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Evaluating the impact of accounting for coral cover in large-scale marine conservation prioritizations

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Abstract

Aim: Mega-diverse coral reef ecosystems are declining globally, necessitating conservation prioritizations to protect biodiversity and ecosystem services of sites with high functional integrity to promote persistence. In practice however, the design of marine-protected area (MPA) systems often relies on broad classifications of habitat class and size, making the tacit assumption that all reefs are of comparable condition. We explored the impact of this assumption through a novel, pragmatic approach for incorporating variability in coral cover in a large-scale regional spatial prioritization plan.

Location: The Coral Triangle.

Methods: We developed a spatially explicit predictive model of hard coral cover based on freely available macro-ecological data to generate a complete regional map of coral cover as a proxy for reef condition. We then incorporate this information in spatial conservation prioritization software Marxan to design an MPA system that meets specific conservation objectives.

Results: We discover prioritizations using area-based representation of reef habitat alone may overestimate the conservation benefit, defined as the amount of hard coral cover protected, by up to 64%. We find substantial differences in conservation priorities and an overall increase in habitat quality metrics when accounting for predicted coral cover.

Main conclusions: This study shows that including habitat condition in a large-scale marine spatial prioritization is feasible within time and resource constraints, and calls for increased implementation, and evaluation, of such ecologically relevant planning approaches to enhance potential conservation effectiveness.

KEYWORDS

coral cover, Coral Triangle, Marxan, reef health, spatial prioritization, systematic conservation planning

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1 | INTRODUCTION

Identifying where and how to allocate scarce conservation resources to ensure the persistence of biodiversity is a fundamental challenge of the 21st century (Margules & Pressey, 2000). Spatial prioritization addresses this issue by informing decisions about what actions to take in space and time, often based on target-driven objectives for biodiversity, threats and socio-economic costs (Wilson, Cabeza, & Klein, 2009). Establishing marine-protected areas (MPAs) is one management action supporting global conservation efforts (Edgar et al., 2014). Four principles have been proposed to underpin the design of MPA systems: ensuring all elements of biodiversity such as habitat classes, species and processes receive protection (representation), securing functional linkages (connectivity), ensuring the persistence of species through time by securing ecological and evolutionary processes (adequacy), and minimizing impacts on people (efficiency) (Groves & Game, 2016). At present, systematically designed MPA systems focus on cost-effectively meeting representation targets, but also increasingly on securing connectivity (Beger et al., 2015; Krueck et al., 2017). However, operationalizing adequacy in spatial conservation planning remains challenging because area-based targets are often set by policy or stakeholder consensus rather than ecological justifications (Jumin et al., 2017, but see: Magris, Pressey, Mills, Vila-Nova, & Floeter, 2017). Ecological assessments may better inform adequate targets, but planners typically lack the resources, time and/or detailed biological information required to comprehensively conduct such analyses, especially for multiple species (McCarthy & Possingham, 2014).

In tropical marine systems, healthy coral reefs are crucial to sound ecological functioning. Loss of structural complexity and diversity on reefs can dramatically impact fish communities (Komyakova, Munday, & Jones, 2013) and compromise ecosystem services (Graham & Nash, 2013). For the adequacy criterion to be met, conservation planning should therefore consider not just the presence, but the *condition* of conservation features to avoid establishing MPAs in locations that are too unproductive to ensure their persistence (Arafeh-Dalmau, Torres-Moye, Seingier, Montaño-Moctezuma, & Micheli, 2017; Klein et al., 2013). Well-designed MPAs would target conservation of, for example, fish biomass and coral cover to promote adequacy (Selig & Bruno, 2010), and, where possible, link these to ecological connectivity requirements (Beger et al., 2015; Magris et al., 2017). Yet such spatially explicit information on reef condition is lacking for much of the marine environment, which necessitates the use of surrogate information such as reef extent or bioregionalizations to make decisions about where to allocate resources (e.g., Fernandes et al., 2005; Green et al., 2014; Beger et al., 2015; Jumin et al., 2017). Some studies have used threats as a proxy for ecosystem condition (García Molinos et al., 2017; Linke et al., 2012; Tallis, Ferdaña, & Gray, 2008). While this may be feasible at smaller scales, large regional prioritizations most often rely on broadly classified morphological features derived from remotely sensed data, and representation is achieved by specifying proportions of each habitat or substrate type to capture their associated biodiversity (Young & Carr, 2015). This strategy falls short of securing adequacy, because it tacitly considers all habitats classed as "reef" to have equivalent conservation value, irrespective of its actual level of cover or condition. This may result in a protected area system that fails to deliver outcomes effectively and efficiently and ignores the warning by Evans et al. (2015) that care should be taken to incorporate appropriate condition metrics in spatial planning to avoid misspending conservation funding.

