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The benefits of heterogeneity in spatial prioritisation within coral reef environments.

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Abstract

Coral reefs are highly vulnerable habitats, threatened by climate change and local anthropogenic impacts. Management is imperative, and spatial prioritisation apportions the area of interest to inform investments of scarce conservation resources. Spatially delineated planning units used to make management decisions are typically large enough to contain significant natural variabilities, but the ecological significance of such variance is seldom considered in planning decisions. On coral reefs, the patchiness of habitat quality within planning units matters both ecologically and functionally. Here, we show that considering within-planning unit variance in spatial prioritisation influences the location and design of reserve networks. Studying Timor-Leste, we statistically model the average and variance in coral cover. We compare conservation priority areas for scenarios informed by coral cover and variance to a baseline scenario with the spatial prioritisation software Marxan. To further explain these differences, and to show the value of including coral variance as a metric in spatial prioritisation, we created a reserve quality score. We show that the similarity between reserve networks was only 57% for protection, and 44% for restoration objectives. For both objectives, the inclusion of cover variance improves the conservation benefit of management. This project has shown a novel way to target areas for restoration. These results demonstrate that not only is mean coral cover (and, by extension, reef condition) a key criterion in selecting marine conservation actions, but its variance must be considered in spatial conservation prioritisation to improve both the efficiency and benefit of management actions within marine reserve networks.

Keywords

Spatial prioritisation; coral cover; species distribution models; coral reef restoration; marine conservation; Marxan.

1. Introduction

There is an increasing need for habitat management, driven primarily by climate change and global ecosystem decline (Harvey et al., 2018). Threats to coral reefs occur at both large (e.g. climate change; Hughes et al., 2017) and small (e.g. fishing) spatial scales. As conservation funds are limited, it is important to select the most appropriate places to allocate resources for conservation or restoration. The most suitable locations will depend not only on the conservation objectives and resources available, but also existing local governance or policies, and potential threats. Marine spatial planning is the process through which areas of the marine system are allocated to different and often conflicting uses, including conservation, tourism or development (Douvere, 2008). Systematic conservation planning focuses on the conservation of natural habitats, and considers social, economic and political factors, in addition to biodiversity targets aiming to find and protect areas that are comprehensive, adequate and representative of biodiversity (Margules and Pressey, 2000). Marine spatial prioritisation is a methodological component of this process which locates areas for new marine reserves. Only recently has the condition of habitats been included in the spatial prioritisation process (e.g. Magris et al., 2016, 2020; Vercammen et al., 2019), as the presence or absence of a conservation feature was previously the primary driver of reserve placement.

Reef management often includes the designation of marine protected areas (MPAs) and restoration. Marine protected areas aim to reduce damaging activities and threats, such as agricultural run-off and offer protection to the habitats and species within their boundaries (Day et al., 2012), while restoration actively rehabilitates a degraded habitat (SER, 2004), for example, in order to increase the amount or cover of a species or habitat. Until recently (e.g. Magris et al., 2016, 2020; Vercammen et al., 2019), marine spatial prioritisation typically omitted habitat quality information and minimised costs, potentially leading to reserves or management areas established in less threatened areas (e.g. Magris and Pressey, 2017), or poor-quality habitat (e.g. Maxwell et al., 2009). Habitat quality is never homogeneous, yet heterogeneity within habitats (e.g. variation in coral cover) is rarely considered (although terrestrial conservation is more advanced in this respect, e.g. Harlio et al., 2019), and the disparities when selecting sites with high variability are unclear.

Hard coral cover is a common ecological measures that can be used as a proxy for reef health in the absence of more comprehensive reef quality data (Bruno and Selig, 2007; Vercammen et al., 2019). However, there are limitations to this metric; it does not indicate disease (Maina et al., 2008), and is too slow to evaluate ecosystem change (Beger, 2015). Habitats with high, mono-specific coral cover may be dominated by few species, and benefits of protecting them may be less than a more diverse, medium cover habitat (Richards, 2013), therefore variability is a vital metric in spatial prioritisation. The benefits of maintaining heterogeneity in landscapes and populations have been previously recognised (e.g. Foley et al., 2010). At the kilometre scale, greater variability in coral cover and complexity increases diversity in coral species (Richards, 2013) and therefore in associated fauna. Habitat variability also indicates that there may be increased rugosity, supporting increased abundance and richness of fishes (Harborne et al., 2012). Further, higher reef complexity can improve recovery after bleaching events (Januchowski-Hartley et al., 2017). Although using coral cover variance as a proxy for habitat quality still has limitations, and should be carefully validated (Stephens et al., 2014), it is a widely available metric that is straightforward to collect and model, compared to more complex measures of local scale habitat variability.

There is no simple method for determining priority areas for reef conservation, and the availability of data in the marine environment is often a limiting factor. Numerous approaches have been suggested to capture important threats and processes, such as dynamic reserves (Tittensor et al., 2019), the value of protecting connectivity (Beger et al. 2010, 2015; Magris et al., 2018), and the inclusion of areas which will remain valuable under future climate scenarios (Makino et al., 2014). Despite this, the value of using the variation in coral cover remains a gap in the literature. Spatial prioritisation apportions the area of interest into planning units (PUs), favouring the selection of areas with certain characteristics (Nhancale and Smith, 2011). The scale at which the area is analysed typically dictates the minimum spatial scale at which biological patterns can be incorporated into spatial prioritisation (Cheok et al., 2016). The need to summarise biodiversity metrics at the PU scale hinders current spatial planning approaches from considering habitat heterogeneity. Incorporating such heterogeneity in biodiversity patterns would enable analyses at a finer resolution and allow more specific allocation of management actions. Here, we tackle this challenge by determining whether inter-habitat variability in hard coral cover and quality has an impact on marine spatial planning for a case study area in Timor-Leste. We use contrasting scenarios to see if different planning objectives, such as protection or restoration, result in different priority areas being selected. We posit that the heterogeneity in hard coral cover will allow us to differentiate priority sites for marine reserves or restoration, and that its inclusion will substantially improve the quality of reserves. This may be especially important in global conservation network sites such as that recently developed by Beyer et al. (2018).

