

ARTICLE

Evaluation of the full set of habitat suitability models for vulnerable marine ecosystem indicator taxa in the South Pacific high seas

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Abstract

In the high seas, regional fishery management organisations are required to implement measures to prevent significant adverse impacts on vulnerable marine ecosystems (VMEs). Our objectives were to develop habitat suitability models for use in the spatial management of bottom fisheries in the South Pacific and to evaluate these and existing models using independent data from high-quality seafloor imagery. Presence-only models for seven VME indicator taxa were developed to complement previous modelling. Evaluation of habitat suitability models using withheld data indicated high mean True Skill Statistic scores of 0.44–0.64. Most habitat suitability models performed adequately when assessed with independent data on taxon presence and absence but were poor surrogates for abundance. We therefore advocate caution when using presence-only models for spatial management and call for more systematically collected data to develop abundance models.

KEYWORDS

ecological niche modelling, fisheries management, marine spatial planning, species distribution modelling, vulnerable marine ecosystems

1 | INTRODUCTION

The United Nations General Assembly (UNGA) passed resolutions that require regional fishery management organisations (RFMOs) to prevent significant adverse impacts (SAIs) on Vulnerable Marine Ecosystems (VMEs) (UNGA, 2006, 2009, 2011). SAIs are impacts that compromise an ecosystem's structure or function, such as a significant loss of species richness, habitat, or community types on more than a temporary basis (FAO, 2009). VMEs are ecosystems susceptible to substantial alteration from acute or chronic disturbance due to inherent characteristics such as slow growth rates, longevity, late maturity, and fragility of component species

(FAO, 2009). Based on these characteristics, RFMOs have identified VME indicator taxa that represent species or broader taxonomic groups considered to be vulnerable to fishing impacts, to have ecological significance, and to be readily identified in trawl or longline catches (e.g., Parker & Bowden, 2010). The presence of VME indicator taxa as fishing bycatch is used to inform VME encounter protocols (so-called move-on rules) (e.g., Parker et al., 2009), and to design and implement spatial management measures (e.g., Durán Muñoz et al., 2012), both of which are intended to help prevent SAIs to VMEs (Ardrón et al., 2014). To design spatial management measures, available VME indicator taxa data for areas under the jurisdiction of RFMOs are assembled and

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analysed, and where site-specific information is lacking or limited, some form of spatial model prediction is typically used to infer 'the likely presence of vulnerable populations, communities, and habitats' (FAO, 2009).

Currently, no specific density thresholds define a VME, but density is key for the formation of structurally complex habitats and ecosystem functioning (Thurber et al., 2014). Recent attempts to develop consensus on what constitutes a VME, however, show this is not a simple task because some VMEs can be identified by a single image (e.g., scleractinian reefs), while a single coral colony providing habitat for other taxa in an image presents a greater challenge (Baco et al., 2023). Broad-scale density information would provide additional context surrounding single images to enable informed density threshold determination across large geographic scales [e.g., following methodology suggested by Rowden et al. (2020)]. However, available imagery data in many regions does not currently permit this approach, and spatially explicit estimates of VME indicator taxa distribution are not suitable for this task (Bowden et al., 2021). Nevertheless, spatial estimates of occurrence can provide useful information for management in the absence of density estimates (Stephenson et al., 2021). Habitat suitability models are statistical models that predict the distribution of broadly suitable environmental ranges for species in relation to available environmental variables (Guisan & Zimmermann, 2000). Such models are seen as useful for marine ecosystem management (Reiss et al., 2014) and particularly for predicting the distribution of suitable habitat (and therefore the likely species distribution) for VMEs in the deep sea, where field surveys are logistically difficult, expensive, and not feasible to directly observe an entire area of interest (Vierod et al., 2014).

Spatial management areas were established in the western portion of the South Pacific Regional Fisheries Management Organisation Convention Area (hereafter referred to as the 'SPRFMO area') in 2019 (SPRFMO, 2023a) with an aim to protect suitable habitat for VME indicator taxa while providing access for sustainable use of fisheries resources. The size and configuration of spatial management areas were based on habitat suitability models for 6 of 13 VME indicator taxa defined for the SPRFMO area (in Annex 5 of CMM-03-2022; Anderson et al., 2016; Georgian et al., 2019; Stephenson et al., 2021) using presence-only modelling (i.e., presence point-sample locations were combined with informed pseudo-absences to estimate environmental ranges of species). Porifera and Scleractinia were represented by more than one taxon (i.e., more than one habitat suitability model). The Order Scleractinia was represented in the SPRFMO area by four species with individual habitat suitability models: *Enallopsammia rostrata*, *Madrepora oculata*, *Solenosmilia variabilis*, and *Goniocorella dumosa*. The phylum Porifera was represented by separate habitat suitability models for the classes Demospongiae and Hexactinellida.

Ten habitat suitability models were developed for the SPRFMO-evaluated area (Anderson et al., 2016; Georgian et al., 2019; Stephenson et al., 2021) and were statistically evaluated using independent (presence-only) evaluation data from seafloor imagery (Stephenson et al., 2021). This independent evaluation (i.e., testing of

the model's predictive power with independent samples) indicated that the models had high predictive power, including parts of the study area where previously there were few records (Stephenson et al., 2021). Despite these promising results, the results of presence-only models must be interpreted carefully because sample data are known to suffer from spatial bias (Wadoux et al., 2021), and therefore data used in the evaluation of a model may also suffer from bias, even if they are independent, thereby resulting in overly optimistic model evaluation metrics (Valavi et al., 2019). Where possible, habitat suitability models should be validated using independent, well-stratified (non-spatially biased) data (Bowden et al., 2019, 2021; Howell et al., 2022).

Since the early 2000s, quantitative information on seafloor taxa has been collected using non-destructive photographic methods in New Zealand and Australia (e.g., Althaus et al., 2009; Bowden et al., 2020; Clark & Rowden, 2009). In New Zealand, imagery data has been collected since 2006 using a towed camera, the Deep-Towed Imaging System (DTIS, Bowden & Jones, 2016; Hill, 2009). These data are quantitative, so they provide the opportunity to generate spatial estimates of the probability of a taxon being present, rather than simply habitat suitability derived from presence-only models, and to model taxon abundance, thereby moving beyond simply predicting occurrences. Additionally, these data have been collected independently of fisheries and have not been used in earlier modelling, so they can also be used for independent assessment of existing and new models generated using conventional data from bycatch and museum records, including presence-only models (Bowden et al., 2019).