We assessed the consequence of this assumption on large-scale planning outcomes and examined the relative impact of alternative approaches to incorporating reef condition in the planning process, using the Coral Triangle as a case study (Beger et al., 2013, 2015; White et al., 2014). Live hard coral cover predicted from a spatially explicit model of 6,412 reef surveys across the CT provided a proxy for reef condition. By incorporating this information into a spatial conservation prioritization, our approach allowed an explicit assessment of the expected versus realized reef cover captured within the MPA system when condition is ignored. Second, it provided opportunity to tailor prioritizations based on different accounting strategies for reef condition. Our ultimate aim is to demonstrate the large-scale feasibility and potential utility of incorporating the condition of the conservation features we seek to protect (i.e. reef habitat). The creation of such a static plan for highly dynamic reef systems should be considered as an initial spatial representation of priorities, not a fully implementable plan. Spatially heterogeneous stress events for instance can alter coral cover in any site within short time frames, suggesting a need to update and ground truth plans before implementation.

2 | METHODS

2.1 | Study region

The Coral Triangle is the globally recognized epicentre of marine biodiversity, encompassing almost 6 million square km of ocean and coastal waters surrounding Indonesia, Malaysia, Papua New Guinea, the Philippines, Timor Leste and the Solomon Islands. The Coral Triangle Initiative on Coral Reefs, Fisheries and Food Security (CTI-CFF) unites the 6 nations in conserving the region's coastal and marine resources. Significant effort has been invested in the implementation of MPAs at local and national levels (White et al., 2014), and a spatial prioritization framework has been proposed to facilitate ongoing regional MPA planning (Beger et al., 2015).

2.2 | Predicting coral cover

Live hard coral cover, a common proxy for reef condition (Bruno & Selig, 2007), was modelled at the level of planning units using a generalized additive model, with a beta regression distribution and a logit link function (using "mgcv" in R v.3.2.5). The aims were to (a) identify significant drivers of coral cover using existing remotely