2. Materials and Methods

Timor-Leste is a small country within the Coral Triangle, a region of the western Pacific Ocean, supporting high levels of marine biodiversity (Fig. 1 a). The country has one MPA (Nino Konis Santana National Park), at the eastern end of the island. The northern coastline and fringing reef matrix of Timor-Leste, including Oecusse, and the islands of Ataúro and Jaco were divided into planning units approximately 500 m wide, extending outwards to the edge of the reef. This created 983 PUs, (725 for north shore/ Jaco; 139 in Oecusse; 119 around Ataúro), covering 245 km^2, with an average PU size of 0.25 km^2 (Smith et al., 2009).

2.1 Introduction to data

Ecological and mapping survey data of benthic habitat and fish biomass was provided by US NOAA (see PIFSC, 2017 for further detail on sampling methods and results) and the XL Catlin Seaview Survey (González-Rivero et al. 2014, 2016; Rodriguez-Ramirez et al., 2020). The XL Catlin Seaview Survey photographed the benthos approximately every 2 m along 1.8 km transects (n = 27; González-Rivero et al., 2016), at locations representing the North shore, Jaco, Atauro and Oecusse. These kilometre (km)-scale transects span several PUs, with the number of photos ranging from 14 to 844 (288 on average) photos per PU, giving an indication of variance in coral cover. NOAA provided benthic habitat maps from a satellite mapping project, which covered the whole study area, and the benthic cover was obtained on 131 sites spaced randomly around the whole site of interest through photo quadrats of approximately 0.7m^2 in area. Here, the mean cover was calculated from 30 photographs taken along a 30 m transect, at depths no deeper than 30 m (PIFSC, 2017). No surveys were conducted on the south shore and it was therefore excluded from our analysis. Reef fish biomass data for 150 sites were also supplied by NOAA (methods as in PIFSC, 2017), to be used as part of a reef quality score.

2.2. Species distribution models

We predicted both the mean and variance in coral cover for PUs not surveyed with species distribution models (SDMs). We downloaded pre-processed, candidate environmental predictors (Table 1) at a spatial resolution of 9.2 km from Bio-ORACLE (V 2.0; Assis et al., 2018; Tyberghein et al., 2012). Environmental data were interpolated through kriging to increase the resolution to approximately 750 m, ensuring the predictor data spanned the entire project areas, including inshore environments. For the model, we must assume these interpolated values are free of error. Candidate predictors were selected based on known relationships between reef benthos and environmental factors (Table 1), and effective predictors were determined using Akaike's Information Criterion (AIC) values (Hu, 1987). Where two predictors were correlated with Pearson's correlation (Pearson, 1920) > 0.6, only one was used, the other was excluded to reduce error. Gravity, a measure of human impact that combines population density with the travel time to a reef was also included as a proxy for fishing pressure (Table 1; Cinner and Maire, 2018).

We developed the coral cover and variance SDMs using seven effective predictor parameters (Table 1); while gravity was used in both models, the environmental parameters differed to explain variance. The final predictors for mean coral cover were maximum sea surface temperature (SST), dissolved oxygen, phosphate concentration, currents velocity and gravity. For coral cover variance, currents velocity, gravity, PU area and the number of habitats in the PU were used.

Meter-scale surveys were used to predict coral cover across all PUs, while km-scale transects allow the prediction of cover variance, measured as the standard deviation in coral cover. The *lm* and *predict* functions ('stats' package; R Core Team, 2017) were used to create the models in R (R version 3.6.0; R Core Team, 2017) and predict coral cover for the PUs not surveyed. The response variable in each model was cube-root transformed to reduce skewness, with AIC values supporting this method

(Table S1). We used a relatively simple model without weightings to avoid overfitting. A stepwise function served to remove unnecessary model terms and determine the best model by the lowest AIC value (e.g. Maire et al., 2016). We validated the models by bootstrapping and estimating model fit with training and validation datasets, containing 70% and 30% of the data respectively (Shimodaira, 2004). Pearson's correlation was also calculated between observed values and predicted values from the model to determine the best fitting model.

2.3 Marxan

We created a broad conservation decision framework to relate potential management objectives to different actions depending on the local coral cover and variance characteristics of the reef habitat (Fig. 2). We then created planning scenarios to reflect potential conservation or restoration objectives. Marxan v 1.8.10 (Ball et al., 2009) was selected as the conservation prioritisation software, and used with standard calibration unless specified otherwise. Marxan uses simulated annealing to solve a minimum set objective-based problem. It selects sets of PUs to reach targets for all conservation features at a minimum cost. Mean hard coral cover was separated into three conservation features, high, medium and low cover, using the natural breaks algorithm. The coral cover variance was separated into high and low variance following the same method (Vercammen et al., 2019). The area of the PU multiplied by population number within a 2.5 km radius was applied as a metric for the cost to remove the bias from variation in PU size. We set targets for the above coral cover and coral cover variance conservation features and 13 baseline habitats (Table S2) based on regional targets (CTI-CFF, 2013) and recent recommendations (Zhao et al., 2020). For each of the five prioritisation scenarios, targeting either protection or restoration, (Table 2), 100 runs were carried out in Marxan. The *Baseline* scenario was based on binary presence-absence data from the 13 baseline habitats to emulate how reef prioritisations are typically run. We used Marxan's selection frequency outputs to analyse the results. The selection frequency output indicates which PUs are important to prioritise, through indicating how important they are for meeting predefined targets. This is a simple measure of how many times Marxan selects the PU in multiple runs, showing how important a PU is in the construction of a reserve network.