The seven SPRFMO VME indicator taxa that have not previously been modelled are Actiniaria (anemones), Alcyonacea (soft corals), Zoantharia (hexacorals), Hydrozoa, Bryozoa, Brisingida (armless seastars), and Crinoidea (sea lilies and feather stars). It should be noted that habitat suitability models were generated for Brisingida and Crinoidea by Anderson et al. (2016) but were not updated for Georgian et al. (2019) or Stephenson et al. (2021) since these were not considered good VME indicators for use in developing the spatial management measures at the time. The absence of habitat suitability models (or updated models) for these seven VME indicator taxa limits the development and evaluation of the performance of spatial management measures and the encounter protocol for protecting these taxa. Therefore, our objective was to generate habitat suitability models for VME indicator taxa not previously modelled and evaluate the predictive power of habitat suitability models for VME indicator taxa. To achieve our objective, we: (1) developed models for seven more VME indicator taxa to provide a full complement of habitat suitability models for all 13 VME indicator taxa listed in Annex 5 of the SPRFMO Convention CMM-03-2022; and (2) used a well-stratified independent dataset with robust absences and high-quality seafloor imagery data that became available after the models were developed to evaluate the full suite of habitat suitability models, including all 17 habitat suitability models developed for all 13 VME indicator taxa, to provide a more objective view of the predictive power of the models.

2 | METHODS

Habitat suitability models (presence-only) were created as described by Stephenson et al. (2021), and closely followed methods used in spatial modelling studies for New Zealand waters (Anderson, Stephenson, & Behrens, 2020; Stephenson et al., 2020). Ensemble models were created based on predictions from boosted regression tree (BRT, Elith et al., 2006), random forest (RF, Breiman, 2001), and maximum entropy (MaxEnt, Phillips et al., 2006).

2.1 | Study area

The SPRFMO Convention Area encompasses southern parts of the Pacific Ocean beyond areas of national jurisdiction (i.e., in the high seas), from 10°N to 60°S and 120°E to 67°W (SPRFMO, 2022). Models of VME indicator taxa distributions were constrained to an area encompassing the southwestern part of the SPRFMO Convention Area, much of the New Zealand Exclusive Economic Zone (EEZ), and parts of the EEZs of Australia, New Caledonia, Fiji, and Tonga in depths of 200–3000m (hereafter referred to as the study area, see Figure 1). This study area included parts of the SPRFMO Convention Area where spatial management measures have been implemented, including Louisville Seamount Chain, Lord Howe Rise, and West Norfolk Ridge (Figure 1). High-resolution (1km×1km grid) environmental data available for modelling the study area and depth range represented the approximate combined bathymetric range of all modelled taxa (Stephenson et al., 2021).

2.2 | Occurrence data

Biological data used to train habitat suitability models included taxon occurrences (presence-only) from New Zealand and Australian museum and collection records, fisheries research databases, and online biodiversity datasets (Geange et al., 2020). Records spanned from the early 1900s to 2020. Data were groomed before modelling, including assigning taxonomy, correcting positional (latitude and longitude) errors (where impossible, records were removed), removing records outside the study area depth range (200–3000m), and removing duplicate records.

Habitat suitability modelling required presence and absence data for modelled taxa. The presence-only models developed here employed the same approach used by Stephenson et al. (2021). Briefly, absence records were not available across the study area at the scale and quantity required for modelling, so target-group background data were used (Phillips et al., 2009). This approach maintained that grid cells with presence records for other taxa in the dataset from the same broad biological group as a modelled taxon, collected using similar methods with the same sampling biases, were treated as absences of the taxon being modelled. This assumes that if a modelled taxon was present in a grid cell where another taxon was present, a record would also have been obtained for the modelled taxon. Absence of a modelled taxon is not a guarantee when using this approach, but absences were more likely to be real than randomly generated pseudo-absences (Phillips et al., 2009; Stephenson et al., 2020, 2021). Target-group background absences within the same grid cell as presences for a modelled taxon were excluded, and absences were only retained if the sampling gear of

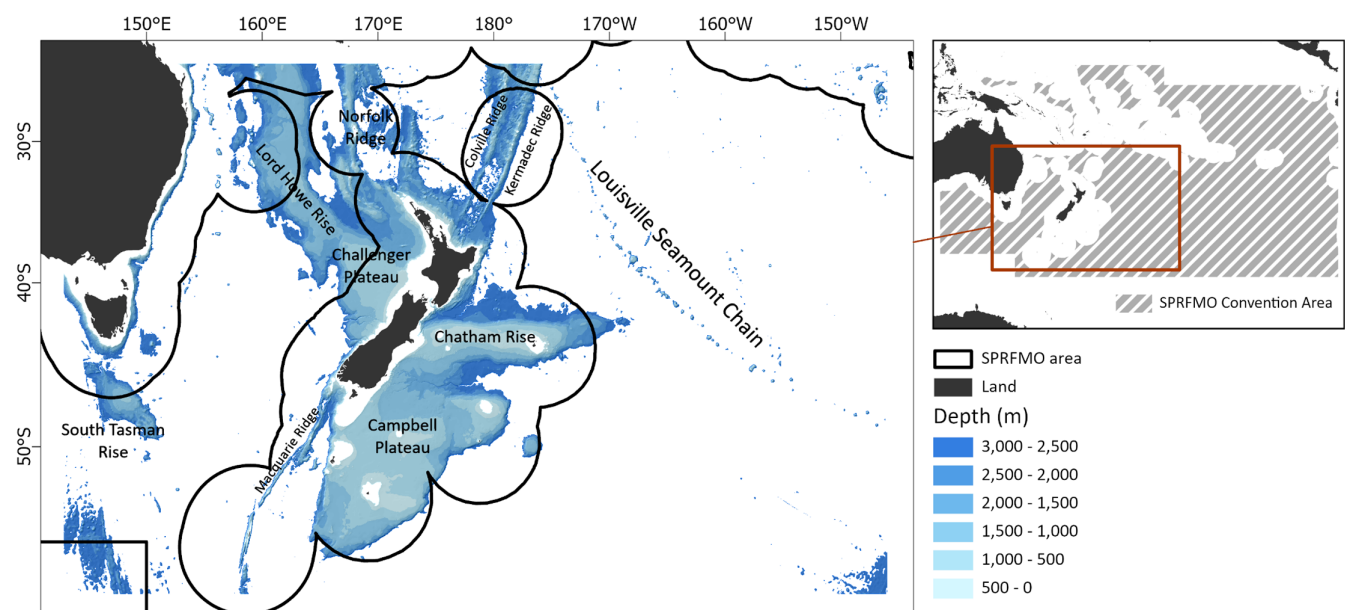


FIGURE 1 Study area (modelled extent indicated by bathymetry) for developing habitat suitability models for vulnerable marine ecosystem indicator taxa in the South Pacific Regional Fisheries Management Organisation (SPRFMO) Convention Area, New Zealand, and Australia. The black line in the main map and the hatched area in the inset indicate the extent of the SPRFMO Convention Area. The SPRFMO area refers to the western portion of the SPRMFO Convention Area (the extent of the SPRFMO Convention Area encompassed within the brown bounding box).

a given target-group background absence was represented in the presence dataset. The number of target-group background absences used in model training was equal to the number of presences for the boosted regression tree and random forest models up to a fixed 10,000 records for Maximum Entropy models (see below and in Stephenson et al., 2021).

