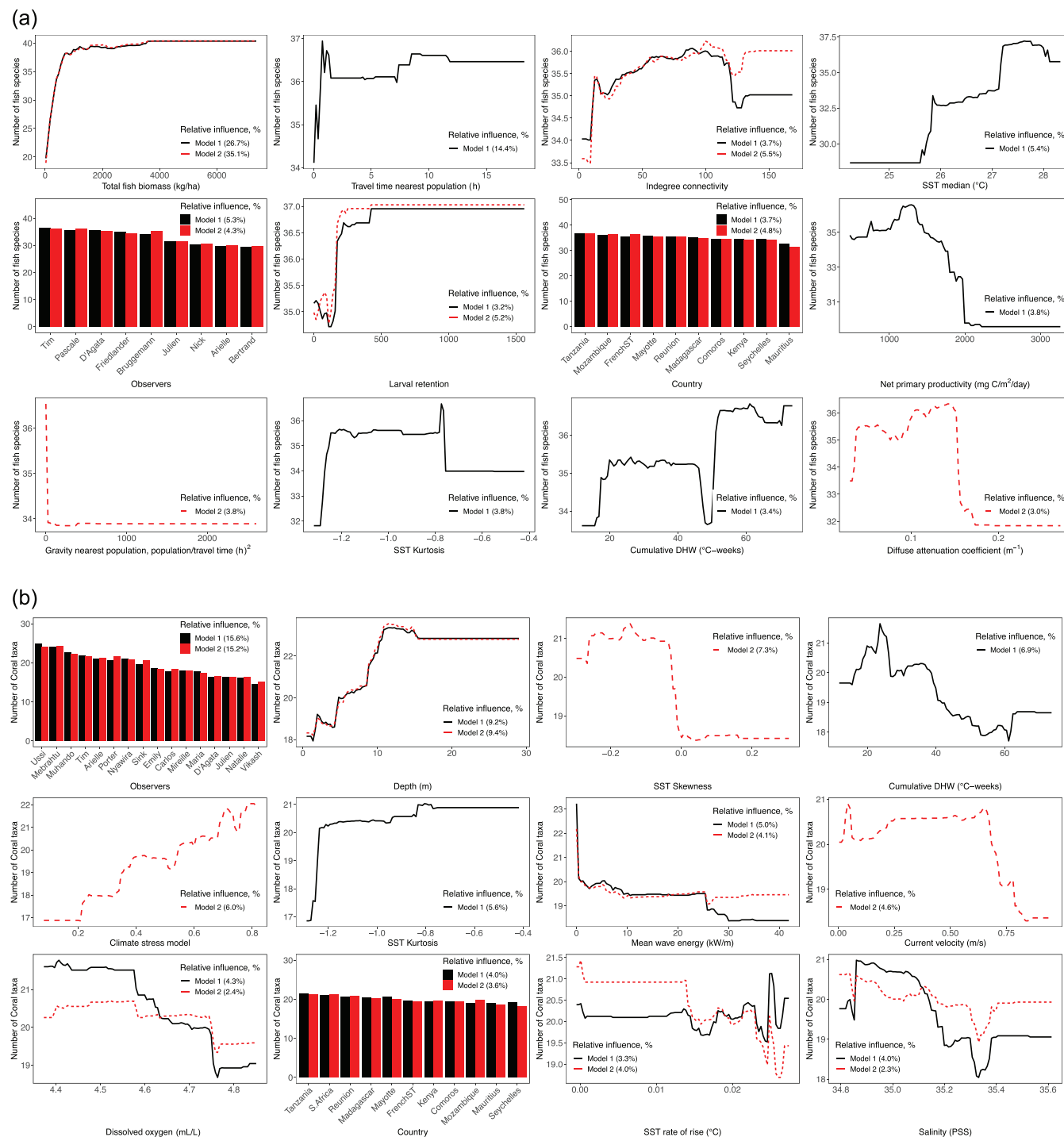
FIGURE 3 Twelve environmental variables used in the 2 combined models associated with the number of (a) fishes and (b) coral taxa based on the boosted regression tree partial plots. Shown are the relative importance for both models (graphs with 2 lines, variable used in both models; graphs with one line, variable eliminated due to high correlation with a variable in another model and therefore used in only one model).

of southern Madagascar were among the lowest number of taxa sites.

When reef cells were delineated and subsequently scaled at the ecoregional level, a shift in scaling reflected the cells position relative to the ecoregional maximum (Appendix S7b). Pooling and evaluating sites at the ecoregional scale indicated the dom-

inance of positive z score deviance in the East African Coral Coast (Table 2). Only the Bight of Sofala had positive deviance; peak numbers of taxa occurred in the north on the boundary with the Coral Coast and in some offshore reefs at the southern chain of the Primeiras Islands. The northern Monsoon Coast was the third-ranked region. It had patchy numbers of taxa

TABLE 2 Model predictions for the mean (+SE: standard error) numbers of fish species and coral taxa by province, ecoregion, and nation and in hotspots (high densities of high-diversity reefs) and coldspots (low biodiversity and reef clustering).