2.4 Analysis and reef quality score

To assess differences between results for each scenario, a dissimilarity matrix of Marxan solutions was created using the *vegdist* function ('vegan' package; Oksanen et al., 2019) and hierarchical clustering was carried out in R (R Version 3.6.0; R Core Team, 2017) using the *hclust* function ('stats' package; (R Core Team, 2017). These results were visualised as a dendrogram, using the *colorDendrogram* function ('sparcl' package; Witten and Tibshirani, 2018). Fish biomass data were interpolated using kriging as data resolution was not sufficient for modelling. The resulting fish biomass dataset and the results from coral cover and cover variance were normalised and applied to a metric estimating habitat quality within the given reserves (hereafter, *reserve quality score*) for each PU (Equation 1):

$$Equation\ 1{:}\ Reserve\ quality\ score = \frac{\sum Cover * Cover\ Variance * Fish\ Biomass}{Number\ of\ PUs\ within\ reserve}.$$

<u>3. Results</u>

3.1 Species distribution models

Predicted hard coral cover varied between 9.98% and 24.85% (range = 14.87%; Fig. 1 b), with a mean of 15.86% and a median of 15.03%. The coral cover variance was predicted with a mean of 10.96% and a median of 10.70%, and between 7.95% and 16.33% (range = 8.38%; Fig. 1 c). Pearson's correlation between actual and predicted hard coral cover values was < 0.4 Fig. S1 a), while Pearson's correlation for coral cover variance was 0.45, averaged for all bootstrapping runs (Fig. S1 b). The range and distribution for measured hard coral cover and predicted values are comparable but slightly lower for predicted coral cover. The high variance seen within km-scale transects was not depicted in mean values from any surveys (Fig. S2). The relationship between coral cover and cover variance was weak for the range of values in this study (Pearson's correlation, $r = 0.24$, $p < 0.005$).

3.2 Marxan

Under the *Baseline* scenario, 60% of PUs were selected across runs, but selection frequency across all runs was low (< 50 for 981 PUs). Under the *Coral Protection* scenario, there is a focus around Nino Konis Santana National Park, as well as a central area of the north coast. Only 5% (n = 45) of the PUs were selected 100% of the time, while 59% (n = 584) was not selected in any of the 100 runs. When the variance in the coral cover of each PU was included in the input data, the selection frequency around Jaco Island, in Nino Konis Santana National Park, was more comparable to that of the *Baseline* scenario, but an increase in small areas with high selection was seen elsewhere. Compared to the *Coral Protection* scenario, almost twice as many PUs (11%, n = 104) were selected in every run, while 62% (n = 613) PUs were not selected at all. For a protection objective, *Coral Protection* and *Coral Variance Protection* scenarios have 56.5% agreement (Cohen's kappa = 0.303, $p < 0.005$).

When considering restoration, the output was very different when assessing coral cover and coral cover variance; large stretches of the northern coastline were prioritised for restoration projects. The selection frequency and spatial configurations of prioritisation solutions differed substantially for different conservation objectives (Table S3). A quarter (25%) of PUs are selected > 75% of the time in the *Coral Restoration* scenario, compared to over a third (36%) in the *Coral Variance Restoration* scenario. The latter scenario had a higher selection frequency around much of Nino Konis Santana National Park. No PUs were selected around Ataúro Island, and very few were selected in Oecusse (n = 11 for *Coral Protection* scenario and n = 39 for *Coral Variance Protection* scenario). C*oral Restoration* and *Coral Variance Restoration* scenarios have 44.2% agreement (Cohen's kappa = 0.329, $p < 0.005$).

3.3 Analysis and reef quality score

Each scenario returns a distinct set of solutions (Fig. 3 a), although the *Baseline s*cenario returns a more variable set of solutions, as seen by the large outer quartiles in figure 3 b. Scenarios for protection or restoration were grouped. The calculated reserve quality score is not significantly different between *Baseline* scenario and any other scenario, but all others are significantly different to one another (One-way ANOVA, $p < 0.005$; Tukey post hoc between all groups $p < 0.05$; Fig. 3 b). The inclusion of cover variance results in the selection of better-quality reefs under both protection and restoration objectives.

4. Discussion

Our study used species distribution models and spatial conservation prioritisation to show that management area priorities change substantially, for both restoration and conservation, if the variance in habitat quality is included. Ultimately, this suggests that it would be beneficial to deploy methods for initial spatial prioritisation that are similar to our conceptual framework (Fig. 2). This conclusion may also extend into other ecosystems, such as mangroves or terrestrial rainforests, although further research is needed to confirm this. The present study has been successful in including predictions of coral cover in spatial prioritisation to distinguish between protection and restoration areas, targeting the most degraded areas for restoration, and avoiding low-quality areas for protection. We argue that areas with low coral cover, but higher cover variance, are preferable for restoration as there is some structure within the habitats that will support the faster colonisation of restored habitat by associated species such as fishes.

