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Modelling biodiversity and marine conservation priorities in Mozambique

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Modelling biodiversity and marine conservation priorities in Mozambique

Supporting the Policy Enabling Environment for Development (SPEED)

Report Author(s): Tim McClanahan, Maxwell Azali, Erwan Sola, Hugo Costa, Acácio Chechene, and Hermegildo Matimele,

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INDEX

ACRONYMS

BRT – Boosted Regression Tree

IUCN – International Union for Conservation of Nature

KBA – Key Biodiversity Areas

m – Meters

MPA – Marine Protected Areas

PAR – Photosynthetic active radiation

RMSE – Root means squared error

SPEED – Supporting the Policy Environment for Economic Development

SWIOFP – Southwest Indian Ocean Fisheries Project

WIO – Western Indian Ocean

WWF – World Wide Fund for Nature

EXECUTIVE SUMMARY

The long coastline of Mozambique transitions from tropical to temperate regions and thus provides a good location to evaluate the efficacy of modelling approaches to conservation decision-making. This report describes a process for modelling marine species diversity in Mozambique with the aim of identifying where the key coral reef biodiversity areas are located and how these compare to both existing and proposed marine protected areas. To achieve this objective, we initially developed 5 different predictive models for two diverse taxa groups (fish and coral) based on field data from regional (WIO marine province) and national (Mozambique) sources combined with relevant environmental variables from satellites and shipboard measurements. First, this included two provincial models with data from the entire WIO region (n~1000 sites) corresponding to a unique set of selected environmental variables. Secondly, we evaluated three Mozambique data-only models (n<113 sites). Mozambique models 1 and 2 used the same environmental variables as selected in the WIO model but based only on fits to data from the Mozambique sites (n<113 sites). Model 3 selected variables independently of the WIO model and fits to Mozambique data only (filtered model). This report focuses on the results of the three Mozambique data-only models. Rankings and responses of the strengths and relationships of the environmental model variables were compared and used to map numbers of taxa in all 1180 cells of a Mozambique grid-map, including those without field data. These procedures and between-model comparisons allowed us to establish a measure of confidence in the number of taxa predictions. The models differed in their ranking and strengths of the specific variables and their responses to environmental conditions, producing somewhat different predictions at the reef cell level and subsequent maps. For instance, the Mozambique data-only models predicted more fish but less coral taxa than the WIO models, however, between-models variation in prediction were generally low. The largest between-model differences occurred along nearshore reefs in the Quirimbas Archipelago, reefs between the Cabo Delgado and Nampula provinces, and for numbers of fish in the southern Primeiras and Segundas Archipelago. The higher variation here may arise from the fact that Mozambique represents a transitional zone and that environmental variability is higher in these particular areas making these locations priorities for ground-truthing field studies. Additionally, further increasing the number of field studies is expected to improve the predictive strengths of these models, as indicated by the higher fits in the provincial models with more data (R2~0.55-65%). Overall, our findings indicated 19 priority locations for coral reefs and fish that were mostly concentrated in Cabo Delgado and Nampula provinces. Many of the identified priority locations overlapped with existing or proposed marine protected areas. Nevertheless, our approach suggests there is a need for more conservation efforts focused on northern Mozambique. This study also aimed at identifying areas with the highest potential to trigger Key Biodiversity Area (KBA[1]) status and where formal assessment should thus be prioritized. Considering that our models predict higher biodiversity in northern Mozambique, there is also a higher probability of including threatened species and increasing the potential to trigger KBA status. The maps produced by the models provide sufficiently low variation among models and thus clearly show where to focus future effort.

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[1] Key Biodiversity areas (KBAs) are areas that contribute significantly to the global persistence of biodiversity.

1 INTRODUCTION

Mozambique is known for its early establishment of Marine Protected Areas (MPAs) in Inhaca Island in 1965 (Reserva Florestal e Marinha da Ilha da Inhaca) and Bazaruto Archipelago in 1971(Bazaruto Archipelago National Park – BANP) (Wells et al. 2007) (Fig. 1; Fig. 2). The Quirimbas National Park (QNP) in Cabo Delgado province in the north followed much later in 2002. There have been subsequent proposals, of which many have not gone past the priority identification stage (EAME 2004; Obura et al. 2012; Everett and van der Elst 2015). Most of these designations were based on short term consultancies and not comprehensive studies that objectively compared biodiversity. Field studies have been few, localized, and rarely cover enough locations and taxa, or used comparable field methods to make broad scale comparisons. With few exceptions, the distribution of fish and coral is still poorly known even within the protected area selections (McClanahan and Muthiga 2017). This creates challenges for national planning based on the key biodiversity area standard (IUCN 2016).

It is expected that biodiversity will decline from north to south away from the equator as is common for most tropical areas (Chaudhary et al. 2021). However, several studies have shown diversity to peak in the WIO are ~10°S or around the Tanzanian-Mozambique border and not the equator in northern Kenya (McClanahan 2015, 2019). This pattern occurs because the equatorial currents are displaced south to Madagascar due to the northern enclosure of the Indian Ocean by the Asian continent. Therefore, the environmental conditions that support coral reefs and their associated high biodiversity are displaced south. Over shorter distances, there can be variability in water temperature and quality that run counter to the expected latitudinal patterns as shown in Cabo Delgado province (McClanahan and Muthiga 2017). Yet, Mozambique has a long coastline and still represents a biogeographic transition from equatorial reefs to more temperate ecosystems that emerge just north of the South African border. Regardless, protected area selection methods have seldom relied on modelled or comparable objective measures of biodiversity, especially among smaller and less space requiring or non-charismatic species. Key Biodiversity Areas have yet to be fully evaluated often because of a lack of empirical data or reliable predictive models, although a several have already been identified (Fig. 2). It is likely that several more sites in Mozambique might be Key Biodiversity Areas (KBAs) as per IUCN's global standard (IUCN 2016). These are sites that contribute to the global persistence of biodiversity that are triggered through quantitative population data that are cross-checked against several threshold criteria. Lack of empirical data or reliable predictive models are preventing the prioritization of sites by the KBA standards (IUCN 2016).

Developments in predictive modelling and subsequent spatial down-scaling provides a new use of emerging technology to evaluate biodiversity (Pilowsky et al. 2022). Emerging tools can provide data for spatial planning activities in the absence of spatially complete field data, and they can also point out areas that should be prioritized for field data collection. The overarching objective of the study was to compile information of the conservation state of coral reef ecosystems in Mozambique and assess what areas have a higher potential to trigger KBA status based on coral reef related features (species and ecosystem per se). Here, we present our efforts to develop multiple models of numbers of taxa and evaluate their utility for predicting total marine diversity. Specifically, we developed a series of models based on field data in the WIO and Mozambique to make predictions and map coral reef taxonomic diversity. The predictions allowed comparison and potential overlap with past prioritization and protected area designations and for the identification of potential coral reef related KBAs along the Mozambican coast.

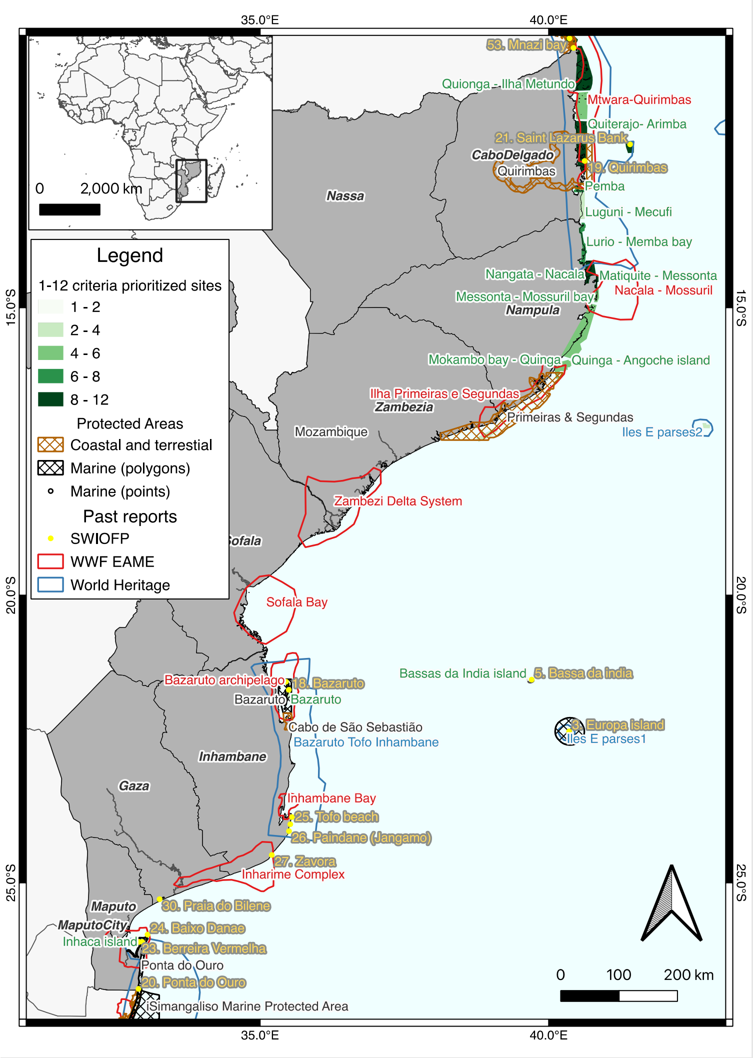


Figure 1. Mozambican coastline showing the history of protected area recommendations. Shown are the priority areas selected in the past by WWF-East African Marine Ecoregion, World Heritage, and SWIOFP programs. The map also shows the distribution of World Protected Areas Database (WDPA) locations. Finally, the green color identifies locations selected for the criteria of having high fish, coral, or total diversity from an unpublished WCS environmental-species predictive model based on 12 biodiversity criteria described below.

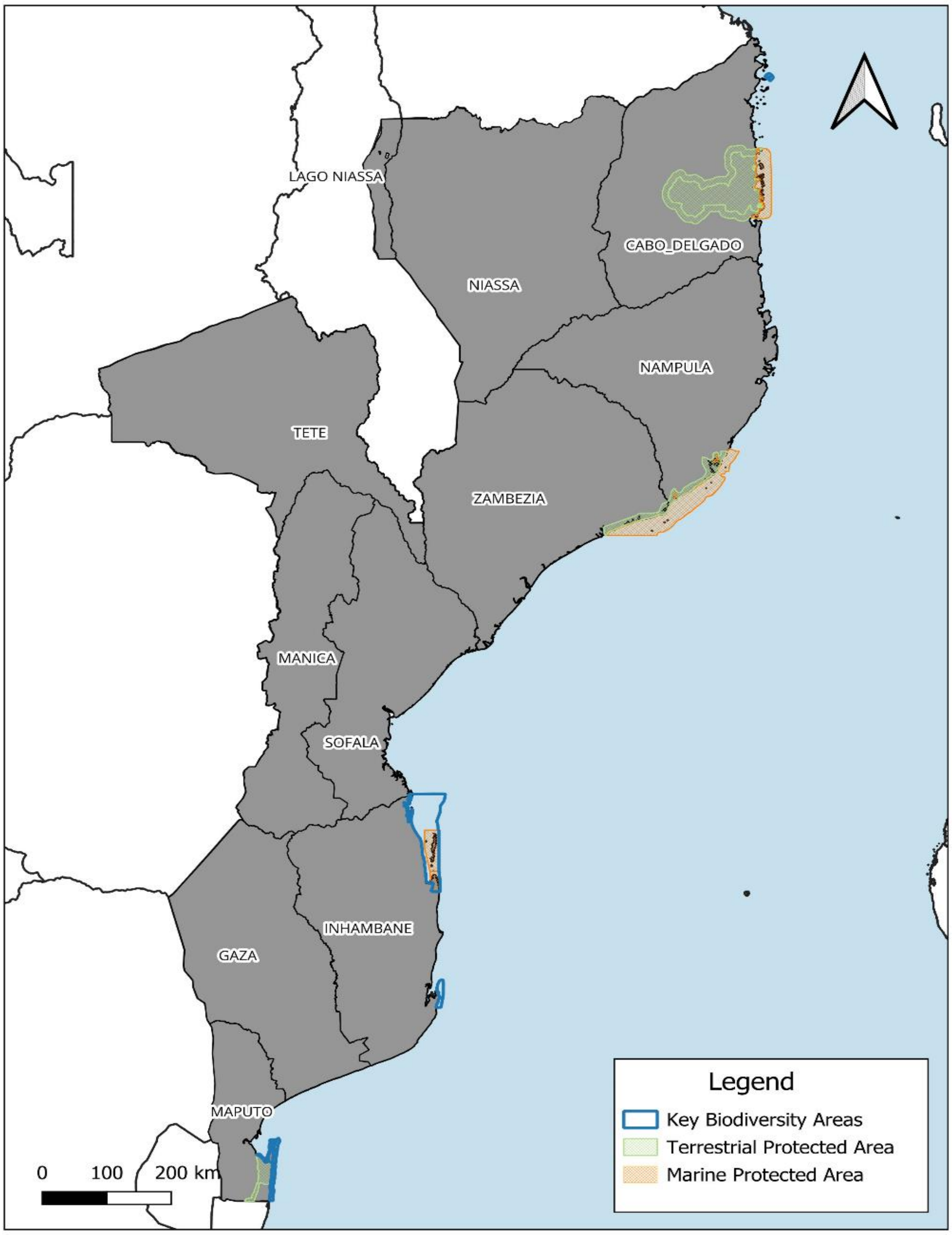


Figure 2. Mozambican coastline showing the existing Key Biodiversity Areas (KBA), established Marine Protected Areas (MPAs) (Note that exclusively terrestrial KBAs and PAs have been omitted from this map for visual clarity, but the map shows also the terrestrial portion of the PAs which cover both terrestrial and marine areas).