	Number of fish species (SE)	Number of coral taxa (SE)	Mean z score (SE)	Number of mapped reef cells*
Province				
Western Indian Ocean	35.6 (6.1)	21.0 (4.7)	0.0 (0.9)	7039
Ecoregion				
East African Coral Coast	39.9 (4.5)	25.3 (2.9)	0.8 (0.5)	2743
Bight of Sofala–Swamp Coast	38.7 (3.4)	20.5 (1.5)	0.2 (0.4)	113
Northern Monsoon Current Coast	32.9 (3.0)	20.5 (1.4)	−0.3 (0.3)	130
Seychelles	31.7 (3.1)	20.4 (1.2)	−0.4 (0.3)	701
Western and Northern Madagascar	33.4 (5.6)	17.9 (3.7)	−0.5 (0.6)	2854
Delagoa	33.4 (3.7)	17.2 (1.4)	−0.6 (0.3)	96
Cargados Carajos–Tromelin Island	30.2 (3.6)	17.2 (2.1)	−0.9 (0.5)	141
Southeast Madagascar	31.6 (4.9)	14.7 (1.1)	−1.0 (0.5)	65
Mascarene Islands	26.9 (3.1)	16.3 (2.2)	−1.2 (0.4)	196
Country				
Tanzania	40.4 (4.3)	25.8 (2.9)	0.9 (0.5)	1524
Mozambique	39.3 (4.9)	24.4 (3.3)	0.7 (0.6)	1180
Comoros	37.6 (4)	23.4 (1.7)	0.4 (0.4)	238
Mayotte	33.2 (4.6)	25.5 (2.0)	0.2 (0.3)	269
Kenya	35.6 (3.9)	21.3 (2.4)	0.04 (0.5)	372
French Eparses Islands	38.6 (4.7)	14.8 (1.8)	−0.4 (0.5)	138
Seychelles	31.7 (3.1)	20.4 (1.2)	−0.4 (0.3)	701
South Africa	28.8 (2.3)	20.2 (0.7)	−0.6 (0.1)	6
Madagascar	32.6 (5.5)	16.5 (1.9)	−0.7 (0.5)	2282
Mauritius	28.2 (3.6)	16.8 (2.2)	−1.1 (0.4)	304
Reunion	27.6 (3.1)	16.4 (1.9)	−1.1 (0.4)	25
Hot- and coldspots				
Hotspot 99% confidence	40.5 (4.3)	25.9 (2.5)	0.9 (0.5)	2440
Hotspot 95% confidence	38.3 (3.3)	22.9 (1.3)	0.5 (0.3)	336
Hotspot 90% confidence	38.0 (3.1)	22.4 (1.5)	0.2 (0.4)	100
Average hotspots	40.3 (4.3)	25.7 (2.6)	0.8 (0.5)	2876
Not significant	35.7 (3.4)	20.9 (1.4)	0.02 (0.4)	892
Coldspot 90% confidence	33.3 (3.2)	19.5 (1.1)	−0.3 (0.3)	193
Coldspot 95% confidence	32.9 (3.6)	19 (1.5)	−0.5 (0.3)	1484
Coldspot 99% confidence	29.9 (4.1)	16.7 (2)	−1.0 (0.5)	1594
Average cold spots	30.4 (4.2)	16.9 (2.1)	−0.7 (0.5)	3271

*For each spatial delineation.

of which the highest reef cells were contained in the northern Kiunga Marine Reserve in Kenya just south of the Somali border. Modeled numbers of taxa were patchy in the Seychelles, but most of the higher numbers of taxa were in the southern part of this ecoregion stretching from Aldabra in the southeast to Farquhar islands in the southwest. Some high numbers of taxa locations were, however, predicted in the more centrally located Les Amirantes group. The Western and Northern Madagascar ecoregion had a high spread of numbers of taxa that generally declined from west to east and north to south. There were some notable exceptions, such as high numbers of taxa in reef cells in the Ambohitrabo region of the southwest. Reef cells and numbers of taxa in the Delagoa ecoregion were patchily distributed, but some high numbers of taxa were predicted on the border between South Africa and Mozambique. The offshore islands of the Cargados Carajos and Tromelin Island and Mascarene ecoregions were among the lowest numbers of taxa sites. There was, however, some spatial structure with Mauritius,

which had 3 hotspots, of which 2 were in northern windward and leeward locations and one in the southeast of the island. The Agalega Islands in the north of the Cargados Carajos ecoregion were predicted to have more taxa than Saint Brandon in the southeast.

Sites delineated at the national level indicated dominance of high numbers of taxa locations in the Coral Coast in Tanzania, Mozambique, Comoros, and Mayotte (Appendix S7c). Kenya and France—Eparses Islands were more transitional and intermediate in numbers of taxa and were followed in declining order by the Seychelles, South Africa, Madagascar, Mauritius, and Reunion. National-scale identification indicated some important transnational locations, such as the Kenya–Tanzania and Tanzania–Mozambique, and to a lesser extent the Mozambique–South African border.

Evaluating reefs by hot- and coldspot cluster analyses again indicated the dominance of hotspots along the African coastline, with an offshore extension to western Mayotte (Appendix S7d). A hotspot cluster was located on the Kenya–Tanzania border extending south to several high-density reef areas in northern Mozambique. The Western and Northern Madagascar ecoregion and the country of Madagascar were notable for lacking hotspots despite having moderate to high numbers of taxa per cell. Madagascar and the satellite islands had dispersed reefs.

Location comparison

Summarizing the top ranked locations by 4 spatial scales and the 3 z score numbers of corals, fishes, and the combined proxy taxa metrics indicated 119 locations fit at least 1 criterion (Figure 1b; Table 3; Appendix 8). There were 12 locations that scored the maximum of 12 criteria. Five of these were in Tanzania, 4 in Mozambique, 2 in Comoros, and 1 in Kenya. Past prioritization publications agreed on 6 locations of which 3 also fit our 12 criteria. The 3 with full agreement were Mtwara–Msimbati in Tanzania, Lazarus Bank, and Quiterajo–Arimba in Mozambique. Two of our top locations were identified by 2 reports, namely, the Mtanga–Lindi in Tanzania and Quiongo–Ilha Metundo in Mozambique. By multiple criteria, the border regions between Tanzania and Mozambique were identified for their high numbers of taxa.