Mean hard coral cover across the planning region was low, with none of our predictions exceeding 25% cover, consistent with previous studies from Timor-Leste (e.g. McCoy et al., 2015; Turak and Devantier, 2013), but lower than elsewhere in Coral Triangle (e.g. Chung et al., 2017; Vercammen et al., 2019). This indicates the importance of considering coral cover and variance of a site relative to both adjacent, local, and global reefs, to get a full picture of the habitat condition.

When considering protection, the inclusion of coral cover variance changed the location of the suggested area network by 43%, and by 56% when the objective was restoration. The coral variance scenarios for both protection and restoration had higher reserve quality scores than their associated coral cover scenarios; indicating clear differences in MPA design when cover variance was considered. These additional criteria of reef quality indicate that we should protect different areas of the reef, so we suggest that without considering these additional characteristics, we may be missing the most suitable sites. While this consideration is an integral part of the planning process, continued monitoring to assess whether objectives are being fulfilled when conservation management is implemented. It is also important to carefully consider the objectives, as a higher quality reef is not necessary or indeed desirable for restoration. It is important to consider a baseline dataset as reserves are often implemented with the aim of representation, regardless of the quality or condition of the habitats they are protecting (Klein et al., 2013). The inconsistencies in the *Baseline* scenario output indicate that these standard representation targets can be met in a multitude of ways, many of which will not be effective in capturing specific management objectives, as they only consider representation. On comparing the similarity of the solutions for each scenario, the two restoration scenarios were distinct from the protection scenarios, while the baseline output contained much more variation. This demonstrates the importance of clearly understanding the conservation objectives before beginning the planning process, as it can influence the data required.

Our results reveal the extent of variance that is hidden when only mean coral cover is considered. Additionally, the loss of reserve quality was highlighted when only coral cover data were considered (Fig. 3 b). The heterogeneity seen within the PUs here suggests that spatial prioritisation at larger scales may be inefficient. Rouget (2003) suggested that broad-scale spatial prioritisation is appropriate in homogeneous landscapes, while fine-scale, high-resolution planning should be used for anything more variable. Heterogeneity in habitats or landscapes makes it difficult to manage for coarse conservation objectives (Game et al., 2008). No significant correlation was found between average coral cover and variance, so cover variance cannot be inferred from knowing hard coral cover, or vice versa. Despite this, the variance is expected to be low in PUs with mean coral cover close to 0% or 100%. Areas with high species richness or biodiversity are more likely to be affected by anthropogenic impacts (Elahi et al., 2015; Quintero et al., 2010), suggesting that areas with medium to high variance should be protected (Fig. 2). We represented heterogeneity with the standard deviation in coral cover, but other elements of heterogeneity are important to conserve; including variance in species traits or responses to climate change (Walsworth et al., 2019). Areas of high biodiversity, and therefore high heterogeneity should be targeted for protection, whereas restoration, as it is focused on degraded habitats, is proposed to target low or declining biodiversity, and low to medium heterogeneity. This area requires further study, as higher variance could potentially improve restoration success.

We were able to use a small spatial scale for PUs, relevant to local communities. Following suggestions from Smith et al. (2009), the size of the PUs was based on the scale of proposed management actions. However, it is more common, particularly where species distribution models are not used (Tulloch et al., 2016), that the analysis scale is determined by the data available for conservation features (Rouget, 2003) or predictor variables (Vercammen et al., 2019). Here, the cost was calculated as the population within 2.5 km multiplied with the overall area of the PU as a proxy for the fishing cost (Ban et al., 2009), however, avoidance of areas around larger towns and cities may occur. Although costs will be higher for active restoration projects, as they still require protection. The opportunity costs for a reef will be the same regardless of the action. Protection should not be favoured over restoration because it is perceived to have a lower cost (Possingham et al., 2015).

With the use of small PUs, within- and between-reserve connectivity should be considered before implementation (Beger et al., 2015a). We did not directly consider connectivity here, but currents velocity was considered in both models, and the strength of these currents around the reefs of Timor-Leste, as well as the small size of the island suggest a well-mixed system (Allen and Erdmann, 2013). However, over a larger study area, integrating connectivity into a reserve can increase the success of a network of small PUs due to its importance in biodiversity persistence. Despite the importance of incorporating components such as connectivity, and due to the urgency of marine conservation, implementing a network of evenly spaced reserves is a sufficiently effective strategy if the local ecology is not well understood (Walsworth et al., 2019). However, here we have shown how variable a reserve system based on coarse habitat presence-absence data can be (Fig. 3 b). As with all models, there is uncertainty associated with our analysis. For example, higher resolutions of predictor datasets would be preferable to predict coral cover in our coastal PUs, however we were constrained by the available resolution in Bio-ORACLE. Such limitations in data makes local and small-scale conservation or restoration planning very challenging, highlighting the long-term need for improved data sources.