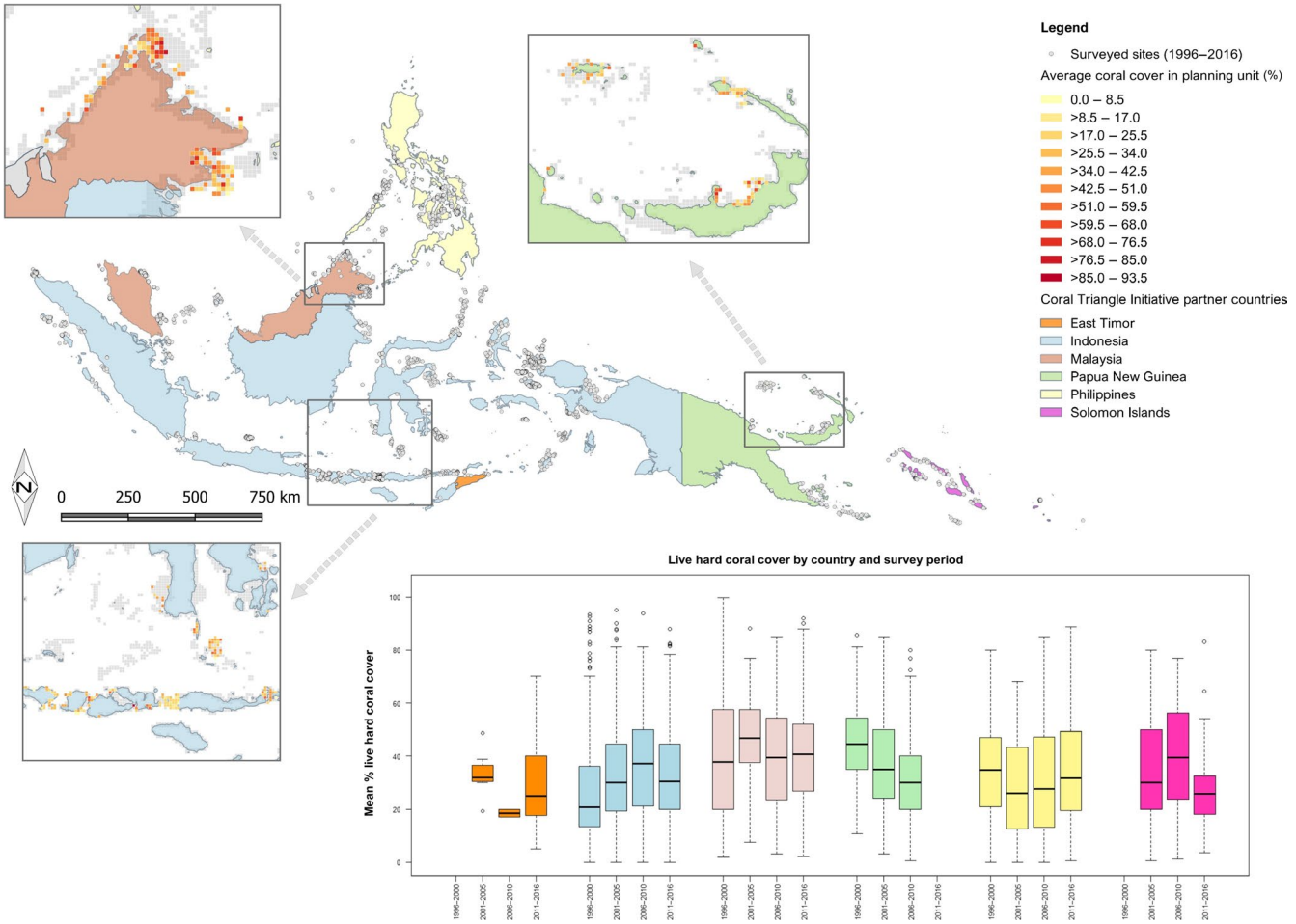

FIGURE 1 Map of coral reef survey locations, with insets demonstrating local variability in coral cover data. Per cent live hard coral cover is averaged across multiple surveys conducted within each of the 10 × 10 km planning units. The box plots demonstrate regional coral cover variability over time. Grey boxes in insets represent planning units with coral reef habitat, but for which no survey data were available. Coral cover in these planning units was estimated using prediction based on the GAM coefficients

sensed and observational data; and (B) generate predictions for previously unsurveyed planning units to produce a region-wide map of coral cover estimates. Georeferenced coral cover data were collated from various sources, comprising 6,412 reef surveys from 3,820 sites (see Figure 1 for the spatial and temporal distribution of surveys). Of these, 3,141 had been surveyed just once between 1996 and 2016 (Table S1). We calculated mean coral cover, aggregating information from multiple survey sites within a planning unit. If multiple records were available for a single survey site, we used the most recent data. We then constructed a statistical model of coral cover, based on biotic and abiotic factors known to impact the distribution of hard scleractinian corals, available at the required spatial coverage and scale. Predictor variables were obtained from the Bio-ORACLE database (www.oracle.ugent.be; Tyberghein et al., 2012): (a) ocean colour bio-optical parameters, (b) nutrients and dissolved oxygen, and (c) temperature and light resources associated with latitudinal patterns. We explored the inclusion of anthropogenic factors as predictors of coral cover, for example, with a composite estimate of human impacts (Halpern et al., 2008), but this did not improve predictive power (Table S2). For highly correlated predictors, one of the paired variables was excluded using expert judgement of their ecological relevance, resulting in a smaller set of predictors to avoid overparameterization and multicollinearity: dissolved oxygen, sea surface temperature (SST) range, maximum SST, pH, photosynthetically available radiation, diffuse attenuation and calcite. Square or log transformations were applied to normalize extremely skewed predictors. To address potential biases in survey effort, we also accounted for potential random effects of different collection methods ("data source") and geographical location ("ecoregion").

2.3 | Spatial prioritization scenarios

We used Marxan (Ball, Possingham, & Watts, 2009), a spatial decision support software, to select sets of planning units which achieve explicit conservation targets, while minimizing the overall cost of the proposed MPA system for two sets of paired prioritization scenarios that account for coral cover in different ways (Table 1; Figure S1). All scenarios were based on the existing planning framework for MPA expansion across the Coral Triangle, consisting of 17,264 planning units, 10 × 10 km in size (Beger et al., 2015; see Figure S2 for a map of the planning region

TABLE 1 Overview of the spatial conservation prioritization scenarios, with paired scenarios A and B representing two distinct methods to account for coral cover in selecting planning units. The workflow is further illustrated in Figure S1

	Prioritization scenario	Accounting for coral cover	Conservation features	Representation target
Paired Scenarios A	Representation Only[a]	None	Basic habitat classes	20%
	Coral Cover Weighted	Extent of coral reef habitat per planning unit multiplied by predicted per cent coral cover	Basic habitat classes; coral reef classes adjusted for coral cover	20%
Paired Scenarios B	No Coral Cover Preference	Coral reef habitats classified by coral cover; equal representation across classes	Basic habitat classes; coral reef habitats classified by coral cover	
			Low	20%
			Moderate	20%
			High	20%
	High Coral Cover Preference	Coral reef habitats classified by coral cover; prioritized representation of high-cover class	Basic habitat classes; coral reef habitats classified by coral cover	
			Low	10%
			Moderate	20%
			High	40%

[a]Baseline scenario used for comparing expected versus realized hard coral cover across the reserve system.

including ecoregions and existing MPA's included in all scenarios). Human population density in coastal areas and artisanal fishing effort in marine planning units served as the best available proxies for opportunity cost at this scale, as in Beger et al. (2015). We applied a minimal boundary length modifier (BLM = 0.2), producing an efficient level of compactness, to all scenarios. Refer to Supporting Information for further details on the definition of conservation features, calculation of costs and other Marxan inputs, processes and outputs.