The Kenya–Tanzania border region was identified by our criteria but less frequently or less specifically by past reports. Past reports identified very large areas, such as Pemba Channel, Pemba, or Unguja Islands. Our scaling identified several locations from the border of Kenya or Vanga town south to Pangani town and east to Pemba Island. All the above locations were in the northern section of Coral Coast ecoregion. In the Western and Northern Madagascar ecoregion, 2 locations on the western or leeward side of Grande Comoros were identified by our criteria and the World Heritage report. The northern windward and leeward sides of the island of Moheli were also identified by 10 of our criteria and the SWIOFP project. Two locations on the northwest side of Mayotte were also identified by 7 or 8 of our criteria and the World Heritage report.

We identified 28 locations that were not selected in past reports and 65 that were selected in 1 report. The remote peripheral ecoregions had a few locations fitting 6 of our criteria. These included Saint-Leu in Reunion and 3 locations in Mauritius (Grand Gaube–Baie la Riviere, Grand Sable–Mahebourg, and Cocotiers–Grand Baie). Only the Farquahr Islands in Seychelles were also identified by the SWIOFP report. There were several peripheral locations with few of our criteria that were chosen by the other reports. For example, WWF-EAME selected locations that included some of our low to moderately ranked sites (i.e., <6 criteria). In decreasing rank, these were Nacala–Mossuril, Bazaruto, Maputo–Machangulo, Tana River Delta, Lamu Archipelago, Greater St. Lucia, Shebela Delta and Bajuni Islands (Somalia), Primeiras and Segundas Islands, and Zambezi Delta. The World Heritage report also listed Lamu–Kiunga, Saya de Malha Bank of the Mascarene Plateau, Bazaruto–Tofo, Iles Eparses, Antongil Bay, northeast Madagascar, and some Comoros sites with similarly low rankings by our criteria. Lastly, SWIOFP identified several locations in South Africa (Aliwal and Protea Shoals and Greater St Lucia Wetland, St Croix Island, Bird Island), Mozambique (Ponta do Ouro, Bazaruto, Tofo, Inhaca Island, Berreira Vermelha), Tanzania (Latham Island, Pemba Channel), Kenya (Ungwana Bay), Madagascar (Grand Recif of Toliara, Nosy Ve, Antongil Bay), France—Eparses Islands (Bassas da India, Europa), Mauritius (Saint Brandon), and Seychelles (Aldabra, Aride, Cosmoledo, Cousin, Curieuse, Desnoufs, Fregate, Mahe, and Sainte Anne) that fit only 1 or 2 of our criteria. In many cases, these differences were due to the report's foci on nesting turtle and birds or sharks and marine mammals.

Existing protected areas comparison

At the time of comparison, there were 479 coastal and marine protected areas in the WIO province. Of the 208 that are strictly marine, 71 (34%) overlapped with our 119 species-rich locations (Table 4). There are 271 coastal terrestrial protected areas, of which 115 (42%) share a coastline with our selected marine locations but without explicit inclusion or protection of marine habitats. Of the 479 protected areas, 179 (37%) either shared a coastline or overlapped with our locations. At the national level, the strict overlap with marine locations varied from 4% for South Africa, due to low coral reef coverage, to 100% for Mozambique, due to the few numbers of MPAs but overlap with many of our identified locations. Kenya (71%), Tanzania (66%), and Mauritius (63%) had modest numbers of MPAs and overlap. Countries with low to modest coverage of MPAs containing our identified locations were Madagascar (39%), Reunion (31%), and Seychelles (34%).

DISCUSSION

Our proxy for total benthic diversity and the predictive BRT algorithm identified several locations of high numbers of taxa as having potential for new conservation activities. Moreover,

TABLE 3 Summary of top 119 priority identified in this western Indian Ocean survey based on the sum of 12 potential criteria and 3 past regional reports.

Ecoregion	Country	Location name	WWF EAME priority sites	World Heritage marine sites of outstanding value	SWIOFP biodiversity hotspots	Sum criteria[a]	Sum criteria (regional reports)	Marine protected areas (WDPA)
East African Coral Coast	Tanzania	Mtwara–Msimbati	Mtwara–Quirimbas	Quirimbas–Mnazi Bay complex	Mnazi Bay, Ruvuma Estuary (53, 54)	12	3	Mnazi bay–Ruvuman estuary marine park
East African Coral Coast	Mozambique	Quiterajo–Arimba	Mtwara–Quirimbas	Quirimbas–Mnazi Bay complex	Quirimbas archipelago (19)	12	3	Quirimbas
East African Coral Coast	Mozambique	Saint Lazarus bank	Mtwara–Quirimbas	Quirimbas–Mnazi Bay complex	Saint Lazarus bank (21)	12	3	
East African Coral Coast	Tanzania	Mtanga–Lindi	Rufiji–Mafia complex		Rufiji Delta, Mafia Island Complex (50, 51)	12	2	Kisarawe mangrove forest reserve, Kilwa mangrove forest reserve
East African Coral Coast	Mozambique	Quionga–Ilha Metundo	Mtwara–Quirimbas	Quirimbas–Mnazi Bay complex		12	2	
East African Coral Coast	Kenya	Funzi–Vanga	Msambweni–Tanga			12	1	Kisite–Mpunguti marine park and reserve
East African Coral Coast	Tanzania	Mahandakini–Sima Beach, Pangani	Msambweni–Tanga			12	1	Maziwe island
East African Coral Coast	Tanzania	Pemba West (Ras Kigomasha–Matumbini)	Pemba island			12	1	Misali island
East African Coral Coast	Tanzania	Pemba East (Ras Kiuyu–Chwale)	Pemba island			12	1	
East African Coral Coast	Mozambique	Nangata–Nacala	Nacala–Mossuril			12	1	
Western and Northern Madagascar	Comoros	Moroni–Singani		Comoros–Glorieuses crescent		12	1	Parc National Coelacanthe
Western and Northern Madagascar	Comoros	Niamaoui–Chomoni		Comoros–Glorieuses crescent		12	1	Parc National Mitsamiouli Ndroude
East African Coral Coast	Tanzania	Kiechuru–Kilwa Kivinje	Rufiji–Mafia complex		Rufiji Delta, Mafia Island Complex (50, 51)	10	2	Bagamoyo mangrove forest reserve
Western and Northern Madagascar	Comoros	Fomboni		Comoros–Glorieuses crescent	Moheli (1)	10	2	Moheli–Zone de transition, Parc National de Moheli