The decision framework, shown in figure 2, is separate to the Marxan scenarios, and provides an overview of factors contributing to habitat quality but is not exhaustive. Local influences (e.g. environmental factors, pollution or fishing pressure) were not included here but may contribute to the distribution of degraded areas. Restoration aims to rehabilitate coral cover and variance and is, therefore, most suitable in partially degraded areas. Spatial prioritisation is a complex process with several factors to consider, ranging from ecological to socio-economic management objectives. As our analysis shows, different ecological objectives change reserve systems, so the inclusion of additional objectives relating to socio-economic or other ecological factors will inevitably change the location of reserve networks and their efficacy (Beger et al., 2015b). Extremely degraded reefs are not the most efficient use of management funding (Loerzel et al., 2017), and no action is suggested. Particularly in places with small-scale fisheries such as Timor-Leste, equitable distribution of management areas (Barr and Mourato, 2009) will increase the likelihood of no-take areas being respected as each village can still access fishing grounds (Rocliffe et al., 2014). Excluding socio-economic considerations from spatial action planning will reduce the efficiency of a reserve or restoration project (Scholz et al., 2004). Despite the evident trade-offs that occur in spatial prioritisation, our framework clearly shows how the theory presented here can be applied to local habitat conservation or restoration projects, based on an understanding of the habitat condition. Within a real-world spatial planning project, this could provide stakeholders with a better understanding of potential reserve networks.

Our results are relevant to Timor-Leste in the present-day environmental climate but could be expanded spatially and temporally in future studies. Through using projected future climate data, similar methods could be used to determine how the heterogeneity of coral cover changes with the climate. This might impact spatial conservation priorities, or the selection of appropriate management actions (e.g. Makino et al., 2014). As well as variance in coral cover, there is heterogeneity in human uses of marine ecosystems (Crowder and Norse, 2008). Here, this was represented by the population count within 2.5 km of the reef, but this is a coarse surrogate, as it does not consider the differences in fishing methods. Furthermore, the distribution of these pressures is likely to change in the future, especially as Timor-Leste is a developing country. Currently, there is a movement of communities protecting their reefs through customary law known as *tara bandu* and these localized protection measures are important to consider in a larger spatial plan (Tilley et al., 2019). There is potential to forecast future fishing pressures, allowing more accurate predictions of mean coral cover and variance over a longer period.

In summary, we have shown that the inclusion of the variance component of coral cover for spatial conservation prioritisation improves reserve design at a relatively small spatial resolution. Additionally, we have used a measure of coral cover variance to target areas specifically for restoration. The results of our study support the inclusion of cover variance in spatial prioritisation and provide a guide for future studies in this field. These methods can be expanded to larger spatial scales and different ecosystems, using similar, widely available datasets. Considering recent and ongoing climate change, in both marine and terrestrial habitats, it is important not to waste conservation effort in ineffective places.

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7. Tables and Figures

Table 1: Parameters and their ecological justification for use as predictor variables for coral cover or cover variance in species distribution models. Environmental parameters were collected between 2000 and 2014 (see Tyberghein et al., 2012 for further detail). PU refers to planning unit.

Parameter	Units	Justification	Reference
Monthly maximum sea surface temperature (SST)	*°C*	Most corals have narrow temperature tolerance.	Kleypas et al., 1999
Dissolved molecular oxygen	*mol* m^{-3}	Used as a surrogate for carbonate saturation state Linked to pH and calcite concentration.	Haas et al., 2014
Phosphate	*mol* m^{-3}	Corals are adapted to nutrient poor waters, thus nutrients influence coral health	Hallock and Schlager, 1986
Currents velocity	m^{-1} *Calculated from u (meridional) and v (zonal) values.*	Ocean currents influence connectivity and recruitment that can aid recovery and control coral cover and impact reef patchiness.	Feng et al., 2016
Gravity	*Population, distance to reef*	Local human populations influence the health (and coral cover) of reefs.	Cinner et al., 2018
PU area	m^2	Correlates with coral reef area while accounting for irregular size of PUs.	-
Number of habitats in PU	*Number*	More habitat types will increase heterogeneity.	-

Table 2: Details of input parameters for Marxan scenarios.

Scenario	Data			Objective	Targets (%)		
	Baseline	**Cover**	**Variance**		High	Med	Low
Baseline	✓			All Habitats		20	
Coral protection	✓	✓		Protection	50	35	10
Coral restoration	✓	✓		Restoration	10	35	50
Coral variance protection	✓	✓	✓	Protection	50	35	10
Coral variance restoration	✓	✓	✓	Restoration	10	35	50