2 OBJECTIVE OF THIS REPORT

The objective of this report is to describes the study modelling marine species diversity in Mozambique with the aim of identifying where the key coral reef biodiversity areas are located and how these compare to both existing and proposed marine protected areas.

3 STRUCTURE OF THE REPORT

The information of this report is organized in article format, there is brief summary of the work that has been done, introduction, objectives and methodology, main achievements, discussion, conclusions challenges.

4 TEAM MEMBERS

Table *1* below shows WCS's team members who were involved in the development of this study which was led by Tim McClanahan, WCS's regional coral reef lead scientist.

Table 1 – List of WCS team members

Name	Institution	Position / role in the study
Tim McClanahan	WCS Kenya	Regional coral reef lead scientist / Activity Manager and Principal investigator, reporting
Maxwell Azali	WCS Kenya	Coral reef scientist / data processing and model development
Erwan Sola	WCS MZ	Coral reef scientist / data collection and reporting
Hermenegildo Matimele	WCS MZ	Project Coordinator / Report revisions
Hugo Costa	WCS MZ	Project Supervisor / Study coordination and report revisions
Acácio Chechene	WCS MZ	Project Assistant / Report revisions

5 METHODOLOGY

Study area

The coast of Mozambique is classified biogeographically as three separate geographic units associated with three ecoregions (Table 2). These are the East African Coral Coast in the north, the Bight of Sofala/Swamp Coast in the middle, and Delagoa Bight / Parabolic dune ecoregion in the south. Most (83%) of the coral reefs are in the north (Table 1). Coral reefs are patchily distributions in the south but extend to South Africa. The Mozambican coast is highly impacted by 1) variable exposure to the East African coastal ocean currents that pass over northern Madagascar before travelling north and 2) the southward-flowing Mozambique Current (MC) characterized by slowly moving mesoscale gyres that periodically form on the leeward side of Madagascar, which also protects northern Mozambique from open ocean storms and cyclones (Lutjeharms et al. 2012). The Southwestern Indian Ocean

(SWIO) is characterized by significant climate variability and frequent tropical cyclones (TC) (Cheng-Seng and Jury 2010), with a peak cyclone season between January and April (Mavume et al. 2009). Dynamics of cyclone activity differ in the MC compared to the greater SWIO. More TCs form in the SWIO but less make landfall compared to the MC (5% vs 55%) (Matyas 2014). The El Niño Southern Oscillation (ENSO) influences TCs in the greater SWIO, but not in the MC and, conversely, La Niña events drive cyclone activity and landfall in the MC (Ho et al. 2006, Cheng-Seng and Jury 2010, Matyas 2014). Generally, Madagascar experiences more landfall than Mozambique for either SWIO and MC generated TCs (Matyas 2014). Interestingly, TC frequency has been showed to decrease in the last two decades compared to the pre-2000 period (Mavume et al. 2009) and various studies have projected decreased TC frequency in the SWIO with future climate change scenarios (Malherbe et al. 2012, Muthige, et al. 2018), although these studies also project a shift of preferred landfall area from the southern African coast to the northern part of the MC. . Offshore deep-water trenches and coastal canyons along the coastline also cool and stabilize coastal water temperatures from Quirimbas to Nacala and the Primeiras and Segundas Archipelago where shelf interactions with the current eddies generate periodical upwelling of these deep cool water (Malauene et al. 2014).

Table 2. Frequency of coral reef cells in Mozambique and its 3 ecoregions and as a percentage of the 7039 WIO reef cells. Reef cells are mapped at the 6.25 km2 scale (map source: Burke et al. 2011).

Ecoregion	**Frequency (%)**
Mozambique	1180 (16.8)
East African Coral Coast	977 (13.9)
Bight of Sofala/Swamp Coast	113 (1.6)
Delagoa	96 (1.3)

Mozambique marine species populations are expected to be largely supplied by larvae connections with Madagascar and southern Tanzania (Crochelet et al. 2016; Gamoyo et al. 2019; Maina et al. 2020). There are strong faunal connections between northern Madagascar, the Comoros/Mayotte island and northern Mozambique (Ridgeway and Sampayo 2005; Obura 2012; McClanahan 2015; Ateweberhan and McClanahan 2016; van der Ven 2021). However, there may be at least 3 distinct regions that share larvae in Mozambique (Crochelet et al. 2016). The mid and southern coastlines may be more influenced by the connections to South Africa and southern Madagascar. Strong cyclones and storms passing around southern tip of Madagascar are also expected to influence the marine fauna in the south. Thus, the connection and state of southern Tanzania, western Madagascar, and South African reefs are expected to influence Mozambique via environmental and larval connections.

Mozambique has received a modest focus on coral reef biodiversity patterns. Interesting patterns between the environment and species distribution are observed when examined for just the Quirimbas Archipelago near the Tanzania border south to Pemba and Nacala cities (McClanahan and Muthiga 2017). For example, light and sea surface water temperature increase and became more centralized and right skewed away from the equator or from 10o to 15o south of the equator. Moreover, water quality decreased to the south along this 5-degrees of latitude. Thus, there is cooler and cleaner water close to the Tanzania border and this water may be protecting coral communities susceptible to thermal stress further to the south and north (McClanahan and Azali 2021). Consequently, the study indicated a location with either tolerance to or refugium from recent thermal disturbances. Despite this north-south pattern there was high coral diversity associated with southern coastal channels in Pemba and Nacala, suggesting these nearshore deep channels also provide stable conditions for corals that may provide refuge from climate disturbances (Obura 2012; Atweberhan and McClanahan 2016). There is some indication that the spatial patterns for corals and fish differed and may be responding to different environmental drivers (McClanahan and Muthiga 2017).

Coral reefs cover less than 0.2% of the ocean's surface but contain over 25% of know marine species and thus make a positively disproportional contribution to marine biodiversity (Reaka-Kudla 1997, Snelgrove et al., 2016). Therefore, it is a good ecosystem to evaluate for total biodiversity. Recent mapping of coral reefs indicated that most of Mozambican reefs are in the complex island structures of northern Mozambique with reefs located around island edges of the Quirimbas Archipelago seascapes and along the Nampula Province coastline (Burke et al. 2011). For perspective, Mozambique's coral reefs are ~17% of the total reef area in the WIO. Published biodiversity distributions over large areas, such as Mozambique's three ecoregions, have poorly differentiated locations when using species distribution information summarized at ecoregional, provincial, or global scales (Jenkins and van Houtan 2016; Bullock et al. 2021), which is an important limitation/caveat addressed in the present study. Indeed, Previous efforts to map key biodiversity and conservation priorities in the WIO and Mozambique have used limited sampling, the presence/absence of key taxa or criteria relying on large-bodies and charismatic species (EAME 2004; Obura et al. 2012; Van der Elst and Everett 2015), rather than the environmental conditions that support species and their distribution. These past and early prioritization decisions represent the historical focus on planning large-scale protected areas (Wells et al. 2016) while no past study has developed a proxy for total diversity and most lacked fine-scale predictions appropriate for spatial planning. Accordingly, the research described below was also undertaken to improve understanding of finer spatial and taxonomic-scale variability of marine diversity in Mozambique and contribute to a better decision-making framework for conservation spatial planning.

Methods

Initially were developed 5 different predictive models for two diverse taxa groups (fish and coral) based on field data from regional (WIO marine province) and national (Mozambique) sources combined with relevant environmental variables from satellites and shipboard measurements. First, this included two provincial models with data from the entire WIO region (n~1000 sites) corresponding to a unique set of selected environmental variables. Secondly, we evaluated three Mozambique data-only models (n<113 sites). Mozambique models 1 and 2 used the same environmental variables as selected in the WIO model but based only on fits to data from the Mozambique sites (n<113 sites). Model 3 selected variables independently of the WIO model and fits to Mozambique data only (filtered model). Detailed methodology for data collection, selection of variables, models' development and data analysis are available here.

6 RESULTS

Model fits

Fits of the models to species survey data indicated a stronger fit and lower RMSE for the large-data provincial than both the lesser-data Mozambique informed and filtered models (

Table 3). For example, the WIO provincial model's R^2 were beween 0.55 and 0.64 with higher fits to the fish (R^2 =0.62-0.64) than the coral data (R^2=0.55-0.56). The pruned and unpruned Mozambique models had similar modest fits (R^2 = 0.43). Therefore, keeping or pruning weak variables had a little effect on predictive strengths.

Mozambique models informed by the selection of variable at the WIO level did not clearly improve fits relative to the standard filtered model. Differences were not large, with the largest difference being between the informed (R2=0.51) and filtered (R2=0.48) coral models. Therefore, variable filtering using uniquely Mozambique environmental and field data, did as well as an informed variable selection process despite some differences in the number and variables selected. For the fish example, the two BRT provincially-informed models selected 10 and 11 large effect variables whereas the filtered model selected 17 (Figure 3). For corals, however, there was less difference and the provincially-informed models selected 14 and 15 large effect variables whereas the filtered model selected 12 variables. Thus, filtering variables could result in different numbers of selected variables depending on the taxa and not influence the models' predictive strengths.

Variable strengths and selection

Fish

The WIO provincial models 1 and 2 both ranked fish biomass as the strongest variable. This was followed by the correlated variables of pH or median temperature and travel time or gravity to nearest population as the top 4 ranked variable depending on the variables included in each model (Table 4; Supplementary Information Find here). Retention connectivity was ranked 3rd and 4th and the strongly corrrelated with the SST variables of kurtosis and skewness that were ranked 5th in each model. The corrrelated variables of net primary productivity and photosynthetically active radiation and depth were ranked 6th to 8th. Therefore, the two models had similar ranks and the differences were due to the inclusion or exclusion of strongly correlated variables. The main finding being that numbers of fish species were influenced by biomass, nearness to people, mean and temperature variability, ocean productivity potential, retention connecity, and depth. Yet, these variables plus many of the medium and lesser variables were used to inform the Mozambique model leading to some changes in rankings.

Rankings of the strongest variables were generally similar among the 3 Mozambique data only models (Figure *3*; Table 4). For the number of fish species, cross validations ranged from $R^2=0.42$ to 0.46 among the 3 models. The highest ranked variables in the informed models 1 and 2 were some mix of biomass, water temperature (bimodality or kurtosis), human gravity and travel time to a cell (reef visitation), water quality metrics (sediments, chlorophyll, nitrogen), calcite, larval indegree flow, depth, and waves. For example, median chlorophyll-a was ranked 1st in model 1 and 2nd in the variable filtered model 3. Andrello-sediments was ranked third in model 2. Chlorophyl-a and the Andrello-sediments were highly correlated and entered separately in the two provincially informed models (Table *4*). The filtered model 3 selected chlorophyll-a and Andrello-nutrients metric was ranked 4th. A similar result occured for correlated temperature variation variables where model 1 ranked kurtosis 2nd and model 2 ranked bimodality 1st.

The filtered model 3 picked the Global Stress Model (a weighted sum of 9 thermal stress variables) as the first ranked variable, SST skewness as the 8th ranked variable, and cumulative DHW as the 15th ranked variable. Wave energy and depth were intermediate ranked variables (7th to 9th) in all 3 models. Photosynthetic active radiation (PAR) was selected but had a low rank in all 3 models (10th in model 1 and 2 and 14th in model 3). Coral cover was selected as weak in models 1 and 3 (11th ranked) and 14th in model 2. The potential human influences estimated by travel time, human gravity, and management variables were weak as was ecoregion in all models. Model 1 and 2 differed mostly by the inclusion of highly correlated variables whereas model 3 selected unique variables, such as the Global Stress Metric, indegree connectivity, habitat, coral cover, sampled area, cumulative degree-heating weeks, and salinity. Therefore, most of the variability among Mozambican models is attributable to the filtered model 3.

Table 3. Predictive performance of BRT models based on full data and pruning or reduction of variables through recursive feature elimination. The model fits are with their own data that is all data for the province and just Mozambique data for the Mozambique model. Models were fitted with repeated 10-fold cross validation 3 times to establish their performance.