(Continues)

TABLE 3 (Continued)

Ecoregion	Country	Location name	WWF EAME priority sites	World Heritage marine sites of outstanding value	SWIOFP biodiversity hotspots	Sum criteria[a]	Sum criteria (regional reports)	Marine protected areas (WDPA)
Western and Northern Madagascar	Comoros	Nioumachoa		Comoros–Glorieuses crescent	Moheli (1)	10	2	Moheli–Reserve Mea, Moheli–Reserve Magnougni et dzaha 1, Moheli–Reserve Magnougni et dzaha 2, Moheli–Reserve Nioumachioua, Moheli–Reserve Ouenefou, Parc National de Moheli
East African Coast	Tanzania	Tumbatu–Makoba	Unguja island			10	1	
East African Coast	Mozambique	Matiquite–Messonta	Nacala–Mossuril			10	1	
Western and Northern Madagascar	Comoros	Dimani–Mohoro		Comoros–Glorieuses crescent		10	1	
East African Coast	Mozambique	Pemba	Mtwara–Quirimbas	Quirimbas–Mnazi Bay complex	Quirimbas archipelago (19)	8	3	Quirimbas
East African Coast	Tanzania	Mafia Island East	Rufiji–Mafia complex		Rufiji Delta, Mafia Island Complex (50, 51)	8	2	Mafia island
East African Coast	Kenya	Malindi–Watamu–Kilifi Chumani	Mida creek–Malindi			8	1	Watamu Marine Park, Malindi–Watamu Marine reserve
East African Coast	Tanzania	Menai bay	Unguja Island			8	1	Menai bay
Western and Northern Madagascar	Mayotte	Longoni bay–Tsingoni		Comoros–Glorieuses crescent		8	1	Ilots M'Tzamboro, Mayotte, Pointes Et Ilots Du Nord, Baie De Dzoumogne–Longoni
Western and Northern Madagascar	Madagascar	Nosy Mitsio		North and Northeast Madagascar, Ambodivahibe–Sahamalaza		8	1	Ankarea
East African Coast	Tanzania	Bagamoyo–Kunduchi				8	0	Dar es Salaam marine reserve
East African Coast	Tanzania	Lindi–Mtwara				8	0	Kisarawe mangrove forest reserve

(Continues)

TABLE 3 (Continued)

Ecoregion	Country	Location name	WWF EAME priority sites	World Heritage marine sites of outstanding value	SWIOFP biodiversity hotspots	Sum criteria[a]	Sum criteria (regional reports)	Marine protected areas (WDPA)
East African Coral Coast	Mozambique	Lurio–Memba bay				8	0	
East African Coral Coast	Tanzania	Mafia Island West	Rufiji–Mafia complex		Rufiji Delta, Mafia Island Complex (50, 51)	7	2	Mafia island
East African Coral Coast	Kenya	Msambweni–Ramisi	Msambweni–Tanga			7	1	
East African Coral Coast	Tanzania	Bomani–Fumba	Unguja Island			7	1	Chumbe Island Coral Park, Menai Bay
Western and Northern Madagascar	Mayotte	Tsingoni–Baie de Kani		Comoros–Glorieuses crescent		7	1	Mayotte, Littoral De Sada–Chiconi, Littoral De Kani–Keli, N'Gouja
East African Coral Coast	Mozambique	Ilha Metundo–Quiterajo	Mtwara–Quirimbas	Quirimbas–Mnazi Bay complex	Quirimbas archipelago (19)	6	3	
Western and Northern Madagascar	France	Glorioso islands		Iles Eparses	Glorieuses (4)	6	2	Archipel des Glorieuses
East African Coral Coast	Tanzania	Pemba South (Panza island)	Pemba island			6	1	
East African Coral Coast	Tanzania	Nungwi–Mtengani	Unguja island			6	1	Menai bay
Western and Northern Madagascar	Comoros	Djomani–Domoni		Comoros–Glorieuses crescent		6	1	
Western and Northern Madagascar	Madagascar	Baie Lotsaina–Ankazomalemy		North and Northeast Madagascar, Ambodivahibe–Sahamalaza		6	1	Nosy Hara
Western and Northern Madagascar	Madagascar	Nosy Sakatia/Nosy Be		North and Northeast Madagascar, Ambodivahibe–Sahamalaza		6	1	Lokobe
Western and Northern Madagascar	Madagascar	Ankazoberavina–Baie Androfiabe		North and Northeast Madagascar, Ambodivahibe–Sahamalaza		6	1	Nosy Antsoha, Ampasindava, Ankivonjy
Mascarene islands	Reunion	Saint Leu		Saya de Malha Bank, Mascarene Plateau		6	1	Reserve Marine de la Reunion
Mascarene islands	Mauritius	Grand Gaube–Baie la Riviere		Saya de Malha Bank, Mascarene Plateau		6	1	Ile D'Ambre, Poudre d'Or