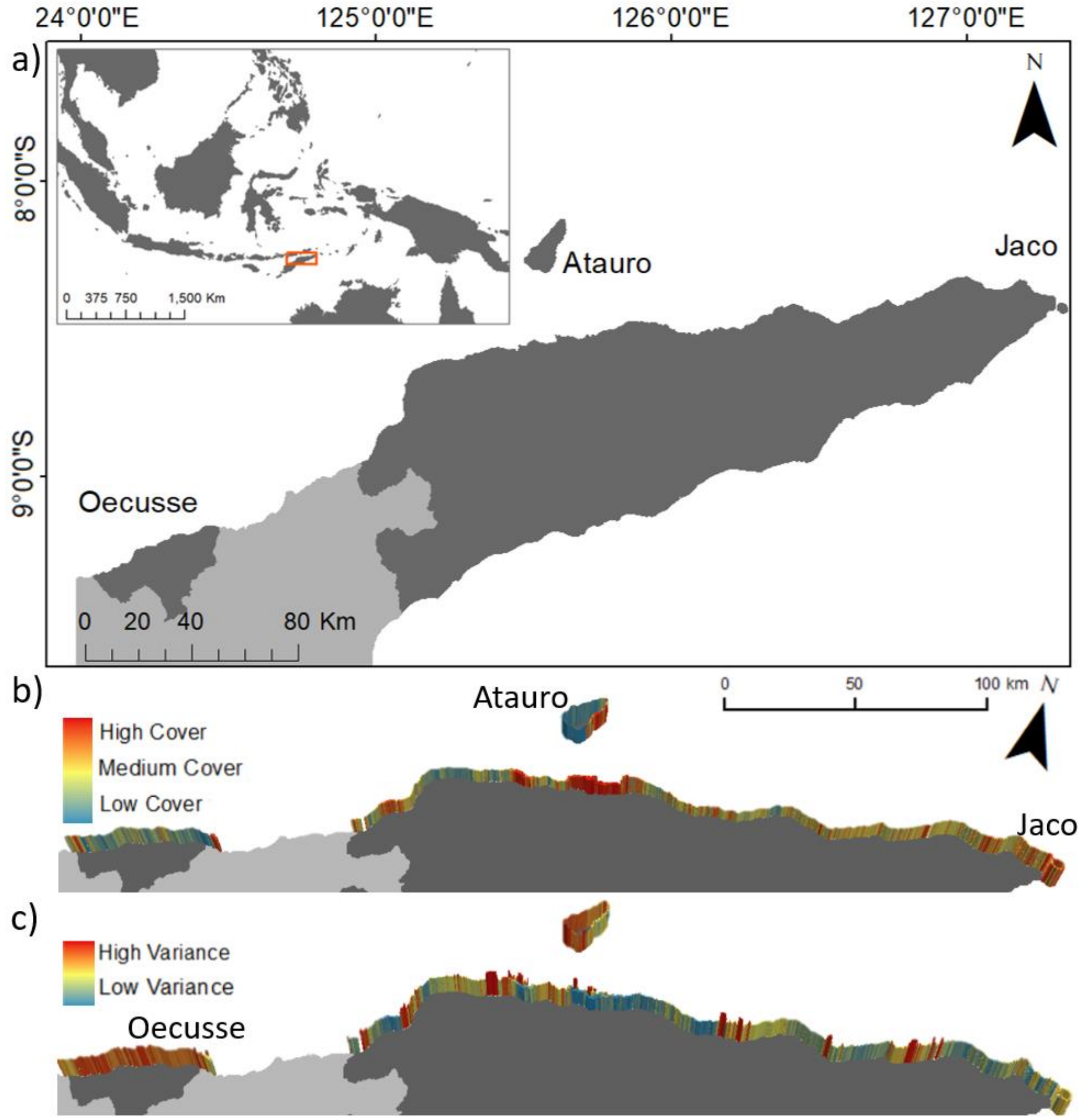

Figure 1: Timor-Leste; (a) location of Timor-Leste within the Coral Triangle; the results of species distribution models showing (b) coral cover and (c) coral cover variance. Spatial limits of our analysis are as follows: xmin 124.50°; xmax 127.38°; ymin 9.38°; ymax 8.12°. Both blue colour and shorter bars represent low cover or variance, while red and higher bars depict high cover or variance. A natural breaks algorithm was used to determine categories. Maps were created using ArcGis 10.6 (ESRI, 2017).

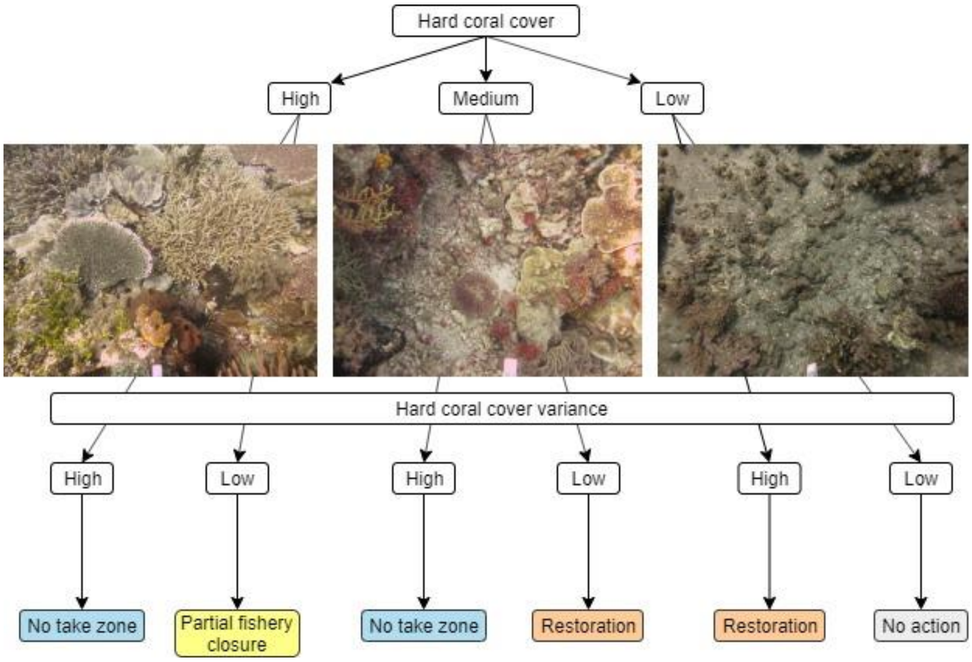

Figure 2: Conservation decision framework. A decision tree showing the suggested actions based on two metrics of habitat quality. For no take zones and partial fishery closures, the conservation objective is protection. Photos from NOAA (PIFSC, 2017).

a) b)