Unpruned includes all selected variables in the model while pruned models select variable within 1 standard error of the lowest RMSE =Root means squared error.

A) Fish

Model	**Method**	**R^2**	**RMSE**
Global number of fish species model 1	Unpruned	0.64	6.15
Global number of fish species model 2	Unpruned	0.62	6.24
Mozambique number of fish species model 1	Unpruned	0.46	7.73
Mozambique number of fish species model 2	Unpruned	0.42	8.02
Mozambique number of fish species model 3	Unpruned	0.43	7.89
Mozambique number of fish species model 1	Pruned	0.42	7.84
Mozambique number of fish species model 2	Pruned	0.44	7.74
Mozambique number of fish species model 3	Pruned	0.43	7.89

B) Coral

Model	**Method**	**R^2**	**RMSE**
Global number of coral genera model 1	Unpruned	0.55	4.47
Global number of coral genera model 2	Unpruned	0.56	4.41
Mozambique number of coral genera model 1	Unpruned	0.50	5.09
Mozambique number of coral genera model 2	Unpruned	0.49	5.13
Mozambique number of coral genera model 3	Unpruned	0.50	5.07
Mozambique number of coral genera model 1	Pruned	0.51	5.11
Mozambique number of coral genera model 2	Pruned	0.50	5.12
Mozambique number of coral genera model 3	Pruned	0.48	5.18

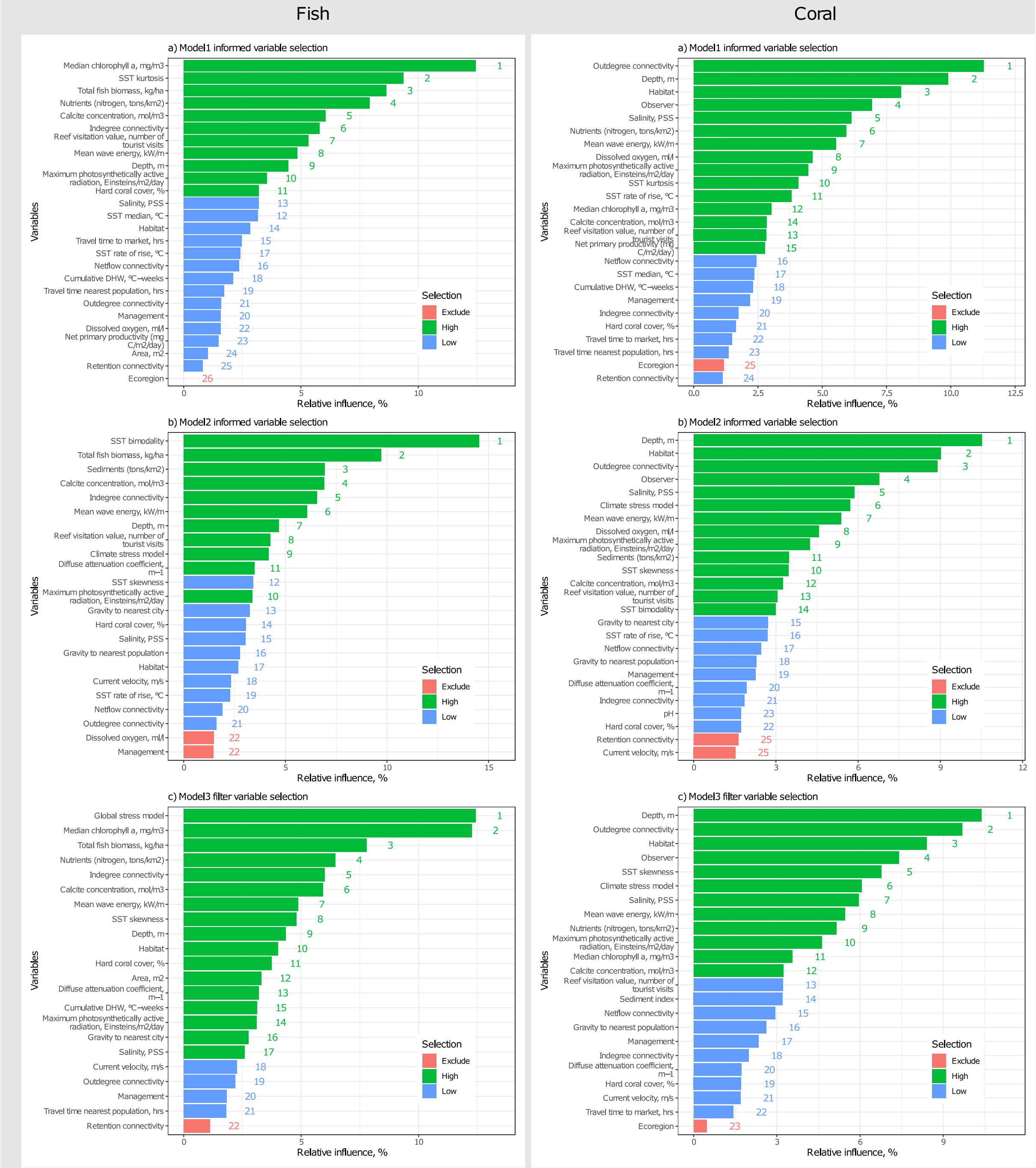


Figure 3.. Relative importance of evaluated variables among 3 Mozambique models based on BRT recursive elimination. Models 1 (a) and 2 (b) were informed by provincially important variables whereas model 3 (c) independently filtered variables prior to testing for fits to data. Shown are rankings and relative importance of BRT selected variables for (left) fish and (right) coral. Relative importance and BRT classifications shown for high, low, and excluded variables. The low and excluded variables were removed for testing the pruned models.

Table 4. Results of the BRT relative contributions (%) of selected variables for numbers of (a) fish and (b) corals taxa for the 5 evaluated models (M) and their respective R-squared fits of models using cross validation methods (see methods). See Supplementary Table 1 for all variables, additional details, and sources of access. BRT selected variables include relative importance values (%) and NI indicates variables not included in the final model (i.e., variables excluded from the corresponding models). RMSE= Root mean squared error

	WIO		WIO informed		Filtered
Variable importance	M 1	M 2	M 1	M 2	M 1
a) Fish					
1. Total fish biomass, kg/ha	42.6	42.7	8.9	10.5	7.8
2. SST median, °C	10.1	NI	2.9	NI	NI
3. Travel time nearest population, hrs	7.5	NI	1.9	NI	2.2
4. Retention connectivity	5.7	6.1	1.1	1	1.2
5. SST kurtosis	4.2	NI	9.5	NI	NI
6. Net primary productivity, mg C/m^2/day	3	NI	1.5	NI	NI
7. Depth, m	2.7	3.1	4.5	4.2	5.2
8. Travel time to market, hrs	2.5	NI	2.4	NI	NI
9. Maximum photosynthetically active radiation, Einstein's/m^2/day	2.4	3.2	2.9	3.4	2.6
10. Median chlorophyll a, mg/m^3	2.1	NI	12.5	NI	10.7
11. Salinity, PSS	1.9	1.7	2.8	2.7	2.1
12. Cumulative DHW, °C-weeks	1.6	NI	2.8	NI	3.3
13. Reef visitation value, number of tourist visits	1.5	1.2	5.5	3.6	NI
14. Mean wave energy, kW/m	1.5	1.2	6	6.9	5.3
15. SST rate of rise, °C	1.5	1.4	2.8	2.3	NI
16. Hard coral cover, %	1	1.5	3.8	3	4.1
17. Nutrients, nitrogen, tons/km^2	0.9	NI	7.6	NI	6.4
18. Indegree connectivity	0.9	1.5	5	6.2	5.1
19. Ecoregion	0.7	0.9	0	0	0
20. Dissolved oxygen, ml/l	0.6	0.7	1.5	1.4	NI

21. Habitat	0.6	0.8	2.9	3.1	4.2
22. Calcite concentration, mol/m^3	0.5	0.8	5.6	6.8	5
23. Management	0.5	0.5	2	1.4	1.4
24. Netflow connectivity	0.5	0.8	1.6	1.4	NI
25. Outdegree connectivity	0.4	0.6	1.7	1.2	1.9
26. Area, m^2	0	0	0.5	0.1	2.7
27. Sediment index	0	0	NI	NI	15.3
28. Sediments, tons/km^2	NI	1	NI	7.5	NI
29. Climate stress model	NI	1.1	NI	3.9	NI
30. Current velocity, m/s	NI	3.1	NI	1.7	3.2
31. Diffuse attenuation coefficient, m^{-1}	NI	3	NI	3	2.8
32. Gravity to nearest city	NI	1	NI	2.7	3.3
33. Gravity to nearest population	NI	5	NI	3.2	NI
34. pH	NI	6.6	NI	0.3	NI
35. SST bimodality	NI	2.7	NI	15	NI
36. SST skewness	NI	4.8	NI	3.6	4.1
Model performance					
Cross validation R^2	0.64	0.62	0.46	0.42	0.43
RMSE	6.15	6.24	7.73	8.02	7.89
b) Corals					
1. Observers	15.6	15.2	6.9	6.8	7.4
2. Depth (m)	9.2	9.4	9.9	10.5	10.4
3. Cumulative DHW, °C-weeks	6.9	NI	2.3	NI	NI
4. SST kurtosis	5.6	NI	4.1	NI	NI
5. Mean wave energy, kW/m	5	4.1	5.5	5.4	5.5
6. Dissolved oxygen, ml/l	4.3	2.4	4.6	4.6	NI
7. Country	4	3.6	NI	NI	NI

8. Salinity, PSS	4	2.3	6.1	5.9	6
9. Reef visitation value, number of tourist visits	3.8	3.2	2.8	3.1	3.2
10. Median chlorophyll a, mg/m^3	3.8	NI	3	NI	3.6
11. Calcite concentration, mol/m^3	3.7	3.9	2.8	3.3	3.2
12. Travel time to market, hrs	3.4	NI	1.5	NI	1.4
13. SST rate of rise, °C	3.3	4	3.8	2.7	NI
14. Maximum photosynthetically active radiation, Einstein's/m^2/day	3.1	3.7	4.5	4.2	4.6
15. Retention connectivity	2.7	2.8	1.1	1.6	NI
16. Indegree connectivity	2.4	1.8	1.7	1.9	2
17. Net primary productivity, mg C/m^2/day	2.2	NI	2.8	NI	NI
18. Habitat	2.2	2.2	8.1	9	8.4
19. SST median, °C	2.1	NI	2.4	NI	NI
20. Travel time nearest population, hrs	2	NI	1.3	NI	NI
21. Hard coral cover, %	1.9	1.8	1.6	1.7	1.7
22. Ecoregion	1.9	0.3	1.2	NI	0.5
23. Netflow connectivity	1.9	1.6	2.4	2.5	2.9
24. Outdegree connectivity	1.9	1.5	11.3	8.9	9.7
25. Fisheries management	1.6	1.6	2.2	2.3	2.3
26. Nutrients (nitrogen, tons/km^2)	1.6	NI	5.9	NI	5.2
27. SST skewness	NI	7.3	NI	3.5	6.8
28. Climate stress model	NI	6	NI	5.7	6.1
29. Current velocity, m/s	NI	4.6	NI	1.5	1.7
30. pH	NI	3.6	NI	1.7	NI
31. Gravity to nearest population, population/travel time, hrs^2	NI	3.1	NI	2.3	2.6
32. Gravity to nearest city, population/travel time, hrs^2	NI	3	NI	2.7	NI

33. Diffuse attenuation coefficient, m^{-1}	NI	2.8	NI	1.9	1.7
34. SST bimodality	NI	2	NI	3	NI
35. Sediments index	NI	2	NI	NI	3.2
36. Sediments, tons/km^2	NI	NI	NI	3.5	NI
Model performance					
Cross validation R^2	0.55	0.56	0.50	0.49	0.50
RMSE	4.47	4.41	5.09	5.13	5.07