The dataset used for training models consisted of 13,825 occurrence records for Actiniaria, Brisingida, Bryozoa, Crinoidea, Hydrozoa, and Zoantharia, combined with the groomed dataset used to train the ten presence-only models for six VME indicator taxa (10 modelled taxa) created by Stephenson et al. (2021), which included Alcyonacea (non-Gorgonians). The final dataset included 23,728 presence point-sample location records for VME indicator taxa for training models (Table 1). The Alcyonacea group was modelled without occurrence records for Actiniaria, Brisingida, Bryozoa, Crinoidea, Hydrozoa, and Zoantharia because it was modelled at an earlier date, before additional data were available. The location of presences and target-group background data were mapped for each modelled taxon (Appendix S1: Figures S1–S7).

2.3 | Environmental data

Environmental variables used in presence-only models were the same as those used by Georgian et al. (2019), with an updated version of particulate organic carbon export to the seafloor used by Stephenson et al. (2021) (Table 2). Environmental variables used for all taxa included ruggedness, slope (SD), bathymetric position index (broad), seamounts, dissolved oxygen and temperature at depth, and particulate organic carbon export. Calcite saturation was used for Alcyonacea, Brisingida, Crinoidea, and Bryozoa. Either percent mud or percent gravel was used for each taxon, and the choice of substrate variable included in each taxon-specific model was selected using a single random forest model (Stephenson, Brough, et al., 2023), implemented using the *extendedForest* package in R (Liaw & Wiener, 2002), that retained the substrate variable that contributed the most to the model (Appendix S1: Table S1).

2.4 | Ensemble modelling and internal evaluation

BRT, RF, and MaxEnt models were bootstrapped by resampling a single dataset to generate sampled distributions 100 times for each VME indicator taxon. For each bootstrap, the dataset was split into two parts: (1) training and (2) evaluation. To create the training set, random samples were taken with a sample size equal to the number of presence records (sampled with replacement). An equal number of randomly selected target-group background data or absence records were then taken, also with replacement. For internal evaluation, an evaluation dataset was then generated by randomly sampling from the remaining data (i.e., data not included in the training dataset) using the same procedure (i.e., random sampling with replacement).

Due to the use of replacement when randomly sampling training and evaluation datasets, the proportion of unique records used for training, and withheld for evaluation was different for each bootstrap. Models were trained with the training set within each bootstrap, and spatial predictions were evaluated using the iteratively withheld evaluation dataset (and the training set).

For each bootstrap, geographic distributions were predicted using predictor variables to a 1km×1km grid cell. On completion of bootstrapping, mean spatial predictions of habitat suitability (as a Habitat Suitability Index or HSI from 0 to 1) were calculated, along with standard deviation (SD). Predictions from the three model types were ensembled using weighting strategies described by Stephenson et al. (2021) and Anderson, Stephenson, and Behrens (2020). Briefly, the procedure derives a two-part weighting (W1 and W2) for each component (BRT, RF, and MaxEnt) of the ensemble model, by taking equal contributions from overall model performance (W1; based on the iteratively withheld evaluation data) and uncertainty in each cell (W2; SD). The area under the Receiver Operating Characteristic curve (AUC) performance metric and SD were used within the weighting procedure for the ensemble (Appendix S1).

Model performance was assessed using the AUC and true skill statistic (TSS) (Allouche et al., 2006; Hosmer et al., 2013; Komac et al., 2016). The TSS ranges from -1 to 1, where 1 indicates perfect agreement, -1 is equal to random chance, and a value >0.6 is considered adequate (Allouche et al., 2006). The AUC metric ranges from 0 to 1, where 0.5 indicates model performance is equal to random chance, >0.7 indicates adequate performance, and >0.80 indicates excellent performance (Hosmer et al., 2013). AUC and TSS scores were derived for BRT, RF, and MaxEnt models for each bootstrap using training and evaluation data. All statistical analyses were done in R (R Core Team, 2022) using the *dismo* (Hijmans et al., 2017), *gbm* (Ridgeway, 2007), and *raster* (Hijmans et al., 2015) packages.

2.5 | Environmental coverage

When predicting into unsampled space, it is important to consider how well the training data used captures the environmental variables in the projected space (Elith et al., 2010), that is, how similar environmental conditions are in data-rich areas compared to data-poor areas (Bridges et al., 2023). Training dataset coverage of environmental space was estimated for presence-only models, as described by Stephenson et al. (2020, 2021) and others (Pinkerton et al., 2010; Smith et al., 2013). In short, environmental coverage was estimated as the extent to which the environmental space (the multidimensional space that considers all environmental variables in sympatry) was captured by the training data. Environmental coverage approaching 1 is considered to be well captured by training data (more confidence in modelled relationships and predictions), whereas environmental coverage approaching 0 is considered to be less well captured by training data, so modelled relationships and predictions are less reliable and should be interpreted with greater caution (Pinkerton et al., 2010; Smith et al., 2013).



TABLE 1 Vulnerable marine ecosystem (VME) indicator taxon, sample size (number of presences), and target group background data available for developing habitat suitability models for VME indicator taxa in the South Pacific Regional Fisheries Management Organisation Convention Area, New Zealand, and Australia.

Group	Taxon	Training data sample size	
		Presences	Target-group background absences
Actiniaria	Sea anemones	8540	2446
Alcyonacea	Soft corals	515	7424 ^a
Brisingida	'Armless' stars	931	9567
Bryozoa	Bryozoans	725	10,173
Crinoidea	Sea lilies and feather stars	793	10,102
Hydrozoa	Hydroids	1159	9860
Zoantharia	Hexacorals	1016	9600

^aTarget group background data for the Alcyonacea model did not contain records for Actiniaria, Brisingida, Crinoidea, Hydrozoa, or Zoantharia. Instead, target group background data only comprised point-sample locations of taxa modelled in Stephenson et al. (2021) from the same dataset used therein.

TABLE 2 Environmental variables used for habitat suitability models of vulnerable marine ecosystem indicator taxa in the South Pacific Regional Fisheries Management Organisation Convention Area, New Zealand, and Australia.