(Continues)

TABLE 3 (Continued)

Ecoregion	Country	Location name	WWF EAME priority sites	World Heritage marine sites of outstanding value	SWIOFP biodiversity hotspots	Sum criteria[a]	Sum criteria (regional reports)	Marine protected areas (WDPA)
Mascarene islands	Mauritius	Grand Sable–Mahebourg		Saya de Malha Bank, Mascarene Plateau		6	1	Rocher des Oiseaux, Iles aux Fou, Ile aux Vacoas, Ile aux Fouquets, Ile aux Mariannes, Ile aux Aigrettes, Ile de la Passe, Pointe d'Esny Wetland
Mascarene islands	Mauritius	Cocotiers–Grand Baie		Saya de Malha Bank, Mascarene Plateau		6	1	
Carajos/Tromelin island	Mauritius	Agalega Island			Agalega island (12)	6	1	
Seychelles	Seychelles	Farquahar			Farquahar (33)	6	1	Farquhar atoll (marine) area of outstanding natural beauty, Farquhar archipelago (marine) area of outstanding natural beauty
East African Coral Coast	Kenya	Diani–Gazi				6	0	Diani Chale marine reserve
East African Coral Coast	Tanzania	Kunduchi–Buuni				6	0	Dar es Salaam marine reserve
East African Coral Coast	Mozambique	Mokambo bay–Quinga				6	0	
Western and Northern Madagascar	Madagascar	Anjiambe–Ampsikanana				6	0	Ambodivahibe, Analamerana, Loky manambato, Oronjia
East African Coral Coast	Mozambique	Messonta–Mossuril bay	Nacala–Mossuril			5	1	
Bight of Sofala/Swamp Coast	Mozambique	Quinga–Angoche island				5	0	
Northern Monsoon Current Coast	Kenya	Lamu Kiunga	Lamu Archipelago	Lamu–Kiunga Archipelago		4	2	Kiunga marine reserve
Northern Monsoon Current Coast	Kenya	Lamu Rubu	Lamu Archipelago	Lamu–Kiunga Archipelago		4	2	Kiunga marine reserve
Northern Monsoon Current Coast	Kenya	Lamu Manda bay	Lamu Archipelago	Lamu–Kiunga Archipelago		4	2	
Delagoa	Mozambique	Ponta do Ouro			Ponta do Ouro (20)	4	1	Ponta do Ouro
Western and Northern Madagascar	Comoros	Anjouan SW		Comoros–Glorieuses crescent		4	1	Parc National Shisiwani

(Continues)

TABLE 3 (Continued)

Ecoregion	Country	Location name	WWF EAME priority sites	World Heritage marine sites of outstanding value	SWIOFP biodiversity hotspots	Sum criteria[a]	Sum criteria (regional reports)	Marine protected areas (WDPA)
Western and Northern Madagascar	Mayotte	Pamanzi bay–Baie de Kani		Comoros–Glorieuses crescent		4	1	Ilots De La Passe, Ilots De Dembeni, Ilots De Bandrele, Mayotte, La Vasiere des Badamiers, Littoral De Mamoudzou, Littoral De Bandrele, Ilots Mbouzi, Pointes Et Plages De Saziley Et Charifou, Cratere De Petite Terre, Littoral De Dembeni, Vasiere Des Badamiers
Mascarene islands	Mauritius	Poste Lafayette–Troud d'Eau Douce		Saya de Malha Bank, Mascarene Plateau		4	1	Poste Lafayette fishing reserve, Bras D'Eau national park
East African Coral Coast	Mozambique	Luguni–Mecufi				4	0	
Western and Northern Madagascar	Madagascar	Ambohotrabo–Tsiadamaba				4	0	Mangoky Ihotry wetland complex, Velondriake, Manjaboaka, Soriake
Western and Northern Madagascar	Madagascar	Vohemar bay				4	0	
Delagoa	Mozambique	Bazaruto	Bazaruto archipelago	Bazaruto–Tofo, Inhambane	Bazaruto Archipelago (18)	3	3	Bazaruto
Delagoa	Mozambique	Praia de Jangamo–Island rock			Tofo beach (25), Paindane/Jangamo (26), Zavora (27), Manta reef (29)	3	1	
Western and Northern Madagascar	France	Juan de Nova Island		Iles Eparses		3	1	
Bight of Sofala/Swamp Coast	Mozambique	Ilha do Fogo				3	0	Primeiras and Segundas
Western and Northern Madagascar	Madagascar	Nosy Boraha–Toamasina				3	0	
Southeast Madagascar	Madagascar	Nosy Faho				3	0	
Delagoa	Mozambique	Inhaca Island	Maputo–Machangulo complex		Baixo Danae (24), Inhaca Island (29), Berreira Vermelha (23)	2	2	Ponta do Ouro

(Continues)

TABLE 3 (Continued)