Coral

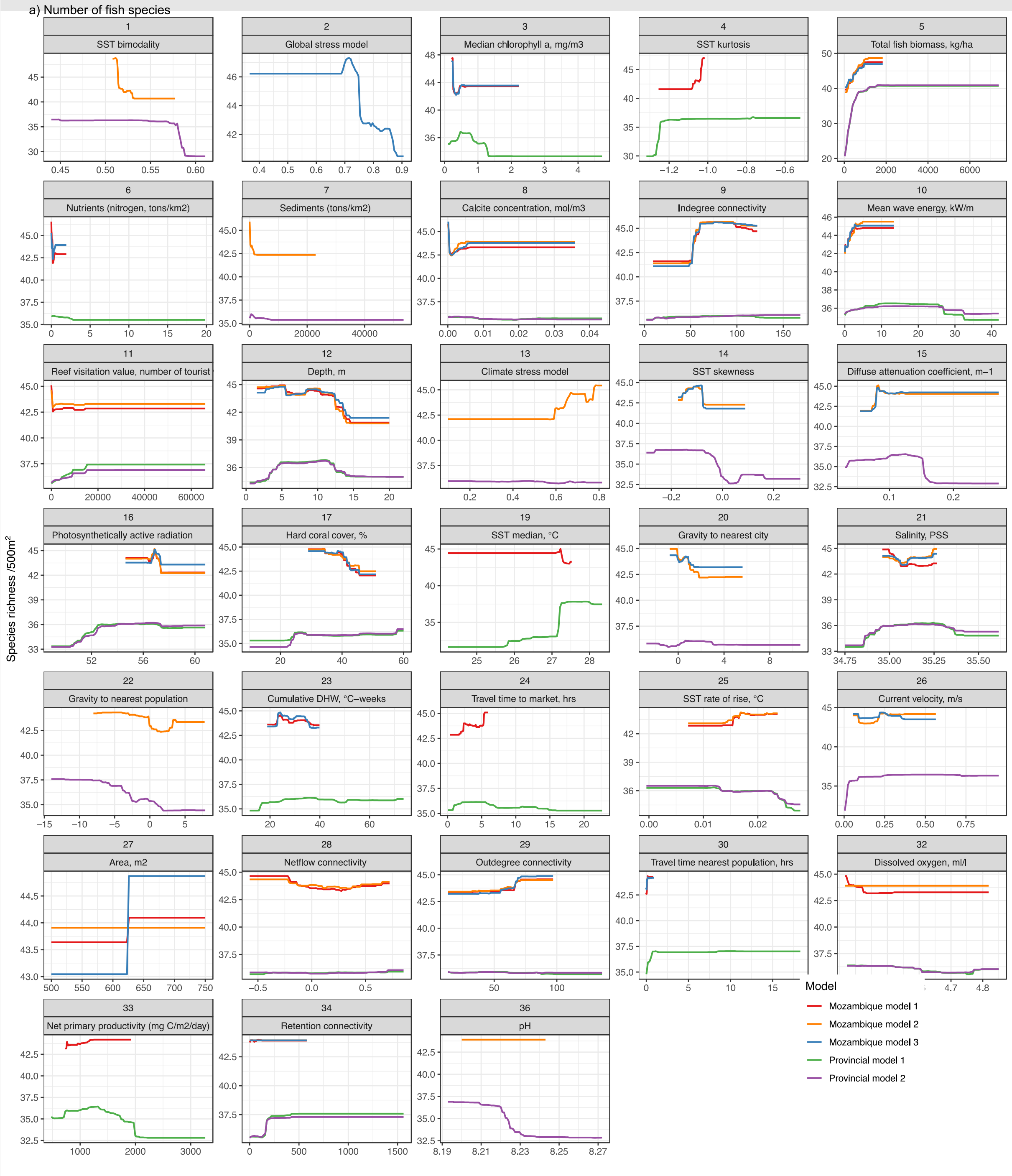
For numbers of corals taxa, the WIO provincial models 1 and 2 ranked the observer and depth as the two strongest variables. For the 3 Mozambican coral models, cross validations were similar with R^2 of 0.49 and 0.50 (Table *4*). There were also strong similarities among the top variables but more differences in the medium rankings (Figure *3*). For the top variables, the Mozambican coral filtered model 3 was not easily distinguished from the provincially informed models 1 and model 2. Temperature skewness was among the most distinguishing variables. It was not included in model 1 but ranked 10th when included in model 2. It was selected in the filtered model 3 and ranked 5th. Another difference was the filtered model selected fewer or 12 compared to 14-15 high importance variables in the 2 informed models.

Response relationships between the environment and numbers of taxa

Response relationships were generally ecologically aligned with ecological theory and empirical studies (Figure *4*). Yet, the Mozambique environmental data often reflected responses within smaller ranges of the independent variables compared to the provincial model. For both fish and coral, temperature, light, water quality, wave energy, and human influence variables had more restricted ranges compared to the WIO models.

The WIO model underestimated the numbers of fish species but overestimated the numbers of coral taxa relative to the Mozambique models (Figure *4*). The 3 Mozambique model responses often followed each other closely but deviated (usually <15%) in the number of taxa predicted by the provincial model. For example, composite thermal and sediment metrics were more important for fish and coral respectively in Mozambique than the WIO. The response to rate of rise in SST was also unique to Mozambique. More coral taxa were associated with faster rates of rise in Mozambique but fewer taxa in the WIO. Additionally, numbers of Mozambican coral taxa were less tolerant of warm-water skewness than in the WIO.

Connectivity metrics were also unique for Mozambican fish and coral compared to the WIO. For example, outdegree connectivity was the 2nd strongest ranked variable for the filtered coral model 3 while indegree was ranked 5th and the highest connectivity variable for fish.


a) Number of fish species
Species richness /500m^2
1 SST bimodality
2 Global stress model
3 Median chlorophyll a, mg/m3
4 SST kurtosis
5 Total fish biomass, kg/ha
6 Nutrients (nitrogen, tons/km2)
7 Sediments (tons/km2)
8 Calcite concentration, mol/m3
9 Indegree connectivity
10 Mean wave energy, kW/m
11 Reef visitation value, number of tourist
12 Depth, m
13 Climate stress model
14 SST skewness
15 Diffuse attenuation coefficient, m−1
16 Photosynthetically active radiation
17 Hard coral cover, %
19 SST median, °C
20 Gravity to nearest city
21 Salinity, PSS
22 Gravity to nearest population
23 Cumulative DHW, °C−weeks
24 Travel time to market, hrs
25 SST rate of rise, °C
26 Current velocity, m/s
27 Area, m2
28 Netflow connectivity
29 Outdegree connectivity
30 Travel time nearest population, hrs
32 Dissolved oxygen, ml/l
33 Net primary productivity (mg C/m2/day)
34 Retention connectivity
36 pH
Model
Mozambique model 1
Mozambique model 2
Mozambique model 3
Provincial model 1
Provincial model 2

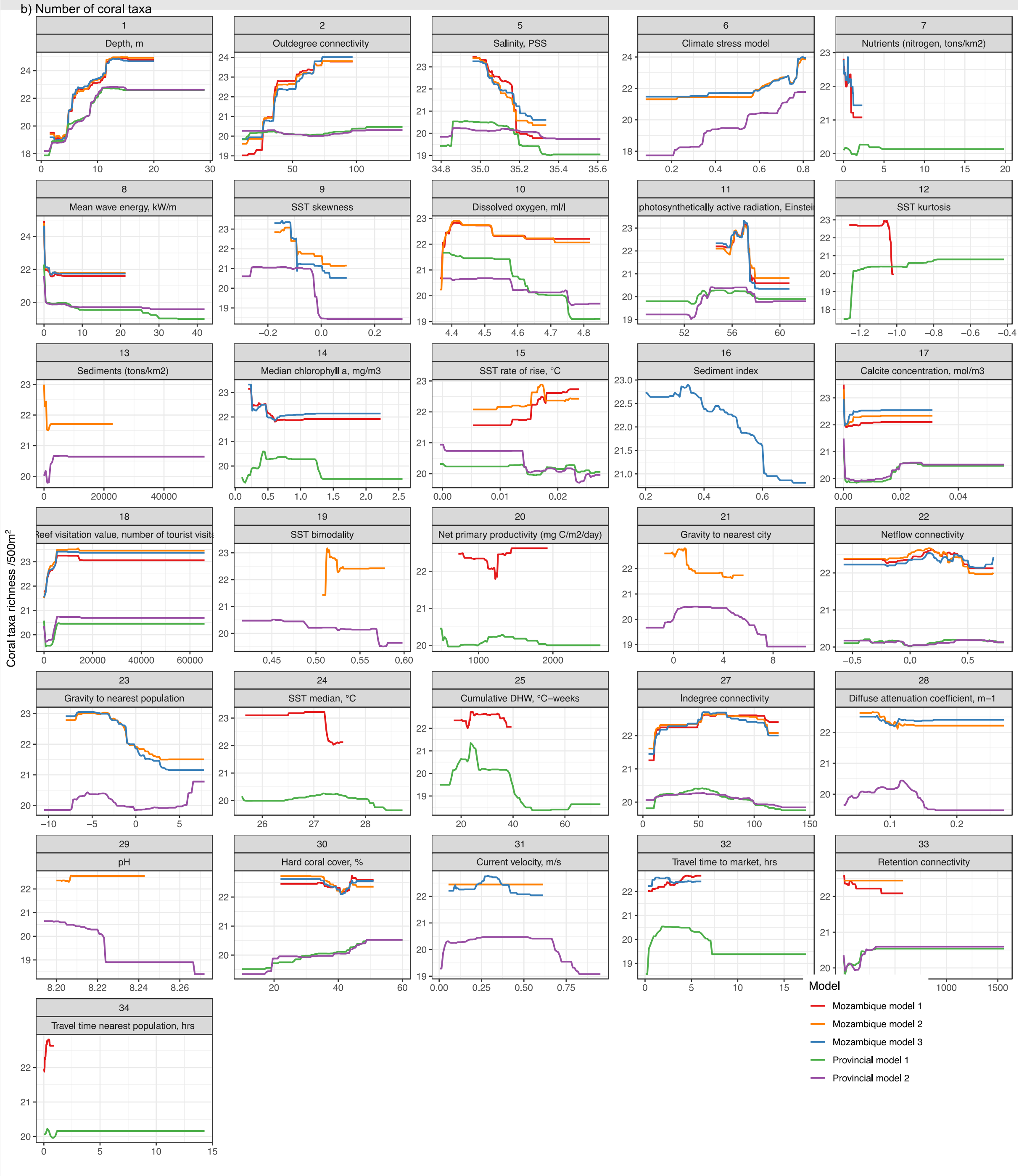


Figure 4. Response relationships between selected environmental variables and (a) numbers of fish and (b) coral taxa. BRT response plots compare 2 provincial models with the 3 Mozambican models. Mozambique models 1 and 2 variables selections were informed by the provincial model whereas model 3 used a standard variable filtering procedure. Some highly correlated variables in models 1 and 2 are missing because they were separated in models to distinguish their effects. Variables ordered from most to least importance based on the average relative influence in each model.

Variable pruning effects

Pruning had a larger effect on the predictive strengths of the provincial models but had little effect on all models (Figure *5*). For example, for fish, the differences were small and had similar mean values (41.5 and 42.1 species per 500 m2) and standard deviations (3.6 and 3.7). The pruned and unpruned model 1 for fish in Mozambique had approximately the same means (46.0 and 46.5 species per 500 m2) and standard deviations (SD=5.8) (Fig. 5a). Patterns between pruned and unpruned versions were even more similar for the 3 other Mozambican models (Figure *5*).

Number of taxa predictions

The predicted numbers of fish taxa differed between models. For example, the WIO predicted fewer fish (41.8 versus ~45.0 species) but more coral taxa (24.3 versus 23.4 taxa per 40 m^2) than the Mozambican models (Figure *4*). Comparing the 3 Mozambican fish models indicated that numbers of species declined from model 1 to 3 from 46 to 45 to 44 species per 500 m^2. Coral model 1 predicted the lowest number of coral taxa (22.8 taxa per 40 m^2) while models 2 and 3 had similar values (~23.6). Thus, there was some variability between models, but it was the variable selection and fits rather than pruning that created the modest model variation.

Relationships between fish and coral

Scatterplots and correlations of the relationships between numbers of fish and coral taxa indicated weak positive relationships (Figure 6). In fact, the relationship was not statistically significant (p=0.11, n=104) for the empirical data but significant for the provincial and pruned and unpruned models (p<0.001, n=1180). It was the strongest for the provincial model (R^2=0.31) while weakest for both the provincially informed and filtered models (R^2=0.05). Therefore, both taxonomic groups appeared to respond to the environment but to be distributed independently. This was most notable when relying on Mozambique-only data and standard variable selection processes. Therefore, the total number of taxa or the sum of these two groups was likely to be a weak proxy for the total number of species in a cell.

Biodiversity maps

Mapped reef cells based on constant biomass, sampling area, and depth reflected mostly the high strength selected variables. Maps indicated that reef cells north of mid-Nampula province had the highest numbers of taxa but with considerable variability both along and offshore from the coast (Figure 7). The provincial map showed the least variable patterns in having a strong onshore-offshore increase in numbers of fish and combined taxa (Fig. 7a). Corals had lower numbers of taxa in the middle of Cabo Delgado, particularly south of Pemba city. The number of coral taxa increased again south of Memba Bay to Nacala city. South of this area, the provincial model maps indicated low numbers of coral taxa until the South African border. Fish had the strongest onshore-offshore pattern that suggests declining species south from the north of Nacala. The provincial model predicted that the Primerias and Segundas islands are not as diverse as northern reefs and with the number of species generally declining to the south along these islands.