Variable	Units	Native resolution	Source
Seafloor characteristics			
Percent gravel	%	1 km ²	Bostock et al. (2019)
Percent mud	%	1 km ²	Bostock et al. (2019)
Ruggedness ^a		1 km ²	Derived from bathymetry (Mackay et al., 2015)
Slope SD ^a		1 km ²	Derived from bathymetry (Mackay et al., 2015)
Bathymetric position index—broad		1 km ²	Derived from bathymetry (Mackay et al., 2015)
Seamounts			Rowden et al. (2008) and Yesson et al. (2011)
Water chemistry			
Calcite saturation at depth		0.5°	Bostock et al. (2013)
Dissolved oxygen at depth	mLL ⁻¹	1°	Garcia et al. (2013)
Temperature at depth	°C	0.25°	Locarnini et al. (2013)
Productivity			
Particulate organic carbon export	mg C m ⁻² d ⁻¹	0.08°	Stephenson et al. (2021)

Note: Variables are listed, along with units (if applicable), and references are provided based on source of data. All environmental variables were sampled at a grid size of 1 km × 1 km.

^aTerrain metrics calculated using window sizes of five cells (1 km × 1 km).

To estimate environmental coverage, all grid cells with a sample were considered 'presences' (=1), and an equal number of background samples were obtained randomly from unsampled space (all grid cells without a sample within their bounds, 1 km × 1 km grid) as 'absences' (=0). A single BRT model was then used to model the relationship between the 12 environmental variables used in the VME indicator taxa distributions (environmental space) and sampling density. The model settings used were the same as Stephenson et al. (2021); BRT models were fitted using a Bernoulli error distribution, a learning rate that yielded 2000 trees, and an interaction depth of 2 (so that only pair-wise combinations of environmental variables were considered).

2.6 | Independent model evaluation

An independent image-based dataset, derived from analyses of seafloor photographic transects (video and stills) collected with the Deepwater Towed Video System (DTIS) during 20 surveys in the waters around New Zealand from 2007 to 2020, was used to evaluate models, including those by Stephenson et al. (2021). The DTIS dataset was originally developed by Bowden et al. (2019) and Anderson, Pallentin, et al. (2020) and has since been added to photographic analyses from multiple other voyages (Anderson et al., 2023). Like occurrence data used for training habitat suitability models, image-based data was limited to 200–3000 m

depths within the study area. For evaluating habitat suitability models, 832 sites were available (785 unique locations or grid cells). The full dataset included abundance estimates for 74 taxa, but the dataset was reduced to include only modelled taxa (17 total; 13 VME indicator taxa). For each taxon, abundance information was converted into binary presence-absence depending on whether any abundance of a taxon was recorded within a grid cell (1 km × 1 km). Various fit metrics were derived using image-based presence-absence data, and the full suite of 17 VME indicator taxa habitat suitability models. AUC, TSS, sensitivity (true positive rate), and specificity (true negative rate) were calculated using the *pROC* package in R (Robin et al., 2011). The relationship between habitat suitability and abundance ($\log(\text{abundance} + 1)$, where abundance = individuals per 1000 m²) in the independent image-based dataset was evaluated with scatter plots [*ggplot2* in R; Wickham (2011)] and a coefficient of determination (R^2).

Some of the data were used to train the Stephenson et al. (2021) models, including 173 unique presence point-sample locations provided to the training dataset for those previous models by this 'independent' dataset. For six models, <50 point samples were provided for training; for four models, 50–100 point-samples were provided; and for Demospongiae, 112 point-samples were provided. At least 720 of the point samples in the evaluation dataset were 'new', so image-based data accounted for <2.5% of the data available for the Stephenson et al. (2021) models. Therefore, we refer to the

image-based dataset as independent, while acknowledging that some data were not strictly independent.

3 | RESULTS

3.1 | Environmental coverage

Taxon models for the Chatham Rise, Louisville Seamount Chain, and shallower areas within New Zealand's and Australia's EEZ were predicted with high environmental coverage (approaching 1). Areas of moderate environmental coverage (~0.4–0.6) were predicted across much of the Campbell Plateau, Challenger Plateau, and much of the northwest space in the study area (Figure 2). Areas of low environmental coverage (approaching 0) were predicted primarily in deeper portions of the study area, north of the Chatham Rise, and in much of the northwest portion of the study area within and between the EEZs of New Zealand and Australia (Figure 2).

3.2 | Habitat suitability models

Presence-only models for seven VME indicator taxa not previously modelled (Figures 3 and 4; Appendix S1: Figures S8–S19) yielded good to excellent model performance scores based on iteratively