2.3.1 | Scenario set A

The *Representation Only Scenario* considered 10 habitats, derived from an unsupervised classification of satellite data delineating four reef types, mangroves, seagrass and another benthic substrate (Kakuta et al., 2010; UNEP-WCMC, 2010), and 24 ecoregions (Spalding et al., 2007). Serving as a baseline, this scenario aims to represent 20% of each conservation feature and does not make any specific demands on reef condition. In direct comparison, the *Coral Cover Weighted Scenario* adjusts the extent of reef habitat based on the amount of predicted coral cover. For example, for two planning units with 500 m^2 of reef habitat, if the model predicts one has 50% average coral cover, while the other has 20%, in this scenario the first planning unit would contribute 250 m^2 of reef and the latter 100 m^2 (see Table 1 for an overview of all scenarios).

2.3.2 | Scenario set B

Two additional scenarios evaluated strategies that allow specification of different objectives based on coral cover, that is, reefs are classified and subsequently prioritized based on their condition. Based on the predicted average coral cover within planning units, we categorized all planning units with reef habitat into "low-cover," "moderate-cover" and "high-cover" classes (refer to Figure S3 for representative images). We used the 20th and 80th percentiles of the predicted coral cover across the region as thresholds. These reef classes were subsequently treated as separate conservation features for which we set distinct targets. In the *No Cover Preference Scenario*, all three coral cover classes were equally represented (20%). In the *High Cover Preference Scenario*, we prioritized reefs in good condition by setting higher representation targets for high-cover reefs (40%), compared with moderate-cover reefs (20%) and low-cover reefs (10%) (Table 1).

2.3.3 | Scenario analysis

To quantify the impact of discounting reef condition in spatial prioritization, we calculated the difference between the total extent of reef habitat that is selected in the best solution for the *Representation Only* scenario and the predicted extent of live hard coral cover in that solution. The difference represents the potential deficit between expected (remotely sensed reef area) and realized (coral cover) contributions towards conservation objectives. We then visually and quantitatively assessed the differences across scenarios using planning unit selection frequencies and Kappa statistics (Landis & Koch, 1977), respectively. Dissimilarity between the four scenarios was quantified using agglomerative hierarchical cluster analysis on the selection of planning units for the 10 best solutions within each scenario.

3 | RESULTS

3.1 | Reef surveys

Analysis of the 6,412 reef survey data points indicated that mean live hard coral cover was 33.9% (*SD* = 19.3; range = 0%–99.8%) across the Coral Triangle, but also revealed significant regional variation. Analysis of variance revealed a significant effect of time period, $F(3,6,391) = 10.24$, $p < 0.001$, country, $F(5,6,391) = 31.73$, $p < 0.001$, as well as an interaction effect between these two

TABLE 2 Results from the Generalized Additive Model with individual contributions of the environmental predictor variables to the outcome, percentage live hard coral cover

	Estimate	Standard error	*z* value	Significance
Intercept	−0.7561	0.1039	−7.279	***
Predictor[a]	**Estimated *df*** [b]	**Reference *df***	X^2	**Significance**
Dissolved oxygen	7.153	8.046	60.13	***
Sea surface temperature (range)	7.333	8.316	38.8	***
Sea surface temperature (max.)	7.709	8.566	41.3	***
pH	5.194	6.181	22.29	**
Photosynthetically available radiation (max.)	5.997	7.198	32.42	***
Diffuse attenuation (max.)	6.515	7.685	56.16	***
Calcite	3.239	4.034	10.22	*
Ecoregion (random effect)	10.557	17	77.33	***
Data source (random effect)	7.899	10	152.62	***

[a]Inclusion of a measure of anthropogenic pressure as a predictor did not substantially improve the model, R^2 adjusted = 0.145; deviance explained = 24.7%, and this term was therefore not included in the final model.
[b]Degrees of freedom.
***<0.001.
**<0.01.
*<0.05.

factors on per cent live hard coral cover, $F(12,6,391) = 11.06$, $p < 0.001$ (Figure 1).

3.2 | Model of coral cover

Our model of coral cover accounted for 24.2% of the variance in live hard coral cover (adjusted $R^2 = 0.14$). Coral cover was significantly associated with all biophysical predictors included in the model (Table 2). The root mean squared deviance between observed and fitted values for the model indicates an average prediction error of 0.16 for the proportion live hard coral cover. Predicted coral cover in the planning units varied spatially (Figure S4a), with relatively high cover in North Borneo and the South China Sea Islands, the Sunda shelf/Java Sea region, some parts of the Bismarck and Solomon Sea and Halmahera. While direct anthropogenic impacts undoubtedly affect coral reefs, the effects of proxy measures such as human population density are not always detectable (Bruno & Valdivia, 2016). The relatively crude measures available at large regional scales may lack power and precision and can be masked by other global influences. The composite estimate of human impacts may have been too crude to provide any additional explanatory power (Table 2). The predicted coral cover was normally distributed (mean = 0.34, Figure S5).