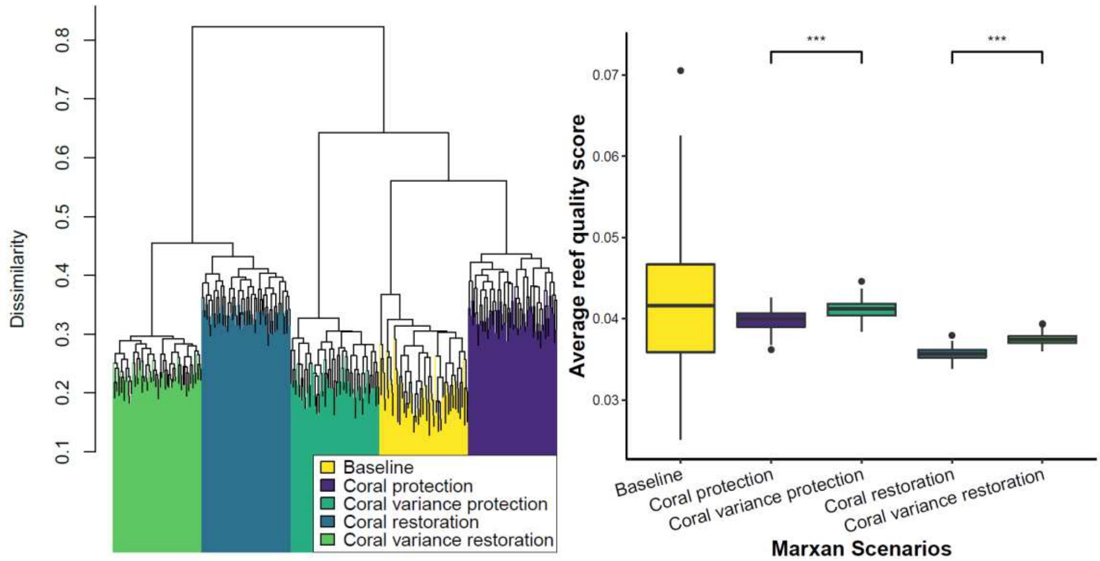

Figure 3: Marxan results: (a) Dendrogram showing reserve design differences for 5 scenarios, as shown on the Y-axis: *Baseline*, *Coral Protection*, *Coral Restoration*, *Coral Variance Protection* and *Coral Variance Restoration*. Dendrogram was created using *colorDendrogram* function ('sparcl' package; Witten and Tibshirani, 2018). (b) The average reserve quality score for the same 5 scenarios, following equation 1. The whiskers represent outer quartiles, excluding outliers. Bars at top represent significance between cover and cover variance scenarios (***: $p < 0.001$).