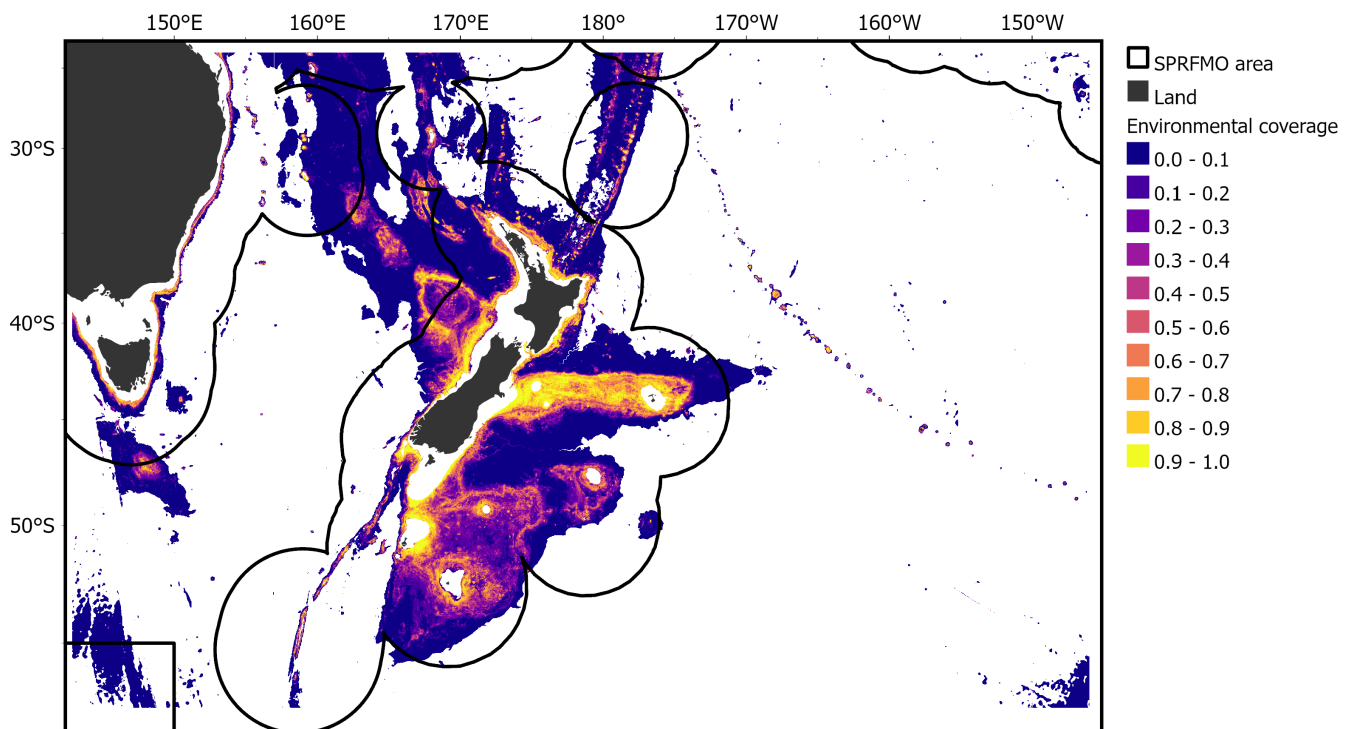


FIGURE 2 Environmental coverage (0–1) between 200 and 3000 m depth, where habitat suitability models were developed for vulnerable marine ecosystem indicator taxa in the South Pacific Regional Fisheries Management Organisation Convention Area, New Zealand, and Australia. Low values of environmental coverage (purple) indicate parts of the environmental space that contained few samples, meaning greater caution should be placed on the predictions. Environmental coverage is generated using the training data used to create the habitat suitability models.

withheld (internal) evaluation data. AUC scores ranged from 0.79 to 0.99, and TSS scores ranged from 0.44 to 0.91 (Table 3). The standard deviation of AUC and TSS scores ranging between 0.002 and 0.04 indicated that models consistently performed across bootstrap samples (Table 3). All three models in the ensemble (RF, BRT, and MaxEnt) performed well, though the RF model (mean AUC/TSS=0.89/0.65) performed slightly better than the BRT model (mean AUC/TSS=0.85/0.56) and the MaxEnt model (mean AUC/TSS=0.82/0.53). The ensemble spatial prediction for Crinoidea (sea lilies and feather stars, Figure 3), as an example, indicated high habitat suitability (0.8–1.0) along much of the continental shelf breaks (including the northwest part of the Challenger Plateau in the SPRFMO area), seamounts (including the Louisville Seamount Chain in the SPRFMO area), the Macquarie, Kermadec, and West Norfolk ridges (the latter is in the SPRFMO area), and parts of the Chatham, Lord Howe, and South Tasman rises (the latter two features are in the SPRFMO area). Moderate habitat suitability (HSI ~0.5) was predicted within some shallower areas of the study area

(<1000m), including parts of the central Challenger Plateau and Chatham Rise in the New Zealand EEZ and parts of the Lord Howe and South Tasman rises and West Norfolk Ridge in the SPRFMO area. Conversely, moderate habitat suitability (HSI ~0.5) was also predicted in some of the deepest areas of the study area (>2500m), including north of the Chatham Rise. Low habitat suitability (HSI <0.2) was predicted across much of the Campbell Plateau and parts of the Challenger Plateau, and the deepest areas (>1500m) were in the EEZs and SPRFMO area. Low uncertainty (low SD) associated with the spatial prediction of habitat suitability for Crinoidea is mapped across most of the Campbell Plateau (Figure 4), moderate-high uncertainty (>0.15, SD) is mapped along much of the northern area of the Chatham Rise in the New Zealand EEZ and along the Louisville Seamount Chain and central Challenger Plateau in the SPRFMO area, and moderate uncertainty (0.1–0.15, SD) is mapped within many of the moderately deeper areas of the SPRFMO area (>2500m) along the western edge of West Norfolk Ridge and South Tasman Rise.