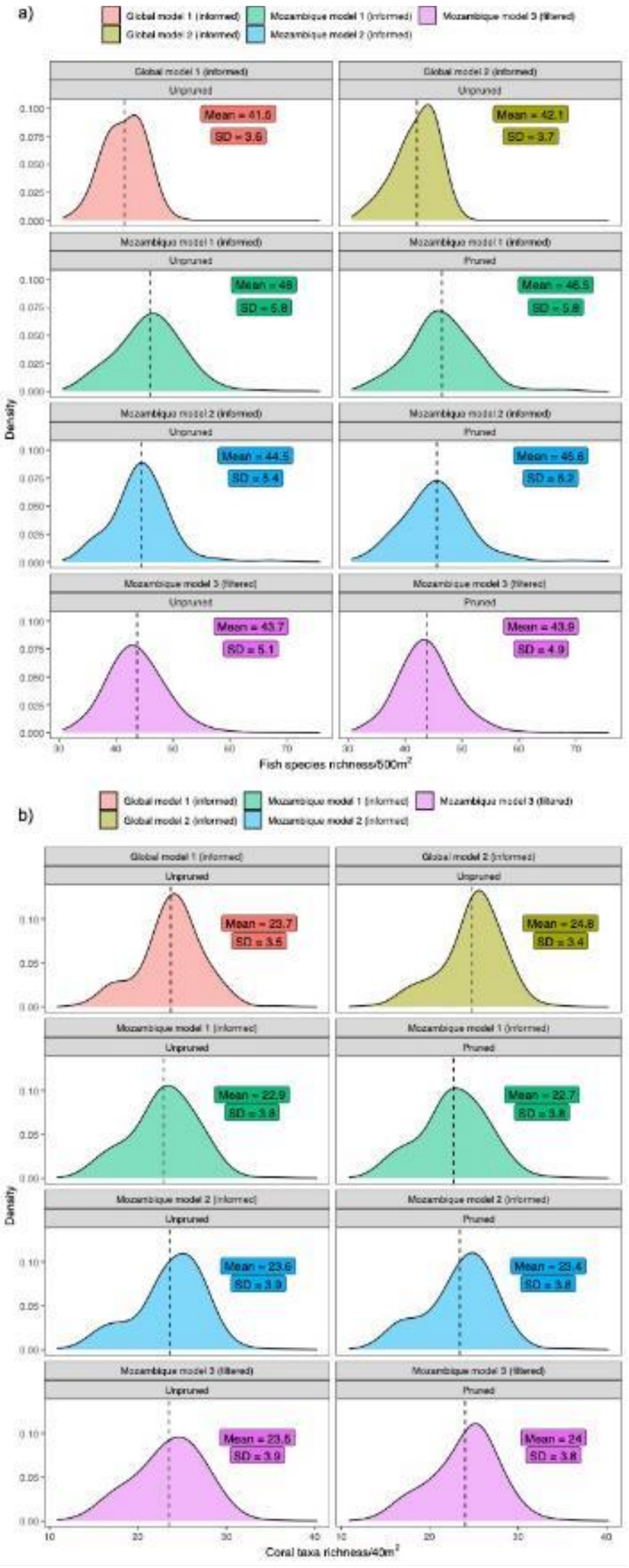

a)
Global model 1 (informed)
Global model 2 (informed)
Mozambique model 1 (informed)
Mozambique model 2 (informed)
Mozambique model 3 (filtered)
Global model 1 (informed)
Unpruned
Mean = 41.5
SD = 3.6
Global model 2 (informed)
Unpruned
Mean = 42.1
SD = 3.7
Mozambique model 1 (informed)
Unpruned
Mean = 46
SD = 5.8
Mozambique model 1 (informed)
Pruned
Mean = 46.5
SD = 5.8
Mozambique model 2 (informed)
Unpruned
Mean = 44.5
SD = 5.4
Mozambique model 2 (informed)
Pruned
Mean = 45.6
SD = 5.2
Mozambique model 3 (filtered)
Unpruned
Mean = 43.7
SD = 5.1
Mozambique model 3 (filtered)
Pruned
Mean = 43.9
SD = 4.9
Density
0.000
0.025
0.050
0.075
0.100
30
40
50
60
70
Fish species richness/500m^2
b)
Global model 1 (informed)
Global model 2 (informed)
Mozambique model 1 (informed)
Mozambique model 2 (informed)
Mozambique model 3 (filtered)
Global model 1 (informed)
Unpruned
Mean = 23.7
SD = 3.6
Global model 2 (informed)
Unpruned
Mean = 24.8
SD = 3.4
Mozambique model 1 (informed)
Unpruned
Mean = 22.9
SD = 3.8
Mozambique model 1 (informed)
Pruned
Mean = 22.7
SD = 3.8
Mozambique model 2 (informed)
Unpruned
Mean = 23.6
SD = 3.9
Mozambique model 2 (informed)
Pruned
Mean = 23.4
SD = 3.8
Mozambique model 3 (filtered)
Unpruned
Mean = 23.5
SD = 3.9
Mozambique model 3 (filtered)
Pruned
Mean = 24
SD = 3.8
Density
0.00
0.05
0.10
10
20
30
40
Coral taxa richness/40m^2

Figure 5. Density frequency histograms of the predictions of the models for (a) fish and (b) coral for Mozambique pruned and unpruned models and the two global models

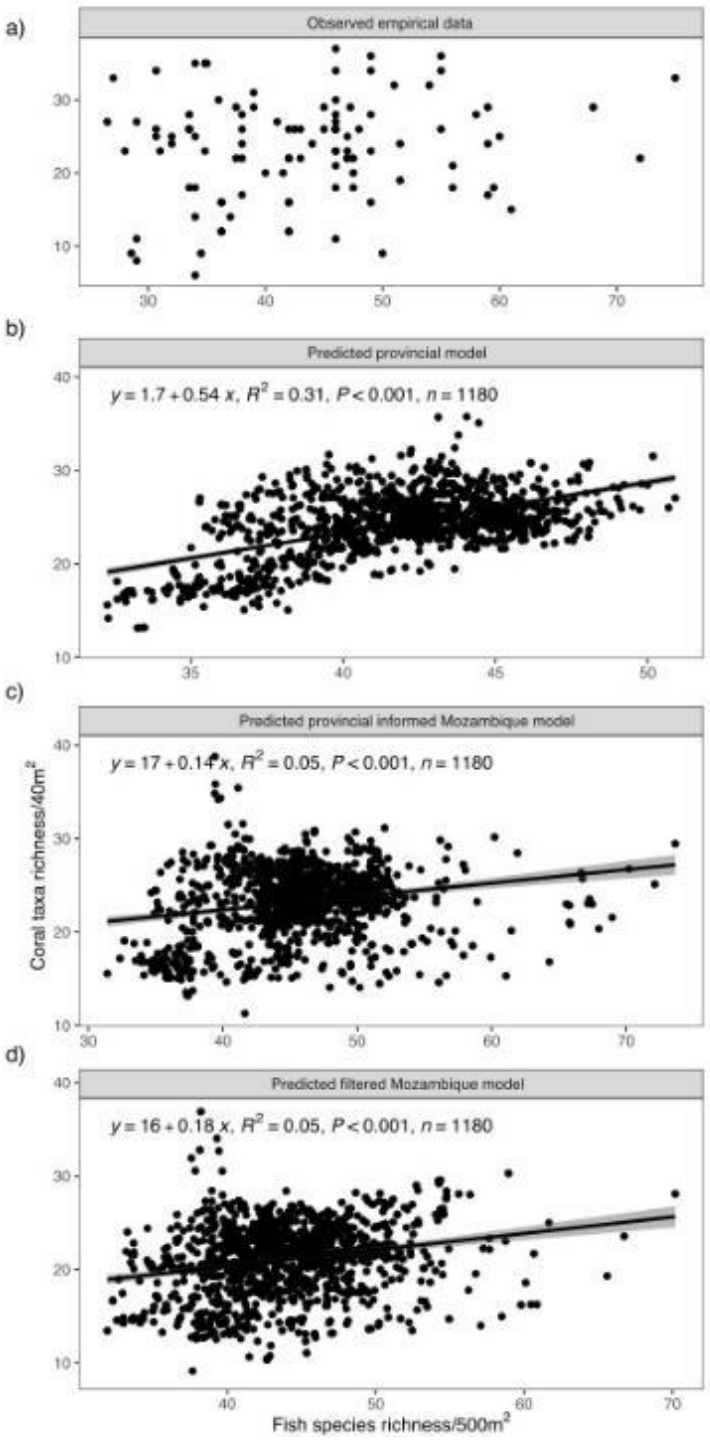


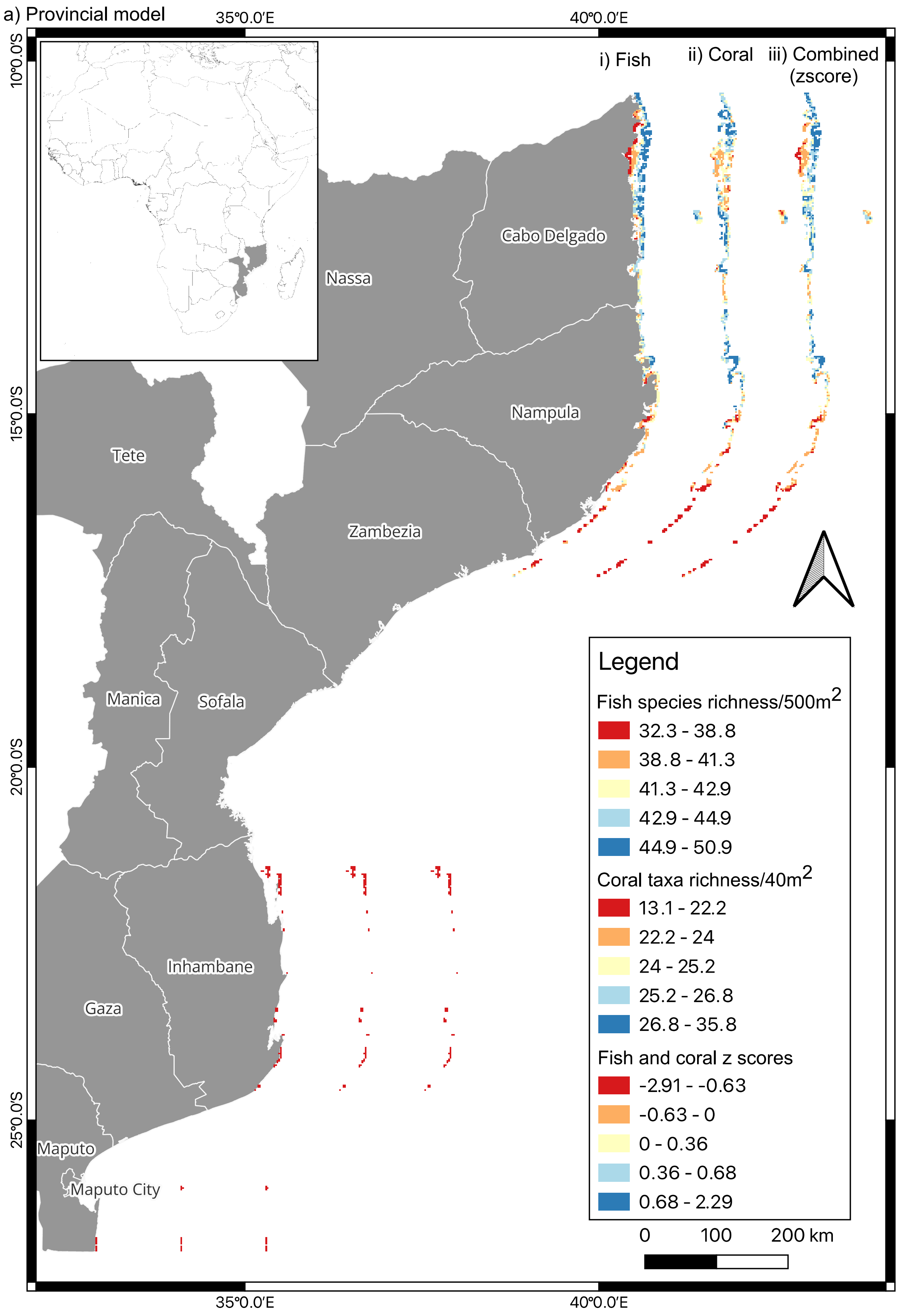
Figure 6. Scatterplot and regression statistics for the relationships between numbers of fish and coral taxa. Presented are the relationships between (a) observed or empirical numbers of fish and coral taxa and modelled values using the average of the (b) provincial models 1 and 2, (c) the provincially informed (models 1 and 2) and (d) variable filtered model 3 for all 1180 reef cells.