Ecoregion	Country	Location name	WWF EAME priority sites	World Heritage marine sites of outstanding value	SWIOFP biodiversity hotspots	Sum criteria[a]	Sum criteria (regional reports)	Marine protected areas (WDPA)
Western and Northern Madagascar	Madagascar	Antisaranana–Masoala		Antongil Bay, Northeast Madagascar	Antongil Bay	2	2	Masoala
Western and Northern Madagascar	France	Bassas da India Island		Iles Eparses	Bassas da India (5)	2	2	
Carajos/Tromelin island	Mauritius	Saint Brandon		Saya de Malha Bank, Mascarene Plateau	Saint Brandon (13)	2	2	
Seychelles	Seychelles	Mahe East		Saya de Malha Bank, Mascarene Plateau	Mahe	2	2	St. Anne marine national park, Anse aux pins shell reserve
Seychelles	Seychelles	Curieuse		Saya de Malha Bank, Mascarene Plateau	Curieuse (38)	2	2	Curieuse marine national park and special reserve
Western and Northern Madagascar	Comoros	Anjouan N, NE		Comoros–Glorieuses crescent		2	1	
Western and Northern Madagascar	Madagascar	Nosy Faly		North and Northeast Madagascar, Ambodivahibe–Sahamalaza		2	1	
Mascarene islands	Reunion	Saint Gilles		Saya de Malha Bank, Mascarene Plateau		2	1	Reserve Marine de La Reunion
Seychelles	Seychelles	Aldabra			Aldabra atoll (31)	2	1	Aldabra group marine national park, Aldabra atoll special reserve
Seychelles	Seychelles	Cosmoledo			Cosmoledo (32)	2	1	Cosmoledo and Astove archipelago (marine) area of outstanding natural beauty
Seychelles	Seychelles	Amirantes (Desnoufs, Marie–Louise, Desroches)			Desnoufs (37)	2	1	Amirantes south marine national park, Desroche's atoll area of outstanding natural beauty, Amirantes (marine) to fortune bank (marine) area of outstanding natural beauty
Seychelles	Seychelles	Praslin		Saya de Malha Bank, Mascarene Plateau		2	1	
Seychelles	Seychelles	La Digue		Saya de Malha Bank, Mascarene Plateau		2	1	Veuve reserve, La Digue shell reserve
East African Coral Coast	Kenya	Tiwi–Waa				2	0	

(Continues)

TABLE 3 (Continued)

Ecoregion	Country	Location name	WWF EAME priority sites	World Heritage marine sites of outstanding value	SWIOFP biodiversity hotspots	Sum criteria[a]	Sum criteria (regional reports)	Marine protected areas (WDPA)
Western and Northern Madagascar	Madagascar	Maintirano				2	0	
Western and Northern Madagascar	Madagascar	Ambatonjanahary–Anjiabe				2	0	
Western and Northern Madagascar	Madagascar	Ivontaka–Anatanambe				2	0	Mananara nord, Seranambe, Vohitralanana, Ambodimangamaro
East African Coral Coast	Kenya	Mpeketoni–Ziwayu island	Tana River Delta		Malindi–Ungwana bay (7 & 8)	1	2	
Delagoa	South Africa	Kosi bay	Greater St. Lucia Wetlands		Isimangliso Wetland Park (47)	1	2	Maputa land marine reserve, Isimangaliso marine protected area
East African Coral Coast	Tanzania	Latham island			Latham island (52)	1	1	
Western and Northern Madagascar	Madagascar	Nosy Ambariovato		North and Northeast Madagascar, Ambodivahibe–Sahamalaza		1	1	
Northern Monsoon Current Coast	Kenya	Ras Tenewi islands				1	0	
East African Coral Coast	Kenya	Kuruwitu–Bureni				1	0	
East African Coral Coast	Kenya	Kanamai–Mradi				1	0	
East African Coral Coast	Kenya	Mombasa MPA–RasIwatine				1	0	Mombasa Marine Park and Reserve
Western and Northern Madagascar	Madagascar	Analalava–Mahabo				1	0	
Southeast Madagascar	Madagascar	Nosy Dombala–Nosy Fonga				1	0	
Southeast Madagascar	Madagascar	Ampanotoamaizina				1	0	
Southeast Madagascar	Madagascar	Vohimasina				1	0	
Southeast Madagascar	Madagascar	Manakara				1	0	
Carajos/Tromelin island	France	Tromelin islands				1	0	

TABLE 3 (Continued)

Ecoregion	Country	Location name	WWF EAME priority sites	World Heritage marine sites of outstanding value	SWIOFP biodiversity hotspots	Sum criteria[a]	Sum criteria (regional reports)	Marine protected areas (WDPA)
East African Coral Coast	Kenya	Tana River Delta	Tana River Delta		Malindi–Ungwana bay (7 & 8)	0	2	
Western and Northern Madagascar	France	Europa		Iles Eparses	Europa (3)	0	2	
Northern Monsoon Current Coast	Somalia	Shebela delta	Shebela delta (SR)			0	1	
Northern Monsoon Current Coast	Somalia	Bajuni	Bajuni (SR)			0	1	
East African Coral Coast	Tanzania	Pemba Channel			Pemba Channel (59)	0	1	
Bight of Sofala/Swamp Coast	Mozambique	Ilhas Primeiras e Segundas	Ilhas Primeiras e Segundas			0	1	Primeiras and Segundas
Bight of Sofala/Swamp Coast	Mozambique	Zambezi Delta system	Zambezi Delta system			0	1	
Delagoa	South Africa	Kwa–Zulu Natal Sardine Run		Kwa–Zulu Natal Sardine Run		0	1	
Delagoa	South Africa	St Croix Island Group			St Croix Island Group (45)	0	1	
Delagoa	South Africa	Bird Island Group			Bird Island Group (46)	0	1	
Natal	South Africa	Aliwal and Protea Shoals			Aliwal (48) and Protea Shoals (49)	0	1	
Southeast Madagascar	Madagascar	Grande Recif			Grande Recif (11)	0	1	
Southeast Madagascar	Madagascar	Nosy Ve			Nosy Ve	0	1	
Southeast Madagascar	Madagascar	Southeast Madagascar		Southern Madagascar (the deep south)		0	1	
Western and Northern Madagascar	France	Geyser bank		Iles Eparses		0	1	Archipel des Glorieuses
Carajos/Tromelin island	International waters	Saya de Malha bank		Saya de Malha Bank, Mascarene Plateau		0	1	
Seychelles	Seychelles	Aride			Aride (34)	0	1	Aride special reserve
Seychelles	Seychelles	Cousin			Cousin (35)	0	1	Cousin special reserve
Seychelles	Seychelles	Fregate			Fregate (36)	0	1	
Seychelles	Seychelles	Saint Anne			Saint Anne (41)	0	1	

Abbreviations: EAME, East African Marine Ecoregion Project; SWIOFP, Southwest Indian Ocean Fisheries Programme; WDPA, World Database on Protected Areas; WWF, Worldwide Fund for Nature.