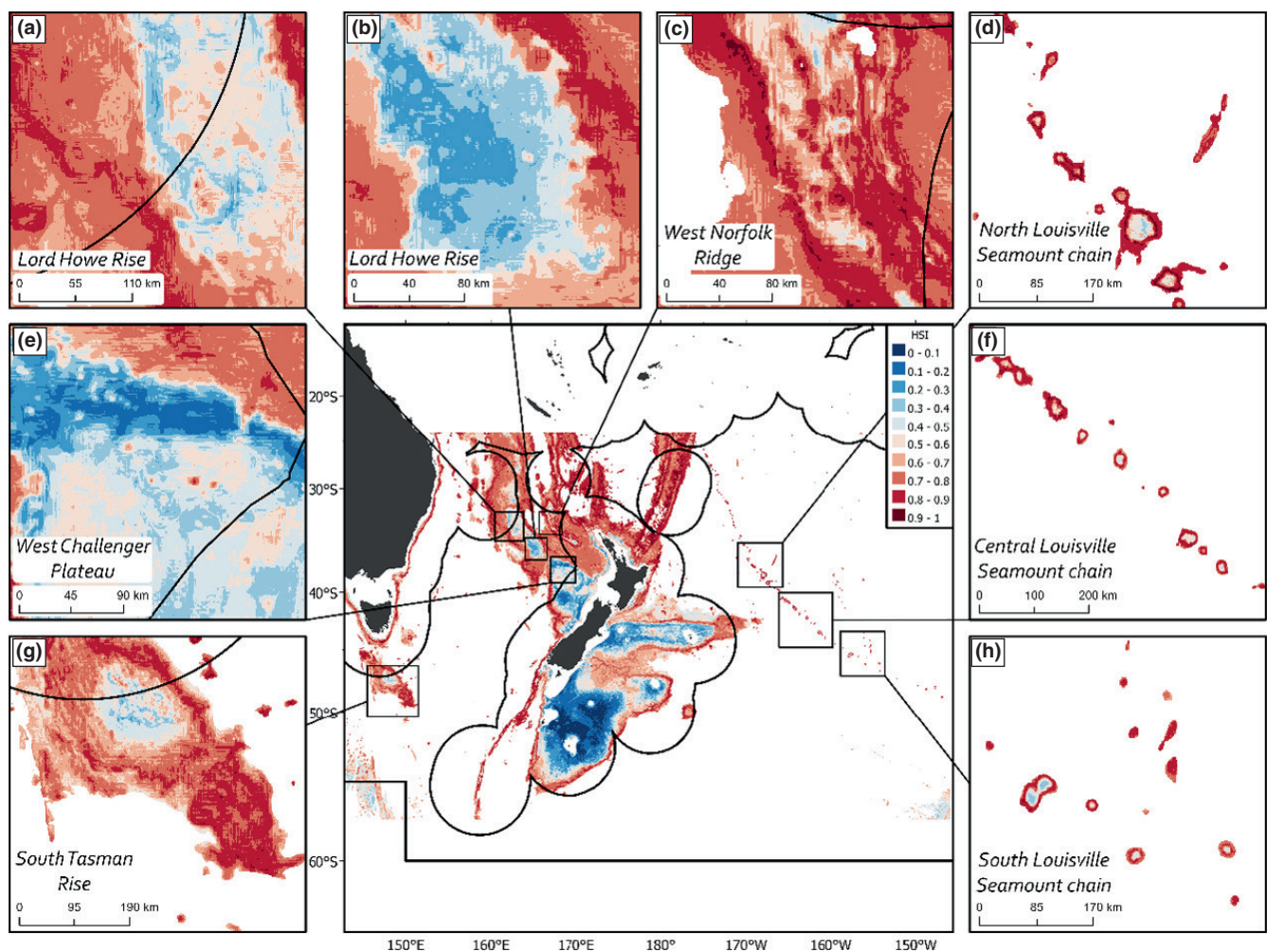


FIGURE 3 Mean predicted habitat suitability index (HSI) for Crinoidea in the South Pacific Regional Fisheries Management Organisation (SPRFMO) Convention Area, New Zealand, and Australia. Black lines indicate the boundary of the SPRFMO area (area outside of exclusive economic zones; see Figure 1). (a–h) Insets are provided for various fisheries management areas (FMAs) within the SPRFMO area.

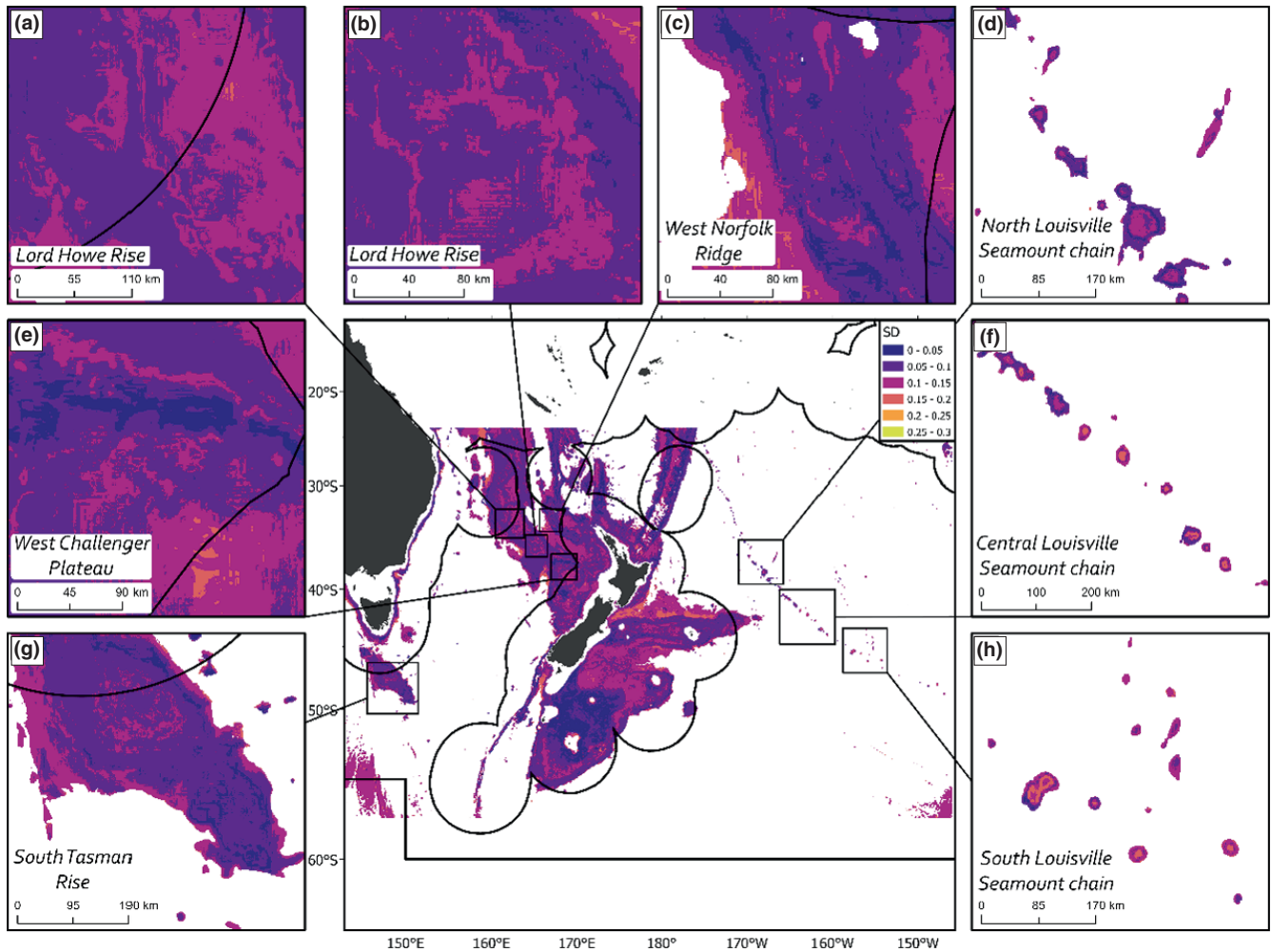


FIGURE 4 Mean predicted ensemble model uncertainty (SD: standard deviation) for Crinoidea in the South Pacific Regional Fisheries Management Organisation (SPRFMO) Convention Area, New Zealand, and Australia. Black lines indicate the boundary of the SPRFMO area (area outside of exclusive economic zones; see Figure 1). (a–h) Insets are provided for various fisheries management areas (FMAs) within the SPRFMO area.

TABLE 3 Performance metrics for habitat suitability models of vulnerable marine ecosystem indicator taxa in the South Pacific Regional Fisheries Management Organisation Convention Area, New Zealand, and Australia.