3.3 | Quantifying the impact of accounting for estimated coral cover

Comparing the area of selected coral reef habitats in the baseline *Representation Only* scenario with predicted coral cover shows that the actual amount of coral cover represented in the resulting MPA system may be overestimated by 64% for the entire Coral Triangle and thus its ability to achieve the conservation objectives (Figure 2). The alternative scenarios we examined consider coral reef condition in different ways to guide the expansion of existing MPA systems across the Coral Triangle. We compare each scenario against the relevant baseline in which coral cover is not considered in prioritizing planning units. As expected, when representation objectives were set based on estimated coral cover, the mean coral cover across solutions exceeded that of solutions based on reef extent alone. Secondly, when we classified all reef habitat into high-, moderate- and low-cover classes, the scenario that prioritized a greater proportion of high-cover reefs also resulted in solutions with higher mean coral cover compared to the scenario with equal objectives for high-, moderate- and low-cover reefs. Across all 4 scenarios, mean coral cover was lowest in the latter scenario. Thus, in both instances, accounting for coral cover achieved solutions with significantly higher coral cover (*t* test, $p < 0.001$) (Figure 3a). These patterns largely hold for all countries with the exception of the Solomon Islands and Timor Leste, where the predicted coral cover is generally low and did not significantly improve in scenarios that preferred coral cover (Figure 3b).

3.4 | Similarity across prioritization scenarios

Overall, there was little variation across scenarios in terms of the number of planning units selected and total cost for countries and for the CT region (Table 3 and Table S3). However, the scenarios delivered configurations of planning units that spatially distinct, as indicated by the cluster analysis (Figure S6). Pairwise comparisons show fair to moderate congruence in the selected planning units of the best solutions, with the lowest overlap in Timor Leste and the highest in Papua New Guinea (Table 3). While there were several

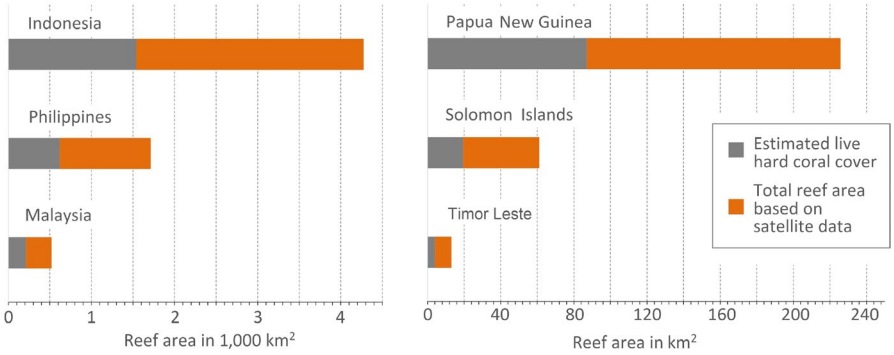

FIGURE 2 Potential conservation shortfall across the Coral Triangle when planning does not account for coral cover. Bars indicate national differences in the extent of coral habitat assumed to be under protection in the *Representation Only Scenario* compared with the modelled amount of actual coral cover in selected planning units

areas of high priority shared by across the *Coral Cover Weighted* and the *Representation Only* scenarios (indicated in purple), a key finding was that Western New Guinea, North-Central Palawan and Eastern Sumatra emerged as new priority areas for conservation when coral cover was taken into consideration (Figure 4). Similarly, many high priority areas remained unchanged under the *High Coral Cover Preference* scenario (purple, Figure 4b), but we also observed new areas that had not been identified in the *No Coral Cover Preference scenario* (Figure 5).

4 | DISCUSSION

The persistence of marine biodiversity can be at risk when planning does not account for ecological context, as sites selected for conservation action may be in poor condition and unlikely to contribute effectively towards conservation outcomes. Yet to date, habitat condition or proxies thereof have rarely been incorporated into MPA design (but see Klein et al., 2013). At large spatial scales in particular, prioritizations are constrained by sparse habitat condition data and