[a]Rankings based on 12 possible criteria from this report are the 4 spatial scales (province, ecoregion, nation, and reef clustering) multiplied by the 3 number of taxa metrics of coral, fish, and the combined proxy. See Appendix S7 for maps of these locations relative to the 4 spatial delineations and Appendix 8 for national maps.

TABLE 4 Number of protected areas in the World Database on Protected Areas (WDPA) showing overlap with the 119 locations of high conservation priority identified based on 12 biodiversity criteria for coastal terrestrial protected areas, strictly marine protected areas, and their combination in the western Indian Ocean faunal province.

Nation	Number of WDPA MPAs			Number (%) of WDPA sites overlapping the 119 priority areas		
	Coastal and terrestrial	Marine	Combined	Coastal and terrestrial	Marine	Combined
Comoros	10	5	15	9 (90)	1 (20)	10 (67)
French Eparses Islands	0	2	2	0	1 (50)	1 (50)
Kenya	2	14	16	2 (100)	10 (71)	9 (56)
Madagascar	22	28	50	3 (14)	11 (39)	13 (26)
Mauritius	11	16	27	3 (27)	10 (63)	13 (48)
Mayotte	18	7	25	15 (83)	4 (57)	19 (76)
Mozambique	3	2	5	2 (67)	2 (100)	4 (80)
Reunion	2	13	15	1 (50)	4 (31)	5 (33)
Seychelles	17	32	49	9 (33)	11 (34)	19 (39)
South Africa	75	68	143	1 (1)	3 (4)	4 (3)
Tanzania	111	21	132	70 (63)	14 (66)	82 (62)
Western Indian Ocean province	271	208	479	115 (42)	71 (34)	179 (37)

these were identified by an objective measure and at finer spatial scales than past efforts. Past efforts delineated locations at the provincial level, whereas the finer scales used here identified additional delineations at the national, ecoregional, and reef clustering scales. However, the method did not include some of the past considerations such as remoteness, large animal body sizes, nesting areas, rarity, and endemism. Previous studies of other diverse unsampled taxa, such as species associated with seagrass and mangroves, also show some coarse correspondence with the patterns elicited here (Table 1). For example, many taxa evaluated in Table 1 had their highest numbers of taxa in the East African Coral Coast Ecoregion (Short et al., 2007; Spalding, 2010). Our methods represent a focus on shallow-water coral-reef-associated species for comparison with past prioritization efforts and existing protected area designations.

The modest fit between numbers of coral and fish taxa suggested that combining the 2 faunal groups provided a general but not accurate proxy for total numbers of species. Past studies have produced coarse predictors because they relied on presence–absence data and overlapping polygon and cumulative species distribution methods (Table 1). These methods have been criticized for failing to articulate the high variability in biodiversity found at finer spatial scales (McClanahan, 2023). Nevertheless, empirically testing the efficacy of our finer scale proxy of total taxonomic richness will require sampling and evaluating other taxa by similar methodologies. Regardless, our approach provided a needed step to modernize predictions based on the many available environmental variables, variable selection, and machine learning methods. Coral and fish are diverse and the most frequently sampled and widespread taxa and therefore useful proxies when comparing prioritization methods and protected areas.

The 3 past prioritization efforts often shared similar selection choices or biases in terms of selected taxa and human threats. Many of these selections were justifiable based on immediate threats and needs of large-bodied, rare, space- and habitat-requiring, sensitive, and threatened species. These decisions focused on large-bodied species with broad distributions where human impacts threaten the viability of their populations. Two good examples of these conservation decisions are the dugong (*Dugong dugon*), which has a moderate size population found only at Bazaruto, Mozambique, and the leatherback turtle (*Dermochelys coriacea*), which nests only in Sodwana Bay. Our method identified Bazaruto as a national high-diversity location. Yet, given the lack of viable dugong populations elsewhere in the province, past prioritization at the provincial and national levels seems justified by the uniqueness, regardless of the species richness status. The same reasoning applies to the leatherback turtle, given our method cannot make predictions where coral reefs are absent. In contrast, our coral and fish selections included smaller bodied and subtidal species that often supply important ecosystem services of long-term value to people, such as fisheries production and shoreline protection. Because of the weak overlap between past and our selection methods, the remoteness and marine umbrella species approaches of past prioritizations would appear to be poor proxies for total numbers of species.

Past prioritization studies focused on reproductive and nesting locations or key habitats. However, the widespread migrations of many of these focal species suggest limits to local area protection to ensure population viability. For example, some species, such as the southern humpback whales (*Megaptera novaeangliae*) and most nesting birds, have broad ranges. Species-specific management applied across their migratory ranges may be more critical than establishing specific location. Nevertheless, mating and nesting sites can be critical for many species and therefore a good criterion for making conservation decisions.