8. Supplementary Information

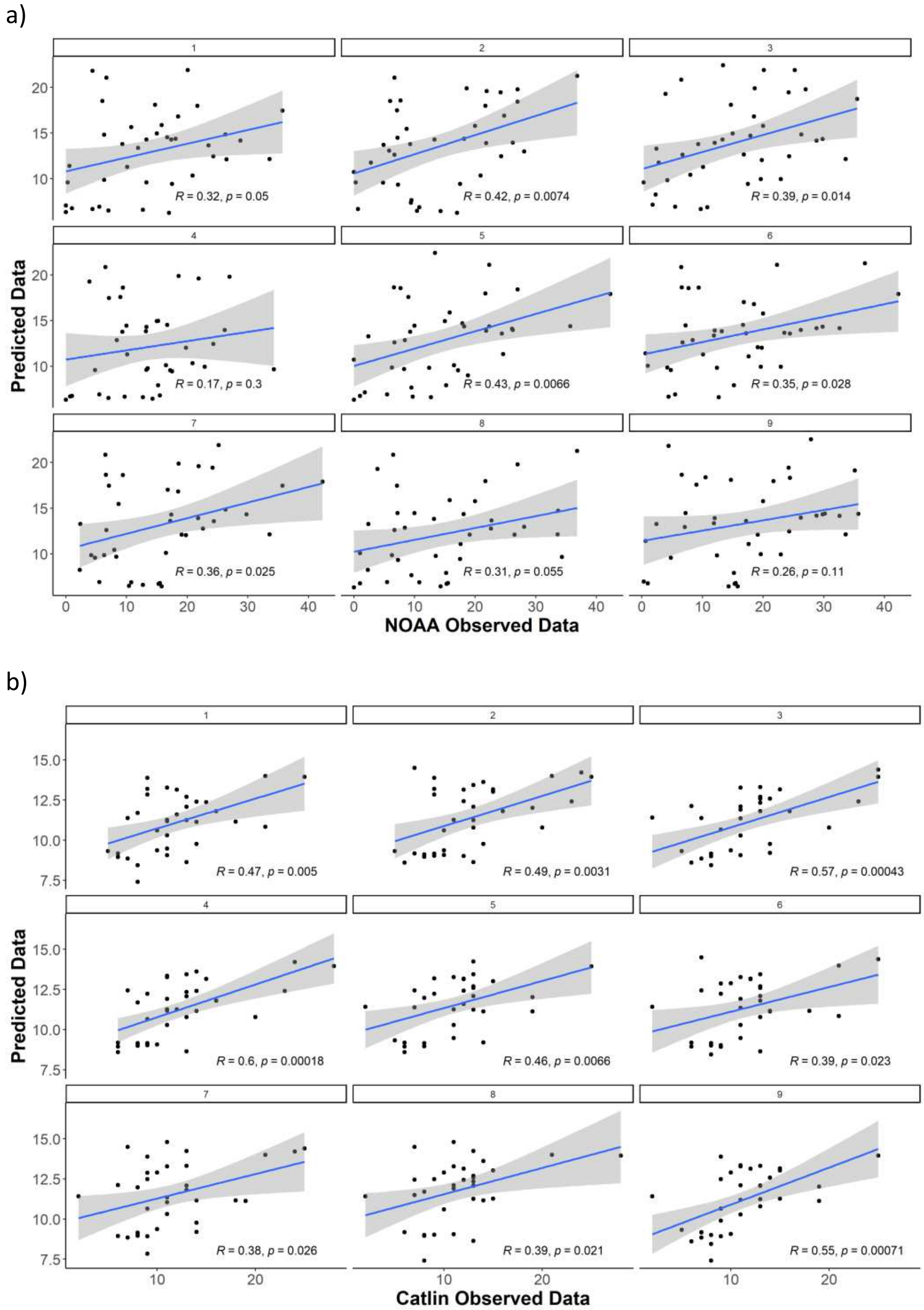

Figure S1: Output of first nine bootstrapping runs for (a) coral cover model and (b) coral cover variance model. Observed data from either NOAA or XL Catlin (as indicated in x-axis titles), averaged by planning unit, is compared against the predicted coral cover from SDMs to assess the accuracy of the model. 1-9 indicate the bootstrapping run. The blue line represents the labelled Pearson's correlation (R) between the observed and predicted data for each run. A correlation closer to 1 suggests a more accurate run. P value is included for Pearson's correlation. Shaded area shows 95% confidence intervals. Plotted in R using the *qplot* function ('ggplot2' package; Wickham, 2016)

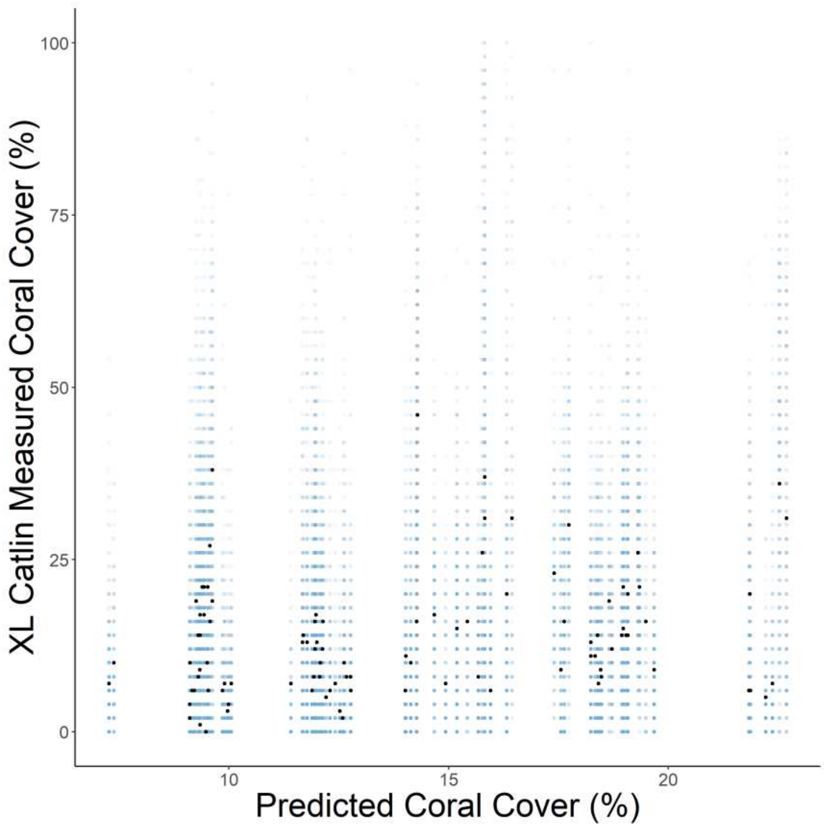

Figure S2: XL Catlin Kilometer-scale surveys show high within-reef variance. Blue points show measures of coral cover as a percentage, with each vertical line showing one PU; blue points are semi-transparent and darker areas show clustering. Black points show the mean coral cover per PU according to m-scale surveys.

Table S1: AIC values used to determine best measure of human pressure.

Measure of human pressure	Mean correlation 500 runs	AIC value	ΔAIC
Gravity	0.380	264.25	0.00
Population within 2.5 km	0.338	267.01	2.76
Population within 25 km	0.371	265.21	0.96
Travel Time to reef	0.355	265.44	1.19

Table S2: Coral reef habitats observed in m-scale NOAA data along the northern coastline of Timor-Leste.

Coral Reef Habitats	
Hard shallow coral	Seagrass
Hard medium coral	Mangrove
Hard deep coral	Intertidal
Soft shallow coral	Emergent rocks
Soft medium coral	Macroalgae
Soft deep coral	Lagoon
	Unknown

Table S3: Table of statistics for each scenario. The Cohen's kappa test was compared to the *Baseline* scenario.

	Number of PUs in best solution	***Mean number of PUs***	***Mean Selection frequency***	***Median selection frequency***	***Results of Cohen's kappa test***		
					% agreement with baseline	***Cohen's kappa***	***p***
Baseline	161	161	16.4	0	-	-	-
Coral protection	213	241	21.8	0	62.3	0.336	< 0.001
Coral restoration	359	354	36.0	17	39.0	0.148	< 0.001
Coral variance Protection	242	242	24.7	0	64.2	0.340	< 0.001
Coral variance restoration	424	420	42.7	27	43.9	0.200	< 0.001