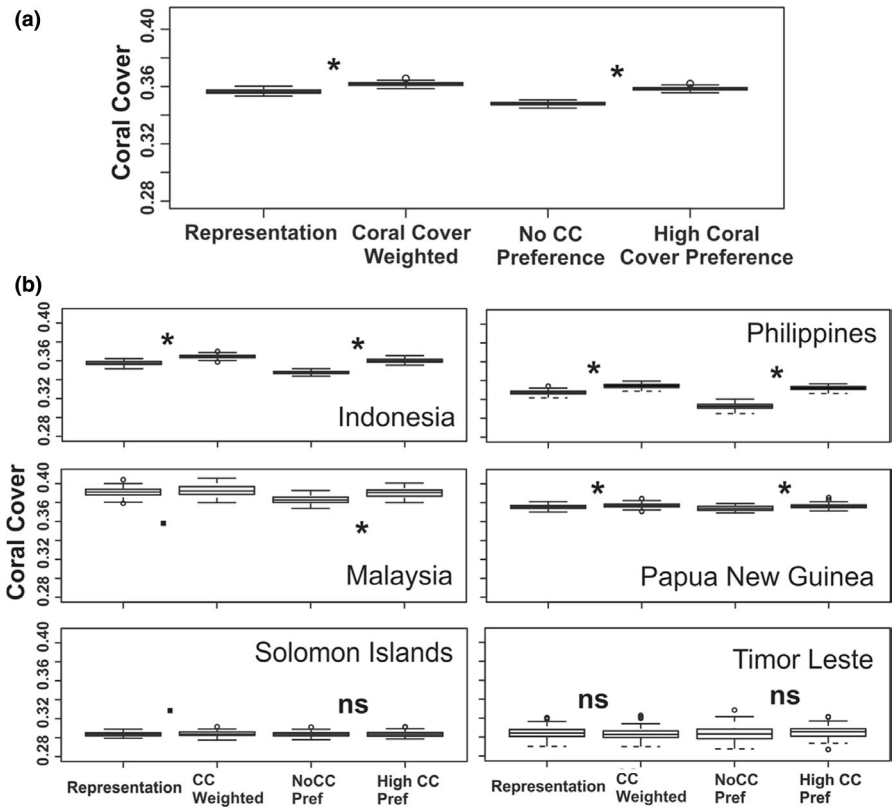

FIGURE 3 Mean coral cover achieved by the four scenarios, demonstrating significant differences between *Representation Only* and the *Coral Cover Weighted* scenarios, and *No Coral Cover Preference* and *High Coral Cover Preference* scenarios, for (a) the region and (b) within the countries of Indonesia, Philippines, Papua New Guinea, Timor Leste and Malaysia. Symbology denotes significance between scenarios for pairwise *t* test: $p < 0.05$; * $p < 0.001$; ns not significant. Coral cover is scaled between 0 and 1

TABLE 3 Country-level and regional planning unit (PU) selections for the best solutions generated by Marxan. Kappa statistics indicate similarity between scenarios that do and do not account for coral cover in selecting planning units

		Pair A		Pair B		Kappa	
	Total number PU's	PU's in Representation only scenario	PU's in coral cover weighted scenario	PU's in no coral cover preference scenario	PU's in high coral cover preference scenario	Scenario Pair A	Scenario Pair B
Philippines	3,140	618	609	586	640	0.53	0.44
Indonesia	9,072	1946	1998	2081	2006	0.46	0.46
Malaysia	1,062	211	236	208	221	0.55	0.54
Timor Leste	81	15	21	14	15	0.33	0.32
Papua New Guinea	2,449	512	506	509	519	0.55	0.57
Solomon Islands	754	129	133	127	122	0.52	0.49
Coral Triangle	17,266	3,593	3,647	3,671	3,661	0.49	0.47

typically make the tacit assumption that all reefs have equal conservation value. We show that this may result in MPA systems that overestimate actual outputs by up to 64%. Furthermore, because prioritization scenarios with low representation targets (e.g., 20%) allow considerable flexibility, selection of planning units for specific habitat types may be driven by minimizing cost when information about condition is not included. It may be reasonable to expect that low-cost reef areas, because they are typically remote and less affected by human activity, incidentally represent high-quality habitat. Yet our findings suggest that explicitly incorporating coral cover data in the planning process prioritized reefs in different locations, resulting in an MPA system with improved overall habitat quality.

While the incorporation of habitat condition into planning is likely to result in improved conservation outputs (Evans et al., 2015; Klein et al., 2013), the approach would benefit from further refinements with updated spatial data layers, more precise habitat classifications and connectivity data to account for spatial dependencies, all of which are likely to affect priorities. For instance, larval dispersal connectivity underpins the recovery potential of reefs and is enhanced by high-quality habitat. Favouring reefs that are in good condition and highly connected could represent and important advance in promoting resilience (Beyer et al., 2018). However, the fact that larval dispersal is difficult to estimate and few spatial planning projects currently consider it (Balbar & Metaxas, 2018) makes it difficult to incorporate connectivity in regional planning. At a finer scale, for example, within the 10 km^2 planning units, assessments should include connectivity. This would allow exploration of different strategies such as prioritizing adjacent high coral cover areas or securing a quality gradient, where medium cover reefs may act as a stepping stone to recolonize low-cover areas.

Ultimately, including the condition of conservation features in planning can only aim to achieve a better representation of conservation "value," which is but the first step in securing improved conservation outcomes. To translate planning into useful action, important additional considerations are required, for example, by assigning "priority" based on an assessment of vulnerability and irreplaceability (for an example, see Pressey & Taffs, 2001) and examining "conservation opportunity," which considers the effectiveness and implementation costs of specific actions to achieve conservation aims (Knight, Cowling, Difford, & Campbell, 2010).