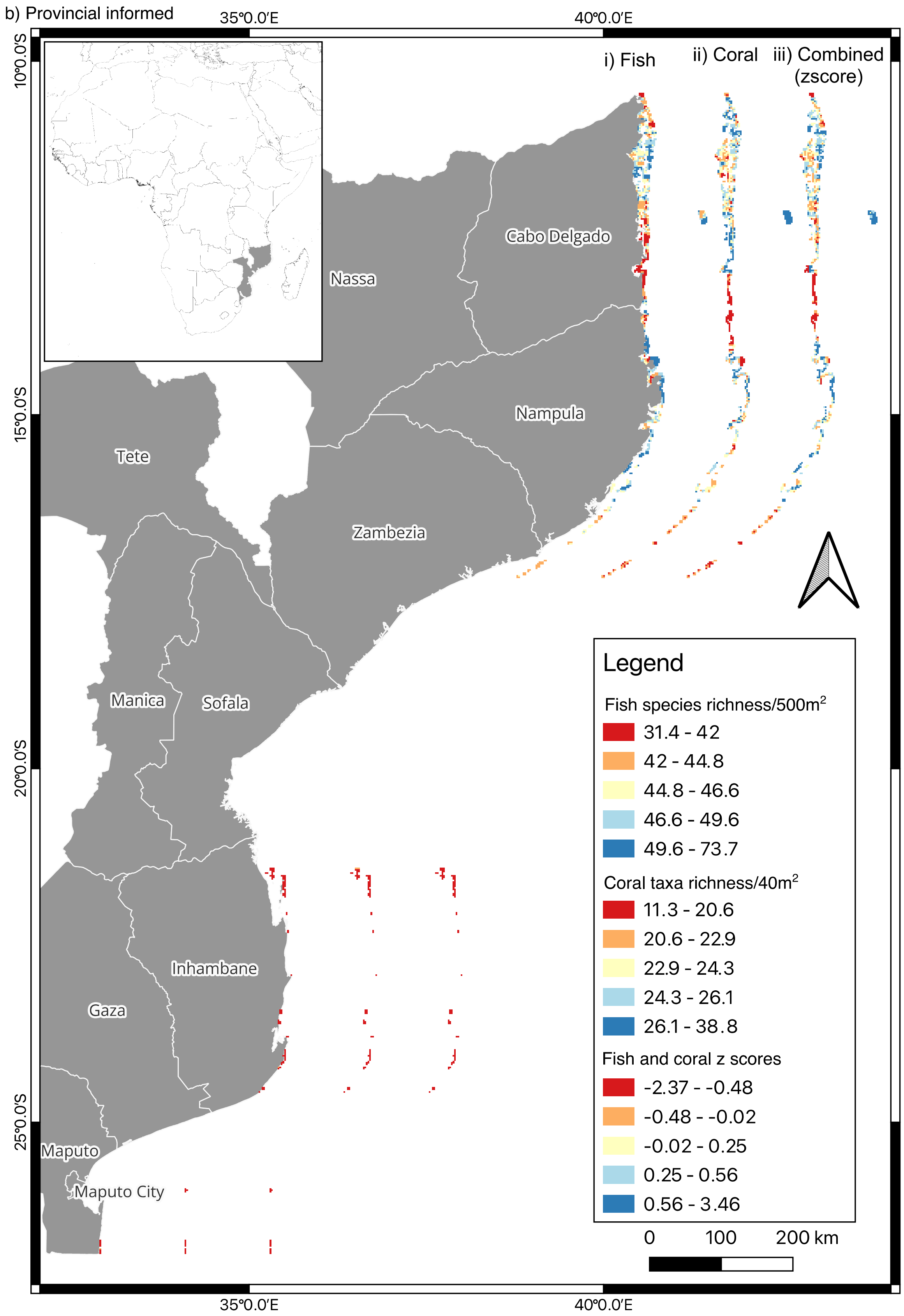
The provincially informed map using Mozambique data predicted a weaker on- to offshore gradient and fewer numbers of fish species in the far north or adjacent the Tanzania border (Fig. 7b). Numbers of fish species also declined in the southern Quirimbas islands reefs and south of Pemba. Numbers of coral taxa were similar to the provincial model predictions for northern Cabo Delgado, but the provincial model predicted lower numbers of taxa for the southern Cabo Delgado and northern Nampula province. Therefore, lower overall taxonomic diversity near the boundaries of these two national provinces.

The Mozambican filtered model 3 predicted high numbers of fish species in the far north as found in the provincial but not the provincially informed model (Fig. 7c). Model 3 also predicted high numbers of fish but not coral for the most southern Primeiras and Segundas islands in contrast to the provincially informed models. Variation among models as reflected in the COV was generally small (Fig. 8). For example, 78.6% of the fish and 87.6% of the 1180 coral cells had COV of <10%. Twenty percent of the fish and 8.7% of coral cells fell within the 10 to 20% COV interval. Only 1.1% of the fish and 3.6% of the coral cells had COV between 20 and 30%. Nampula province had more variation in the fish predictions than coral. Cell variation in fish extended to the Primeiras and Segundas Islands while between-model coral variation was highest on the border between the Cabo Delgado and Nampula provinces.

Priority locations

Nineteen locations in Mozambique fit at least 1 of the 12 provincial high biodiversity criteria (Table 4). All top locations were stretches of coastline in the Quirimbas Archipelago. The following top location outside the Qurimbas Archipelago were stretches of coast in the Nampula province, which included the Lúrio–Baixo Pinda, also followed by Mocambo Bay–Quinga and Angoche and Messonta–Mossuril Bay. One site in the southern end of the Primeiras and Segunda Archipelago was selected by 3 criteria. Model 3 suggested Ilha do Fogo has high numbers of fish but not of coral taxa.


a) Provincial model
35°0.0′E
40°0.0′E
10°0.0′S
15°0.0′S
20°0.0′S
25°0.0′S
i) Fish
ii) Coral
iii) Combined (zscore)
Cabo Delgado
Nassa
Nampula
Tete
Zambezia
Manica
Sofala
Inhambane
Gaza
Maputo
Maputo City
Legend
Fish species richness/500m^2
32.3 - 38.8
38.8 - 41.3
41.3 - 42.9
42.9 - 44.9
44.9 - 50.9
Coral taxa richness/40m^2
13.1 - 22.2
22.2 - 24
24 - 25.2
25.2 - 26.8
26.8 - 35.8
Fish and coral z scores
-2.91 - -0.63
-0.63 - 0
0 - 0.36
0.36 - 0.68
0.68 - 2.29
0
100
200 km


b) Provincial informed
35°0.0′E
40°0.0′E
10°0.0′S
15°0.0′S
20°0.0′S
25°0.0′S
i) Fish
ii) Coral
iii) Combined (zscore)
Cabo Delgado
Nassa
Nampula
Tete
Zambezia
Manica
Sofala
Inhambane
Gaza
Maputo
Maputo City
Legend
Fish species richness/500m^2
🟥 31.4 - 42
🟧 42 - 44.8
🟨 44.8 - 46.6
🟦 46.6 - 49.6
🟦 49.6 - 73.7
Coral taxa richness/40m^2
🟥 11.3 - 20.6
🟧 20.6 - 22.9
🟨 22.9 - 24.3
🟦 24.3 - 26.1
🟦 26.1 - 38.8
Fish and coral z scores
🟥 -2.37 - -0.48
🟧 -0.48 - -0.02
🟨 -0.02 - 0.25
🟦 0.25 - 0.56
🟦 0.56 - 3.46
0
100
200 km

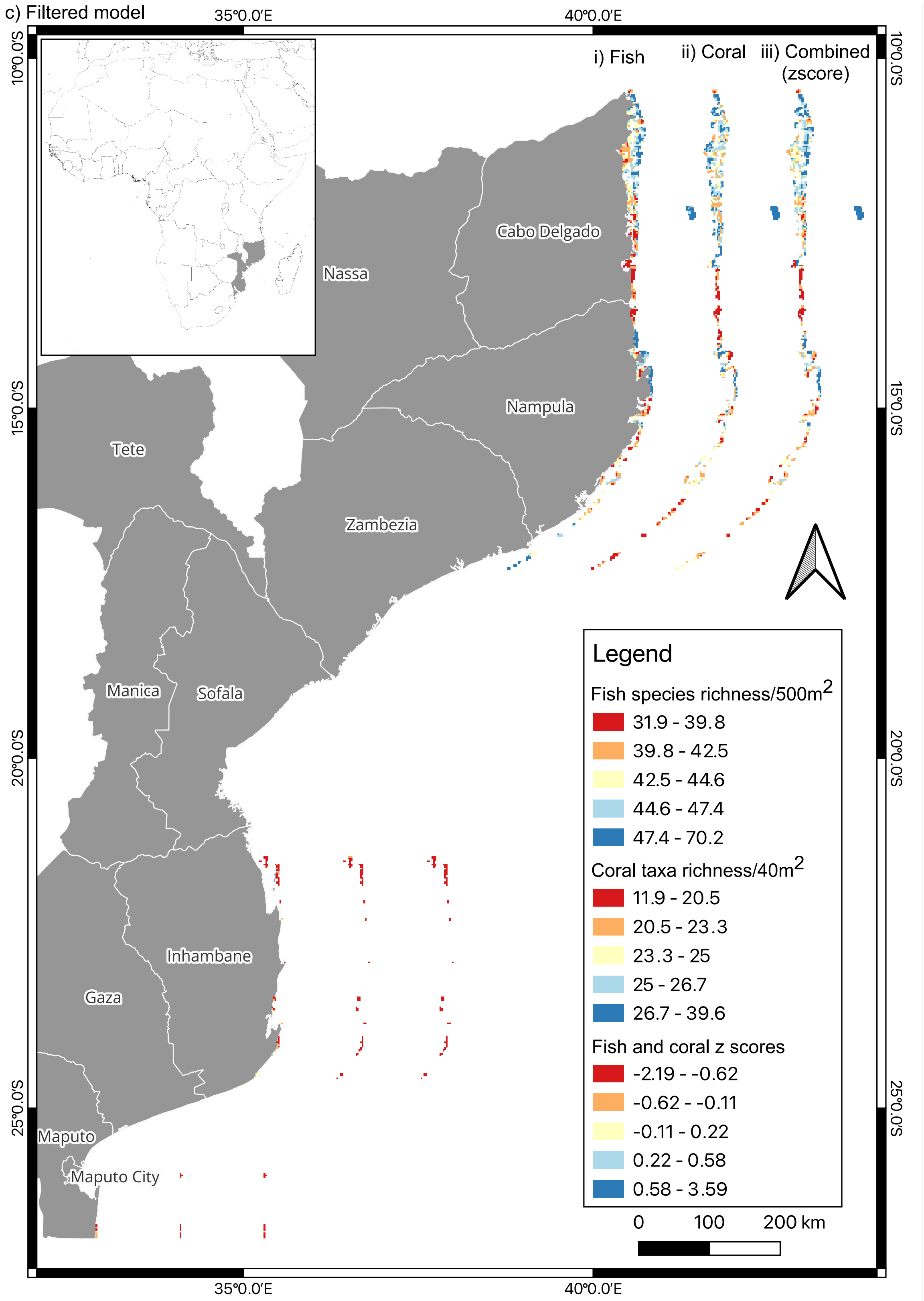


Figure 7. Maps showing the 1180 cellular predictions for (a) the average of the two provincial models for Mozambique, (b) two provincially informed variables but calibrated using Mozambique data, and (c) filtered or uninformed Mozambique models. Each map contains outputs for the number of fish species, coral taxa, and their normalized sums.