Group	HSI model fit metrics (mean AUC and TSS)					
	BRT		RF		MaxEnt	
	AUC	TSS	AUC	TSS	AUC	TSS
Actiniaria	0.86 (0.01)	0.58 (0.02)	0.89 (0.01)	0.64 (0.02)	0.84 (0.01)	0.56 (0.02)
Alcyonacea	0.83 (0.01)	0.51 (0.02)	0.99 (0.002)	0.91 (0.01)	0.82 (0.01)	0.50 (0.02)
Brsingida	0.85 (0.02)	0.58 (0.03)	0.88 (0.01)	0.61 (0.03)	0.82 (0.02)	0.55 (0.03)
Bryozoa	0.83 (0.02)	0.54 (0.03)	0.86 (0.02)	0.57 (0.03)	0.80 (0.02)	0.48 (0.04)
Crinoidea	0.86 (0.02)	0.60 (0.03)	0.88 (0.01)	0.63 (0.03)	0.83 (0.01)	0.54 (0.03)
Hydrozoa	0.82 (0.01)	0.51 (0.02)	0.85 (0.01)	0.56 (0.03)	0.79 (0.01)	0.44 (0.02)
Zoantharia	0.88 (0.01)	0.62 (0.03)	0.89 (0.01)	0.63 (0.03)	0.87 (0.01)	0.63 (0.03)

Note: Values provide means (and standard deviation) from 100 bootstraps based on iteratively withheld evaluation data. For habitat suitability models, fits are provided for the boosted regression tree (BRT), random forest (RF), and MaxEnt (MaxEnt) models. Fits provided are based on binomial sensitivity and specificity, the area under curve (AUC), and the true skill statistic (TSS).



TABLE 4 Performance metrics for ensemble habitat suitability models using an independent image-based dataset of vulnerable marine ecosystem indicator (VME) taxa in the South Pacific Regional Fisheries Management Organisation Convention Area, New Zealand, and Australia.

VME indicator taxa	Taxa	AUC	TSS	Sensitivity	Specificity	R ²	Presences	Absences
Porifera	Demospongiae	0.733	0.451	0.643	0.808	0.086	499	286
	Hexactinallida	0.678	0.292	0.558	0.734	0.032	360	425
Scleractinia	<i>Enallopsammia rostrata</i>	0.966	0.818	0.952	0.866	0.213	21	811
	<i>Goniocorella alumosa</i>	0.871	0.605	0.783	0.823	0.216	69	716
	<i>Madrepora oculata</i>	0.869	0.644	0.722	0.921	0.113	18	814
	<i>Solenosmilia variabilis</i>	0.970	0.862	0.933	0.930	0.412	104	681
Antipatharia	Antipatharia	0.820	0.479	0.860	0.619	0.102	179	606
Alcyonacea	Alcyonacea (non-gorgonian)	0.656	0.258	0.573	0.685	0.097	239	546
Gorgonian Alcyonacea	Gorgonian Alcyonacea	0.708	0.314	0.549	0.764	0.081	344	441
Pennatulacea	Pennatulacea	0.632	0.227	0.427	0.800	0.043	370	415
Actiniaria	Actiniaria	0.683	0.270	0.773	0.497	0.034	608	177
Zoantharia	Zoantharia	0.755	0.418	0.734	0.683	0.051	128	657
Hydrozoa	Hydrozoa	0.522	0.047	0.607	0.440	0.000	399	386
Stylasteridae	Stylasteridae	0.928	0.730	0.833	0.898	0.366	209	576
Bryozoa	Bryozoa	0.541	0.106	0.442	0.664	0.001	371	414
Brisingida	Brisingida	0.615	0.187	0.490	0.697	0.015	247	538
Crinoidea	Crinoidea	0.759	0.395	0.758	0.637	0.133	289	496

Note: The number of presences and absences available for the evaluation of the respective VME indicator taxa is shown.

Abbreviations: AUC, area under curve; R², coefficient of determination; TSS, true skill statistic.

3.3 | Independent evaluation

The performance of our seven models and 10 models by Stephenson et al. (2021) varied from adequate or excellent to poor, depending on taxon and performance metric (Table 4). AUC and TSS ranged from very poor (AUC=0.52 and TSS=0.05) for Hydrozoa to excellent (AUC=0.97 and TSS=0.86) for *S. variabilis*. The mean AUC for all 17 VME indicator taxa was 0.75 (SD=0.14) and the mean TSS was 0.42 (SD=0.24). For 13 of 17 models, AUC >0.65, and for 8 of 17 models, TSS >0.4. Sensitivity and specificity measures highlighted taxon-specific false-negative and false-positive effects (Table 4). For example, for Pennatulacea, specificity was high (0.8), but sensitivity was very poor (0.427). In contrast, for Antipatharia sensitivity was high (0.86), but specificity was poor (0.619). For seven taxa, specificity >0.8, including Pennatulacea, Demospongiae, *G. dumosa*, Stylasteridae, *E. rostrata*, *M. oculata*, and *S. variabilis*. In contrast, for four taxa, sensitivity >0.8, including Stylasteridae, *S. variabilis*, *E. rostrata*, and Antipatharia. The relationship between observed abundance and HSI for the full set of 17 VME indicator taxa models was taxon-specific (Appendix S1: Figure S20). Three of the four Scleractinia (stony coral) models and the Stylasteridae model had R^2 >0.2, models for *M. oculata*, Crinoidea, and Antipatharia had R^2 values >0.1, and models of all other taxa ($n=10$) had R^2 <0.1 (Table 4).

4 | DISCUSSION

Here, we generated habitat suitability models for seven VME indicator taxa in the western portion of the SPRFMO Convention Area that were not previously modelled (Stephenson et al., 2021). Together, this modelling effort has resulted in the availability of habitat suitability models for all VME indicator taxa currently identified by SPRFMO (2022). The development of additional models meant that SPRFMO was able to fully complete its evaluation of the effectiveness of spatial closures implemented in 2019 (SPRFMO, 2023b). Without habitat suitability models for all VME indicator taxa, the effectiveness of these measures was uncertain. The latest evaluation of the effectiveness of recent adjustments to spatial closures indicated that at least 70% of suitable habitat (HSI values above a receiver operating characteristic determined threshold; generally, HSI >0.45) for all VME indicator taxa was protected within the Fishery Management Areas (SPRFMO, 2023b).