Our achievement here is therefore not (yet) an implementable plan, but a quantitative demonstration of the assumed (and highly intuitive) importance of incorporating habitat condition into large-scale spatial prioritization. We used the Coral Triangle case study to illustrate how predicted coral cover, based on free, globally available data on recent climatic, biotic and abiotic conditions can be included in the planning process. In one scenario, weighting conservation features by their predicted coral cover allowed representation of reef habitat based on reef extent *and* condition. In another scenario, we classified reefs into three distinct classes based on predicted coral cover and constrained the selection problem by setting higher targets for high-cover reefs compared with low-cover reefs. Both approaches resulted in improved MPA systems from the point of

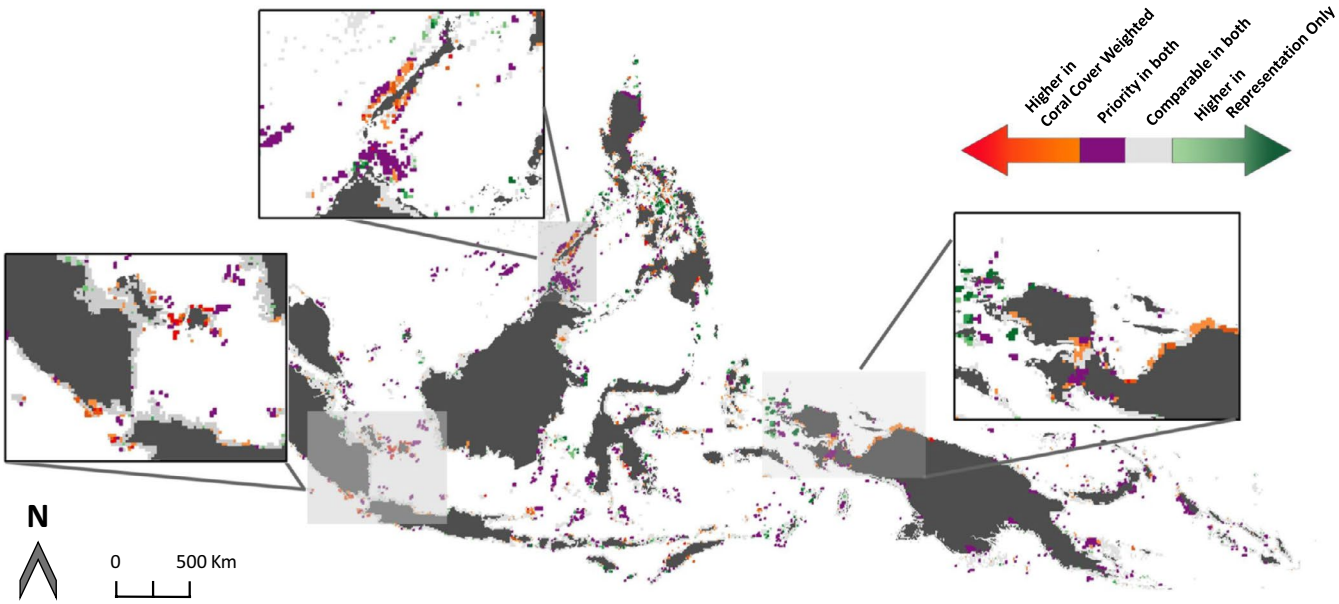

FIGURE 4 Map showing differences in priorities based on planning unit selection frequency between scenario pairs A, comparing the *Representation Only* and the *Coral Cover Weighted* scenarios

habitat condition, but only the former was more cost-effective. The case study further highlighted considerable subregional variation in the extent to which accounting for coral cover altered priority areas for MPA expansion, and better coral cover is not achieved in the relatively small countries. For instance, despite large spatial differences between the different scenarios in Timor Leste, the percentage of locally protected coral cover did not significantly increase when coral cover was accounted for. This suggests that a simple representation-based approach incidentally maximizes representation of coral cover, arguably due to a small number of planning units available for selection, all of which supporting relatively low cover. In Malaysia and the Solomon Islands, coral cover is generally higher, and more moderate shifts in the distribution of priority areas produced a significant improvement in overall condition of the MPA system. Overall, the proposed approach may be most suitable where subregional refinements based on both reef condition and cost-effective spatial redistribution within an existing MPA system are required.

Conservation actions are often determined by preferences for specific mechanisms and resource availability (White et al., 2014). Setting representation targets based on reef condition provides this kind of flexibility to align planning with specific management goals. In our second set of scenarios, by setting higher representation targets for high-cover reefs, we make the reasonable assumption that they will offer greater return-on-investment than low-cover reefs. Conservation