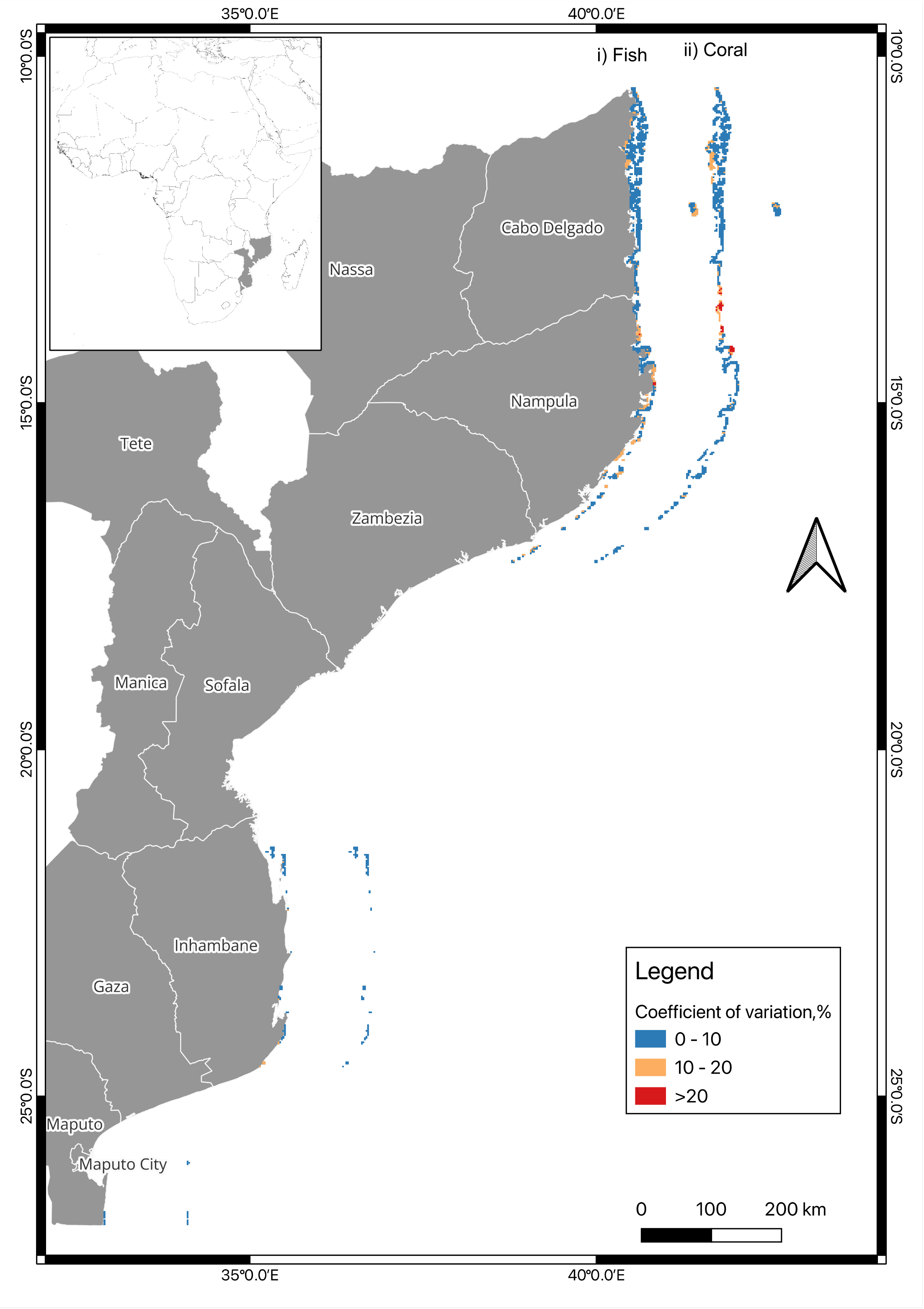


Figure 8. Map of the coefficient of variation (COV) in the predictions for each cell based on the 5 models per ta

7 DISCUSSION

The ability to model biodiversity has improved significantly following several scientific advances (Pilowsky et al. 2022). Progress has been primarily dependent on the wide coverage of ocean surface data and associated environmental metrics and proxies. Nevertheless, the low availability of field data collected beneath-the-sea surface is often a major limitation to using these tools. This can produce errors associated with low sampling intensity and the possibility of unknowns, biases, overfitting, and other problems arising from preferred theories and variables, low samples sizes, and weak field sampling designs. Arguably, this could be the case for Mozambique. However, the study here suggests these problems were not large and the Mozambique data-only filtered or model 3 produced similar results to the provincial and provincially informed models. Moreover, when model 3 produced some differences, they were ecologically insightful. Therefore, overreliance on large-scale environment-biodiversity theories and models and spatial extrapolations of models beyond the data may fail to reveal some unique marine environmental and biodiversity features. Our approach of comparing common modelling decisions produced differences and novel insights that should stimulate further investigations.

Mozambique provided a good test location due to limited data but a long coastline with 3 ecoregions and a tropical to temperate environmental gradient. Nevertheless, we did find comparable data from several observers, and used partial effect methods that can partially account for many sources of variability. Additionally, the BRT methods used here can hold some key values constant, such as sampled area, biomass, and depth to make fair comparisons between cells. For the number of fish, BRT simulations held biomass above the saturation level (> 500 kg/ha) required to make comparable evaluations of numbers of taxa between locations. This flexibility and ability to control many factors is a key strength of BRT algorithms. Clearly, ground-truthing the model predictions will be an important next step in testing the predictive power of our methods. Locations with higher between-model variation are priorities for future investigations.

The prior development of the WIO provincial model allowed us to examine the efficacy of the different predictive modelling approaches. Mozambique was likely to challenge any modelling methods as the coastline extends from dense tropical reefs in the north to sparse reefs and more temperate conditions in the south. Therefore, the 3 model options allowed testing the consequences of extrapolations of prior knowledge versus relying on local but limited sampling. During the early stages of data collection and predictive model building, most location or nation-specific studies would be unable to compare these decisions and consider the limits set by the empirical data. However, despite a limited number of study sites we believe the local model made reliable predictions and contributed to understanding Mozambique. Variable selection processes comparing local and larger geographies allowed differentiation of universal from local environmental influences. Thus, a model primarily developed with equatorial data may miss or underestimate the importance of some variables when applied to subtropical locations. Our approach contributed to a persistent debate in science of the value of theories emergent from viable hypotheses versus local scale empiricism. We find support for both approaches.

Several of the findings provide insights into the consequences of making model choice decisions. First, all models had reasonable fits to data considering the scale and complexity of the studied reef environments relative to the field sampling intensity. All models leave some variance unexplained whether due to unmeasured variables or natural variability. Having more data reduced the variance and improved the fits, as reflected in the larger-n WIO model. Higher fits would be expected given the large number of environmental variables used to make tree-based predictions. However, the selected variables did not predict cellular map patterns better than the national model when fit to local data. Additionally, there were no strong losses of predictive ability when pruning weaker variables. Also, no clear differences were observed in the number of variables selected as strong in the informed and uninformed models. All models shared several variables but the rankings between models were insightful into local versus provincial patterns.

The shared variables among all 3 models varied between the taxa. However, the selected fish species variables were often a mixture of biomass, depth, waves, heat and its variability, distance to human populations, ocean productivity, some specific connectivity metrics, and some water quality metrics. For numbers of coral taxa, the depth, and thermal heat and temperature variability metrics were strongest and followed by a number moderate physio-chemical metrics including currents, waves, calcite, various water quality variables including dissolved oxygen, and salinity metrics. Human influences and connectivity metrics were among the weakest variables for both coral and fish. Despite having several shared variables, numbers of fish and coral taxa were not well correlated in Mozambique relative to the WIO. The qualitative literature has speculated about the patterns of biodiversity in Mozambique and some of the large-scale patterns, such as sediments and temperature variation, are supported by this study (Rodrigues et al. 2000).

The unique features of Mozambique

Comparisons between models made it possible to distinguish the environmental conditions that influence Mozambique. The first indication of some important differences between Mozambique and the WIO region was the higher number of fish and lower number of coral taxa in the Mozambique than predicted by the provincial models. Secondly, we see factors such and temperature variation (bimodality and kurtosis) and connectivity were more important in Mozambique than in the WIO. Possibly due to the transitional nature of this part of the coastline characterized by high environmental variability. Thereafter, key distinguishing variables included some connectivity metrics, habitats, nutrients, sediments, weak human effects, and temperature variation, possibly most influenced by temperature bimodality. The bimodality and kurtosis metrics were likely to reflect the latitudinal gradient but correlated with other temperature variable metrics associated with latitude. Unexpectedly, bimodality was the strongest variable for numbers of fish species for both versions of model 2 but ranked 14th for corals. Consequently, seasonality would appear to be more influential for numbers of fish than coral taxa.

The correlated variables of SST bimodality, SST skewness and kurtosis indicated that taxa declined as these metrics increased. High negative kurtosis and high positive bimodality are proxies of chronic temperature stress, and positive skewness is a measure of the frequency of reoccurring hot water or acute stress. These metrics combined indicated that numbers of both corals and fish taxa declined as chronic and acute stress increased towards the southern Mozambican border. Typically, acute warm water stresses are common in tropical locations during episodic ocean conditions, such warm El Nino Southern (ENSO) and Southwest Indian Ocean Oscillations (SWIO) but also episodic cyclones (Bruggemann et al. 2012). However, the northern Mozambique (10-12°C) reefs appeared to be buffered from these acute stresses as warm skewness was shown to increase from the Tanzanian border south to Pemba and Nacala (McClanahan and Muthiga 2017). In contrast to the WIO findings, numbers of both coral and fish taxa increased with the rate of SST rise, although with a moderate effect. This would suggest that conditions for high reef biodiversity will improve more in transitional than equatorial regions with climate change.

Connectivity metrics were stronger in Mozambique than in the WIO. Greater isolation or the peripheral location of these reefs might be the cause. Reefs in Madagascar to the east are numerically dominant and those in Tanzania and the East African Coral Coast Ecoregion to the north have the highest diversity. A high diversity corridor of WIO reefs is observed to exist between northern Mozambique, east to Comoros, Mayotte, and the northwestern Islands of Madagascar (Obura, 2012; McClanahan and Azali 2021; McClanahan et al. in review). The WIO models predicted numbers of taxa were more influenced by larval retention rather than in- and outdegree connectivity metrics found for fish and corals in Mozambique. Indegree connectivity was strongest for numbers of fish but outdegree for coral taxa. Understanding these intriguing differences will require more research. Regardless, differences in connectivity influences between fish and corals may partly explain the lack of correlation between their numbers of taxa in Mozambique.

Mozambique Channel currents are gyres created when the South Equatorial current bifurcates and produces eddies that travel south along the Mozambique coast (Halo et al. 2014; Gamoyo et al. 2019). Genetic connections between Madagascar and Mozambique were observed in a coral relatedness study (ven der Ven et al. 2021). Moreover, connectivity relationships appear to be divided between northern reefs and mid-channel reefs. The transition in connectivity occurs near the border of the Cabo Delgado and Nampula provinces for species with short larval durations (<15 days) (Crochelet et al. 2016; Gamoyo et al. 2019; O'Donnell et al. 2017). Halo et al. (2014) predicted ~4 eddy cycles per year, which suggests regular connectivity within these divisions depending on the larval duration of the specific taxa. The consequences of this gyre system appear to differ between coral and fish connectivity patterns.

An increase in numbers of fish species associated with indegree connectivity suggests that species travel east to west and north to south, which would fit with the overall current movement patterns and connectivity of northern Mozambique (Crochelet et al. 2016; Gamoyo et al. 2019). However, the outdegree importance for corals suggests a different connection system or possibly unstudied hidden variables correlated with the outdegree connectivity metric. For example, one viable hypothesis is outdegree connectivity correlates with remnant or climate change refuges of high numbers of coral species in the deep-water Pemba and Nacala bay channels (McClanahan et al. 2011; Obura 2012; Halo et al. 2014; McClanahan and Muthiga 2017). These locations are likely associated with the anticlockwise gyre systems that pull cool water offshore, creating some weak upwelling. In other words, the causes of the high numbers of species could be attributed to their adjacency to deep, cool, and stable water or thermal refuge created by gyres rather than larval outdegree dynamics. Future research will need to consider these among other options responsible for these unique deep-water high diversity refuges.

Water quality effects on numbers of taxa was generally greater in Mozambique than the WIO. The latitudinal gradient should produce these patterns often associated with increased nutrients and sediments typical of cooler and more variable oceanic waters found in temperate latitudes. Yet, high sediment concentrations are observed in reefs south of Pemba and particularly south of Nacala Channel. Shallow reefs and associated species are missing along a long stretch of central Mozambique and high sediments and low water quality are the likely causes. Variability in numbers of species with habitats may also reflect differences in exposure to water quality and temperature variability.

Human influences on numbers of taxa appeared weaker in Mozambique than the WIO. Coastal populations are more sparsely and evenly distributed (~40 people/km^2) than elsewhere in the WIO. This combined with stronger environmental temperature and water quality effects may explain these patterns. In many countries of the WIO, fish biomass has declined greatly, and this has reduced the numbers of species (McClanahan 2022). Most Mozambican reefs are also overfished but not to the same extent as many reefs in Kenya, Tanzania, Reunion, and Comoros (McClanahan et al. 2023). A model estimating the recovery times of Mozambican reefs predicted it would take ~5 and 15 years of no fishing to recover biomass to optimal yield and the higher conservation levels (McClanahan et al. 2016). Additionally, the existing fisheries management classifications were probably ranked low due to small differences between protected, managed, and unmanaged reefs (McClanahan et al. 2015; Gill et al. 2017). This is potentially an attribute if the biomass of fish is more evenly distributed across the management systems. However, most Mozambican reefs have low to moderate fish biomass regardless of management.

It is likely that the influences of the above environmental variables led to the underprediction of numbers of fish and overprediction of corals when comparing the provincial and national models. The implication is that conditions are better for fish and worse for coral taxa in Mozambique than the WIO. This finding should provoke speculations but the complexity or number of variables in the model imply several different environmental forces. Perhaps this is an attribute of comparing a model developed largely for equatorial reefs versus latitudinal transition reefs. Our findings suggest that the transition from tropical to temperate systems provokes a decoupling of strong coral-fish species associations among these two tropical taxa. Therefore, fish are likely to adapt better than corals to transitional subtropical environments. This would be expected given that corals rely more on light and clear water than fish to survive.