However, weak concordance with our proxy again suggests limits to coverage of total species protection when using nesting criteria. Mammals and birds are the taxa typically used as proxies but are generaly poor predictors of total diversity (Branton & Richardson, 2011; Roberge & Angelstam, 2004). Our selection of coral and fish taxa indicated a positive correlation between taxa, despite their responding to different environmental influences. However, this overlap of coral reef taxa is less common when compared with past prioritization choices that relied on other, often large, animals and remoteness. Moreover, the aesthetic values of taxa may be a poor proxy for establishing conservation priorities (Langlois et al., 2022). Nevertheless, although our methods and maps are useful in tropical locations with reefs, other approaches will be required outside of reefs habitats.

Past consultancy efforts have selected only priority locations at the faunal province delineation. The scale of delineation decisions can, however, be quite important in terms of the numbers, areas, and distribution of selected sites (Grace et al., 2022). Past reports selected from 36 to 47 locations in the WIO province that matched our mapping and spatial scale of selection. Yet, we identified 119 locations when we used our 4 scales of spatial delineation and finer spatial resolution (Appendix S7). Thus, multiple delineations and finer scales increased the numbers of identified high-richness sites. Despite the large and coarse scale of most past reports, there was seldom agreement among them; only 6 of the 91 past selections overlapped. Therefore, there is a concern that common prioritization decisions are subjective or anecdotal. Thus, high-resolution data, proxies, and predictive models provide a more objective alternative.

Numbers of taxa are only one of many potential metrics that should be considered for conservation planning and actions (Beger et al., 2015). Moreover, many priority decisions will need the support of national and local governments. Thus, our provision of national-level delineations should better provoke political engagement in decision-making. For example, some remote islands and Madagascar lacked locations with high numbers of taxa when evaluated at the provincial delineation. Large distances from source populations and sparse reef clustering reflect the geomorphological conditions found in Madagascar. These biogeological factors are outside the control of national governments and should not prevent the establishment of national and local priorities. Moreover, the ecoregional delineation helped to identify high numbers of taxa in transboundary areas that should provoke intergovernmental cooperation.

Past prioritization decisions represent the historical focus on planning large-scale protected areas (Wells et al., 2016). Yet, the generally poor overlap (34%) between MPAs and high numbers of taxa sites found here suggests inadequacy in fully protecting locations with high numbers of species. Moreover, this past approach of multiple use management in larger protected areas is losing favor to small- or community-scale proposals (McClanahan et al., 2016; Rocliffe et al., 2014). High resource dependency and low funding for conservation in this province have often undermined the effectiveness of large, protected areas, where outcomes seldom differ from effective national fisheries restrictions (McClanahan et al., 2015). Thus, evaluating finer scales of biodiversity should be helpful for identifying high-species-richness locations under the existing social needs–conservation tradeoffs (McClanahan, 2023). One provocative finding is the notable overlap (42%) between our identified locations and coastal terrestrial protected areas. Extending biodiversity protection offshore from these coastal terrestrial parks could include more species than purely marine-focused efforts.

The smaller ∼6.25-km^2 scale of our analyses relative to past efforts should be useful for the current governance and conservation actions. Moreover, species functions, ecological services, and vulnerabilities are among key current priority concerns and include fisheries production, shoreline protection, and local biodiversity conservation. A global analysis by Auber et al. (2022) showed that vulnerability generally declined as species richness increased for fishes but not marine mammals. It is expected that ecological functions provided by fishes and corals align well with policies that prioritize ecological services. Indeed, sustaining high and stable fish catches is a major concern throughout this province (Kerwath et al., 2013; McClanahan, 2021). In contrast, past prioritization criteria relying on visible and charismatic species may better promote ecotourism, but they also face the problems of economic limits and instability in poor countries (Spash, 2021). Therefore, decision-makers need biodiversity information that includes the services and economics of food production, shoreline protection, and tourism potential (McClanahan et al., 2016; Perry et al., 2018).

Several technical advancements in conservation science are represented in our approach and outcomes (Pilowsky et al., 2022). Nevertheless, the availability of field data and collaboration among experienced observers were core prerequisites for our analyses. Fortunately, the collaborators used methods that were comparable (McClanahan, Ateweberhan, et al., 2007; McClanahan, Graham, et al., 2007). Moreover, the BRT algorithm's ability to control for variable effects can account better for observer, sampling, and differential impacts on fish biomass. These variables need to be held constant when making predictions of potential underlying richness for comparisons between cells. In the case of fishes, our BRT simulations held biomass high and constant among cells for making comparable evaluations. Therefore, predictions were not influenced by local biomass depletion by variable fishing impacts. The observer effect was also controlled for in the coral distribution analyses by making predictions based on the experienced observer who sampled the most in each country. These were largely 3 or 4 observers who contributed the most data and knew the fauna best in the sampled countries. The flexibility and ability to control for many specific factors when making predictions are key strengths of the BRT algorithm. Clearly, ground-truthing the model predictions will be an important next step in testing the efficacy of the identification process.

Tests of model performance indicated good predictive ability. Yet, when making predictions for many cells on large scales, there is the possibility of overfitting and missing important local conditions, especially below the ∼6.25-km^2 scale. Moreover,

the model cannot account for local unmodeled variables, such as damaging fishing methods or point-source effluents. Nevertheless, access to 70 relevant variables, variable selection, and cross-validation methods represents a considerable advance in marine spatial modeling. Challenges remain to test predictions and account for human and other local factors not currently available at large scales. The outcomes will, however, depend on the metrics and values of the assessments, such as ecological functions of taxa, their various values, uniqueness, evolutionary relatedness, and threats (Auber et al., 2022; Brooks et al., 2006; Parravacini et al., 2014). These and additional concerns are not well addressed by presence–absence compilations and maps. Ultimately, decisions to act on the numbers of taxa findings will depend on governance bodies and their institutional values and conservation goals.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.