Previous efforts produced models for some of the VME indicator taxa modelled herein, including Brisingida and Crinoidea (Anderson et al., 2016). Despite somewhat differing datasets, the habitat suitability maps we produced were visually similar to those by Anderson et al. (2016). For instance, for both Crinoidea and Brisingida, low habitat suitability (<0.2) was predicted across much of the Campbell Plateau and Chatham Rise, and high habitat suitability (>0.8) was predicted in the Bounty Trough and on Lord Howe Rise. Furthermore, several areas of high habitat suitability (>0.8) common to many VME indicator taxa we modelled matched those of other VME indicator taxa previously modelled, including high habitat suitability along the

Kermadec and Macquarie ridges for Stylasteridae and Hexactinellida (Anderson et al., 2016; Georgian et al., 2019) and Brisingida, Hydrozoa, Crinoidea, and Bryozoa (this study). Finally, while habitat suitability for Actiniaria was visually dissimilar to other modelled VME indicator taxa (this study), some patterns were similar to habitat suitability for Hexactinellida; for instance, areas of the Chatham Rise, Challenger Plateau, and large areas of the Campbell Plateau were predicted to have moderate (>0.6) to high (>0.8) habitat suitability, and areas along the North Chatham Rise and Bounty Trough were predicted to have low habitat suitability (<0.4) by Georgian et al. (2019) and Stephenson et al. (2021). Reliability of predicted distributions from presence-only models depends on the quality of available response data, the quality and ecological relevance of predictors, and how the models were constructed. Many issues identified with habitat suitability models require attention if such models can be confidently and routinely used in decision-making for the management of marine resources (Stephenson et al., 2021; Winship et al., 2020). Therefore, the accuracy of habitat suitability model predictions must be evaluated and improved to support the design and implementation of existing spatial management measures (Bowden et al., 2021).

We used spatially independent evaluation data to build on an earlier evaluation of habitat suitability models using independent data, which had the same spatial biases as the data used to develop the models (Stephenson et al., 2021). Importantly, the towed video surveys used as the independent dataset purposefully targeted unfished areas, compared to the model fitting dataset that was somewhat biased towards fished areas. Validation metrics for both the model-fitting dataset and the independent dataset provide context about model performance. In contrast to an earlier study, we found that model predictive power was generally lower and more variable among taxa when assessed using independent, well stratified, presence-absence data (Stephenson et al., 2021). Contrary to expectations of presence-only models, presence was not more consistently classified than absence (i.e., higher sensitivity compared to specificity) when assessing model fits with presence-absence data, similar to another study, where comparably poor sensitivity was ascribed to under-representation of aspects of a taxon's ecological niche in the dataset used to build the model (Howell et al., 2022). Despite lower predictive power, we found that most habitat suitability models performed adequately, with only two VME indicator taxa (Hydrozoa and Bryozoa) considered to be performing poorly (AUC <0.55), although both models were at class and phylum taxonomic levels, and therefore comprise many different (hundreds in the study area) species. Coarse taxonomic resolution means that many species, with different life-histories and environmental requirements, are included under a single nominal taxon, so models may not accurately represent a niche (Winship et al., 2020). Mixed-species models of VME indicator taxa might therefore overly predict broad distributions regardless of whether they are developed using presence-only, presence-absence, or abundance data, because interspecific environmental niches are conflated in the model.



Habitat suitability models predict relative habitat suitability of a taxon (i.e., the likely distribution of the taxon), rather than expected abundance of a taxon. In the absence of abundance models, habitat suitability models provide best estimates of distributions of modelled VME indicator taxa in an environment that is data-limited in faunal distributions and physical habitat characteristics. However, knowledge of spatial variation in taxon abundance is of greater value for informing the management of VMEs (Ardron et al., 2014). For example, the functional significance of the presence of a single stony coral colony at a site will be different from the functional significance of a high density of stony coral colonies that provide complex physical structures upon which other taxa and ecological processes are highly dependent (sensu the definition of VMEs in paragraph 42 of the FAO International Guidelines for the Management of Deep-sea Fisheries in the High Seas, FAO, 2009). Although several studies have assessed whether habitat suitability models can be used as surrogates for abundance distributions (Pitcher et al., 2019; Rullens et al., 2021), our findings and Bowden et al. (2021) illustrated that they do not provide accurate proxies for abundance for many models produced here and by Stephenson et al. (2021). Some taxa were exceptions, notably *S. variabilis*, likely because a species-level model was used for a taxon with a comparatively narrow environmental niche (typically present on seamounts) in the study area. In contrast, phylum- and class-level models for Bryozoa and Hydrozoa were poor. Some relationships between predicted habitat suitability and abundance may be non-linear (Monnier-Corbel et al., 2023; Vanderwal et al., 2009). We found that habitat suitability for some taxa corresponded well with the upper limit of abundance, while mean abundance was less well indicated.

Despite our success in developing habitat suitability models for VME indicator taxa for the SPRFMO area and the use of those models for evaluating the effectiveness of spatial management measures implemented to prevent SAIs in VMEs, abundance models are now needed for these taxa (Stephenson et al., 2021). Similar sentiments have been voiced by scientists mapping VME distributions in the northeast Atlantic, given that habitat suitability models do not predict aggregations (Howell et al., 2022). Though taxon-specific, density is central to the VME concept (Baco et al., 2023), because density of habitat for species is inately linked to assemblage diversity, functionality, and structural complexity (de la Torre et al., 2020). Where systematically collected data are available, more useful models can be developed to predict abundance of VME indicator taxa (Piechaud & Howell, 2022; Rowden et al., 2017) and also to relate to one or more of the FAO (2009) functional definitions of what constitutes a VME (e.g., Baco et al., 2023; Rowden et al., 2020) or translated into maps for VME indices (Stephenson, Bowden, et al., 2023). Outputs from abundance models, even if geographically limited, can be used to fine-tune boundaries of spatial closures that have been based on information from presence-only models, to provide more reliable management for specific areas or taxa.

5 | CONCLUSION

Our findings complement previous studies that produced habitat suitability models for the study area, thereby contributing to a full suite of models for VME indicator taxa identified by SPRFMO in Annex 5 of CMM-03-2022. Past studies have shown that these types of models 'have reached their predictive limit' (Stephenson et al., 2021) or were not suitable proxies for abundance (Bowden et al., 2021). Our findings were similar, with the seven new models performing well when evaluated with independent data of taxon presence and absence but were poor surrogates for abundance. Given that density is central to the VME concept, abundance information is required to identify and locate them. While this study was based in the South Pacific high seas, New Zealand, and Australia, the results also have implications for modelling efforts aiming to conserve biodiversity beyond national jurisdictions elsewhere. Future efforts must strive for spatial datasets of abundance, as only they can provide the information needed to identify and test VME density thresholds and thereby enable more effective spatial management of extractive activities such as fishing (Gros et al., 2022).

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The code used to develop the models here is available online (Stephenson et al., 2021) from GitHub: https://github.com/Fabrice-Stephenson/VME_Predictions_South_Pacific. Much of the data used to produce the models in this paper are freely available online; see Geange et al. (2020) for details. Modelled spatial datasets will be provided upon request to the corresponding author.

ETHICS STATEMENT

No new data were collected for this manuscript, therefore information on ethical treatment of humans and animals is not applicable.

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SUPPORTING INFORMATION

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

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