Comparing models

Differences between models were less influenced by their predictive ability than the rankings of the medium to high strength variables. Shifts in rankings will affect numbers of taxa predictions for specific cells and therefore influence the biodiversity distribution maps. Overall, the between-model variation map was the best reflection of the variability in rankings (Figure *8*). Most locations exhibited modest variation between models. However, patterns of variation indicated less confidence in predictions for nearshore reefs located between the Cabo Delgado and Nampula provinces. There was also less between-model confidence for numbers of fish than corals particularly in Nampula province and the southern Primeiras and Segunda Islands. However, limited and uneven sampling combined with a lack of field data and ground truthing in southern Nampula could have influenced the variability in the model's predictions. From the perspective of improving modelling, sampling in southern Nampula province is a high priority. One prediction is that fish would have relatively more species than corals after accounting for any fishing effects.

Tests of model performance indicated good predictive ability. Yet, when making predictions for many cells on large scales, overfitting and missing important local conditions are concerns, especially for predictions below the cell's ~6.25-km^2 scale. Moreover, the model cannot account for local unmodelled variables, such as damaging fishing methods or point-source effluents. Nevertheless, consideration of 70 relevant environmental variables, variable selection, validation, and comparative model methods represents a considerable advance in marine spatial modelling and predictions for Mozambique. Challenges remain to test predictions and account for human and other local factors not currently available at large scales. Moreover, it is important to choose model variables that are amenable to management and human concerns. Nevertheless, all predictive models had good skill. Similar methods evaluating coral cover and fish stocks and yields made good large-scale predictions (McClanahan and Azali 2021; McClanahan et al. 2023).

Proxy for total numbers of species

Estimating the total numbers of species using the sum of the fish and coral was expected to produce a good proxy for total numbers of species. However, our analysis found numbers of taxa of fish and coral were not strongly related ($R^2 \sim 0.05$). The modest fit in the provincial model ($R^2=0.31$) likely arose from a variable selection process weakly influenced by the Mozambican data. Consequently, the sum of the two taxa have limited ability to predict the total numbers of species. As suggested above, the environmental conditions in Mozambique cause these two taxa to respond differently to environmental conditions. Interestingly, ecoregion was also not significant in our model suggesting that this faunal delineation was not influencing numbers of coral and fish taxa apart from the environmental variables used in the model. Therefore, Mozambican ecoregions likely represent different environments and qualitative aspects of the fauna and not the numbers of our studied taxa. It remains to be discovered if there is a proxy for total number of taxa for transitional locations like Mozambique.

Priority locations

Past conservation efforts by the national government of Mozambique and NGOs identified several priority locations in Mozambique (EAME 2004; Obura et al. 2012; Everett and van der Elst 2015). WWF-EAME, World Heritage, and SWIOFP identified some locations that overlapped but many were large, particularly for WWF-EAME and World Heritage selections. These large areas included Mtwara-Qurimbas, Nacala-Mossuril, Premeiras-Segundas, Zambezi Delta, Sofala Bay, Bazaruto-Inhambane, Inharime complex, and various locations from Praia do Billene to Ponta do Ouro north of South Africa or the iSimangaliso MPA (Figure 1). These are large areas that cover a large portion of the Mozambican coastline. Our predictive model identified more specific high biodiversity locations for 6.25 km^2 cells. This resulted in overlaps with proposed or existing MPAs but also in identifying some new smaller localities (Figure 1; Annex I,Table *5*). Our model also identified the taxa by the specific environmental associations, which resulted in variability in the number of criteria used to make site selections. For example, high numbers of fish but not coral taxa were predicted in Ilha do Fogo.

Our method was localized and specific to taxa and did not consider some of the past considerations such as remoteness, animals with large body sizes, nesting areas, rarity, and endemism. Nevertheless, we did combine hard coral, a well sampled invertebrate representing a diverse host taxon, and fish, a vertebrate taxon known for high numbers of species. Regardless, our approach provided a needed step to modernize the number of species predictions for Mozambique. Coral and fish are diverse and the most frequently sampled and widespread taxa and therefore useful proxies for examining the relationships between protected areas and biodiversity.

The three past prioritization efforts often relied on large-bodied, rare, space-and habitat-requiring, and threatened sensitive species. Past selection decisions have focused on large-bodied species with broad distributions that pose threats to their population viability. A good example is the dugong (*Dugong dugon*), which has a moderate population size found only in Bazaruto. Our method also identified Bazaruto as a national priority for corals and fish. In contrast to the large bodied species that attract conservation attention, our selections criteria included smaller-bodied and subtidal species of fish and corals.

Past and early prioritization decisions represent the historical focus on planning large-scale protected areas (Wells et al. 2016). Yet, the methods used here suggest this approach identified many areas in southern Mozambique near the capital and South African border that are not as diverse as northern Mozambique. The approach used here provides an alternative basis for site selection. The Quirimbas NP is one of the few exceptions but has struggled to maintain strong conservation impacts (Gill et al. 2017). This is likely due to high resource dependency, multiple use management, and political conflicts. High resource dependency combined with low funding to achieve compliance and alternate livelihoods has undermined the effectiveness of some large, protected areas in the WIO (McClanahan et al. 2015).

In many WIO MPAs, outcomes seldom differ from effective national fisheries restrictions (McClanahan et al. 2015). Some of these challenges may indicate why large MPAs are losing favor to smaller- or community-scale proposals (Rocliffe et al. 2014; McClanahan et al. 2016). The smaller ~6.25-km^2 scale of our analyses relative to past efforts should be useful if smaller MPAs or community closures become conservation priorities. Moreover, species studied here provide ecological services including fisheries production, shoreline protection, and local biodiversity conservation. Therefore, ecological functions provided by fishes and corals aligns well with policies that prioritize ecological services. Indeed, sustaining high and stable fish catches is a major concern throughout the African coastline (Kerwath et al. 2013; McClanahan 2021). In contrast, past criteria relying on visible and charismatic species promote ecotourism but often face economic limits and instability in poor countries (Spash 2021). Therefore, decision makers need information that considers the services and economics of food production, shoreline protection, and tourism potential (McClanahan et al. 2016; Perry et al. 2018).

7 CONCLUSIONS AND RECOMMENDATIONS

Between-model tests indicated good predictive ability (i.e., R^2 >45%) with few exceptions. Yet, when making predictions for many cells on large scales, overfitting and missing important local conditions is a possibility, especially for biodiversity distributions below the 6.25-km^2 scale of this study. Moreover, the findings indicate the importance of having large replicates and well-designed sampling to improve the models' predictive strengths. Future sampling for the purposes here will want to use similar methods (corals ~40m^2, fish at 500 m^2) and to sample any of the identified gaps.

The availability of field data and collaboration among experienced observers using similar methods was critical to making the predictive model. The ability to deal with many factors is a key strength of the predictive modelling approach which allowed us to provide a more spatially refined view of the biodiversity of Mozambique's coast than shown in previous studies. The environmental modelling methods we used provided a broad- and fine-scale approach by accounting for smaller scale environmental spatial variability and ecological processes. With these methods we identified new areas that can better fit conservation and confirmed the relevance of the location of some existing protected areas. With our study in this specific region, it was noted that high-quality spatial data at finer scale is key to informing the process of identifying priority areas for biodiversity.

Our model allowed the identification of 19 coral reef hotspots located in the Mozambican waters that can now be prioritized for additional field work to collect data which can be used to potentially trigger these areas as KBAs and define site-specific management, conservation and protection measures. Here, we see that most existing protected areas overlapped with our modern predictive modelling methods except for the lesser protected area coverage in northern Mozambique. Our predictive species richness models suggest a need to increase conservation and scientific focus in the north.

Clearly, filling spatial gaps, ground-truthing, and evaluating other environmental and important demographic influences will be an important next step to improve the prediction and prioritization process. However, the current models were useful for providing some new smaller size priority locations in Mozambique (Table 5). These may be locations to consider for modest sized conservation actions that may be aligned with the current approach that accounts for community-based alongside state-managed conservation strategies.

Past scientific work has shown that one of the best indicators of resource status and biodiversity is fish biomass. Therefore, managing biomass on a large scale is important for maintaining fisheries yields and biodiversity (McClanahan 2019; 2022). Biomass is manageable through regulations concerning fisheries and their food production potential (McClanahan et al. 2023). A modelling study of reef fish stocks in Mozambique indicated that ~90% of the modelled reef cells were overfished and 42% were severely overfished (McClanahan et al. 2023). Much of the stocks above sustainability levels were either along coastline with low human population densities or in the national parks. However, designations of marine habitats as parks, reserves, and community closures does not necessarily provide evidence for protection or the status of the resources (McClanahan et al. 2015). Managing biomass on large scales is likely to be one of the simplest and most effective targeted approaches to protect biodiversity while maintaining optimal fisheries yields. Therefore, ensuring that stocks do not fall below optimal yield levels (~500 kg/ha) is a practical goal to get both food security and conservation benefits. By focusing on this goal, it is possible to indirectly protect fish biodiversity, maximize yields, and manage other ecological processes which promote the integrity of coral reef ecosystems (McClanahan 2018).

Biomass is managed through the usual restrictions on access, fishing gear, times, locations, and capture choices. People are more willing to agree to restrictions when local governance is effective (McClanahan and Abunge 2020). In general, managing fisheries for maximum sustained yields on large scales combined with closure areas approaching 30% of the nearshore fishery is expected to optimize management tradeoffs (Kerwath et al. 2013; McClanahan 2021, 2022). Moreover, these closures need to exceed 5 km^2 in area to achieve their potential to restore fish biomass.

In our study, coral reef biodiversity was primarily driven by environmental forces of temperature stresses, water quality, currents, and waves. Our model found that both coral quality and fish stocks were affected by the historical patterns of acute and chronic stress and not just by a period of excessive heat. In fact, modest amounts of increased heat appeared to promote corals acclimation to climate change. Therefore, high environmental variability around Mozambique suggests low tolerance to excess heat but some resilience via high environmental spatial variation. Consequently, it is recommended to monitor coral communities in various environmental locations, such as many of the smaller priority locations identified in this report, to better understand the responses to environmental conditions and ultimately protecting a greater diversity of coral habitats (McClanahan 2019).

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ANNEX 1:

Table 5. Summary of the locations identified in the WIO survey of high biodiversity locations for Mozambique. The sum of criteria from this report is the four spatial scales times the 3 metrics of coral, fish, and the combined proxy. Selection in the 3 past prioritization publications for the WIO are shown. Orange shading represents new locations identified in the WIO report.

Ecoregion name	Country	Location name	WWF EAME Priority Sites	World Heritage Marine Sites of Outstanding value	SWIOFP Biodiversity hotspots	Sum Criteria (This report)	Sum Criteria (Regional Reports)	Marine protected areas (WDPA)
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	Mozambique	Quionga - Ilha Metundo	Mtwara - Quirimbas	Quirimbas-Mnazi Bay complex		12	2	
East African Coral Coast	Mozambique	Nangata - Nacala	Nacala - Mossuril			12	1	
East African Coral Coast	Mozambique	Matiquite - Messonta	Nacala - Mossuril			10	1	
East African Coral Coast	Mozambique	Pemba	Mtwara - Quirimbas	Quirimbas-Mnazi Bay complex	Quirimbas archipelago (19)	8	3	Quirimbas

Ecoregion name	Country	Location name	WWF EAME Priority Sites	World Heritage Marine Sites of Outstanding value	SWIOFP Biodiversity hotspots	Sum Criteria (This report)	Sum Criteria (Regional Reports)	Marine protected areas (WDPA)
East African Coral Coast	Mozambique	Lurio - Memba bay				8	0	
East African Coral Coast	Mozambique	Ilha Metundo - Quiterajo	Mtwara - Quirimbas	Quirimbas-Mnazi Bay complex	Quirimbas archipelago (19)	6	3	
East African Coral Coast	Mozambique	Mokambo bay - Quinga				6	0	
East African Coral Coast	Mozambique	Messonta - Mossuril bay	Nacala - Mossuril			5	1	
Bight of Sofala/Swamp Coast	Mozambique	Quinga - Angoche island				5	0	
Delagoa	Mozambique	Ponta do Ouro			Ponta do Ouro (20)	4	1	Ponta do Ouro
East African Coral Coast	Mozambique	Luguni - Mecufi				4	0	

Ecoregion name	Country	Location name	WWF EAME Priority Sites	World Heritage Marine Sites of Outstanding value	SWIOFP Biodiversity hotspots	Sum Criteria (This report)	Sum Criteria (Regional Reports)	Marine protected areas (WDPA)
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	
Bight of Sofala/Swamp Coast	Mozambique	Ilha do Fogo				3	0	Primeiras and Segundas
Delagoa	Mozambique	Inhaca Island	Maputo - Machangulo complex		Baixo Danae (24), Inhaca Island (29), Berreira Vermelha (23)	2	2	Ponta do Ouro
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	