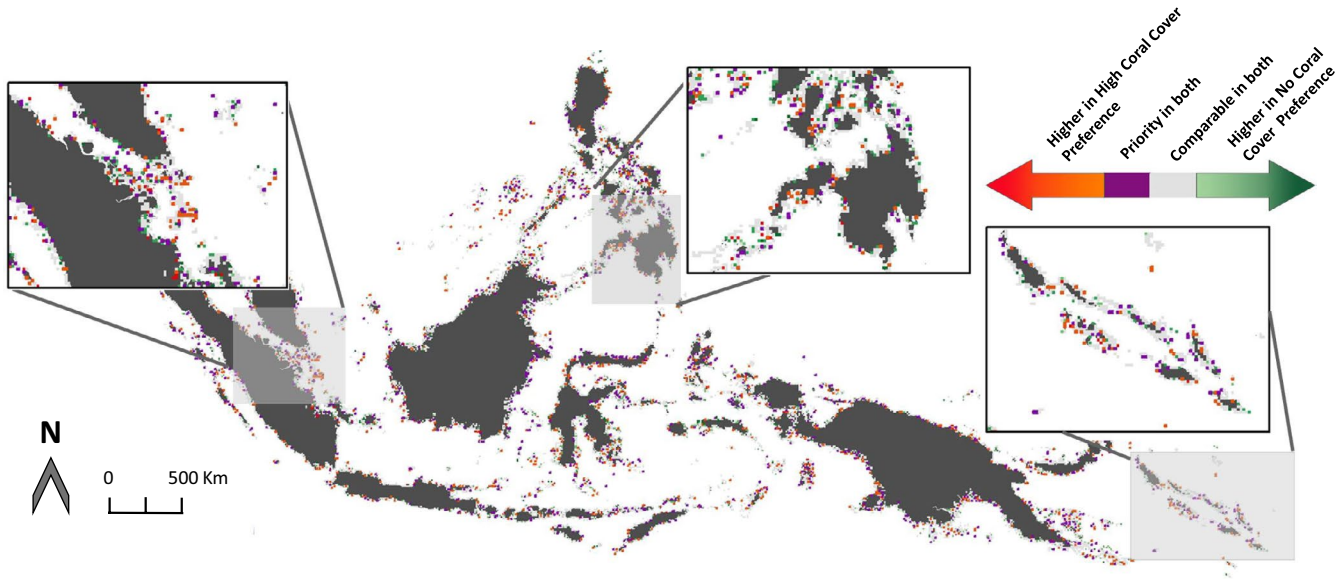

FIGURE 5 Map showing differences in priorities based on planning unit selection frequency between scenario pairs B, comparing the *No Coral Cover Preference* and the *High Coral Cover Preference* scenarios

action should be directed preferentially towards reefs with the best coral cover for the region, as they are more likely to provide propagules, support a high number of species and recover from stress (Richards, 2013). Indeed, we found that this scenario resulted in substantial changes in the spatial arrangement of the MPA system, which improved overall habitat quality. In future, it would be useful to explore scenarios that instead prioritize low-cover reefs as potential restoration sites. However, the lack of evidence for its effectiveness (Bayraktarov et al., 2016) and the potential for high implementation costs currently render the value of prioritizing restoration areas questionable.

Our approach is based on the premise that a planning process aiming to protect the "best available" reefs within a region is unlikely to result in comparative loss of efficiency, and we demonstrate feasibility at scale, with existing data. However, some limitations should be considered. The coral cover model's explanatory power is constrained because predictor variables were limited to those globally available, in a ready-to-use format, to the exclusion of other potentially viable factors such as wave exposure. This maximizes applicability in other geographic regions, and in resource-poor contexts, but does not preclude further refinements of such models at local scales, for example, by inclusion of more precise metrics of ecological function and specific threats or pressures. Further validation of predictions through ground truthing would be valuable, but uncertainty associated with the model is a known parameter (Figure S4b), and potential users can adjudicate whether this is within acceptable limits for their specific purpose, in their specific geographic region. Second, while live hard coral cover is arguably the most commonly used reef condition parameter in many reef monitoring programmes, allowing the best possible spatial coverage, it is a coarse surrogate for fine-grained temporal and spatial variability in reef condition. The model cannot differentiate between naturally occurring low-cover reefs that may well be productive and reefs that are under significant pressure and declining in function. For many sites, the most recent available data may not be representative of the current reef state (e.g., due to recent thermal stress events, but see Hughes et al. (2018) indicating relatively limited bleaching in the CT). Our approach will therefore not fully capture functional reef adequacy in these highly dynamic systems. Future applications should explore more complete operationalizations of the conservation principle of adequacy, for example, including other ecological processes where possible, such as larval dispersal, connectivity or other ecological linkages. Finally, the reef survey data set has unavoidable spatial and temporal biases resulting from different survey effort across the region. Nevertheless, our approach demonstrates a pragmatic solution based on best available, free-to-access data for marine conservation planning at the regional scale, and is fit-for-purpose in the context of rapid spatial prioritizations.

In summary, reef-building corals are foundational species, create critical three-dimensional reef structure and support the biodiversity and productivity of reefs (Graham, 2014). Not accounting for reef condition in planning processes will therefore ultimately constrain the ability to deliver an adequate MPA system that supports the persistence of biodiversity. Here, we demonstrate that incorporating this information into management decisions for tropical marine habitats is feasible on a large spatial scale and provides significant opportunities for improving conservation outcomes.

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DATA AVAILABILITY STATEMENT

The coral cover data used in this study were obtained from third parties, either through open access digital repositories or through formal data sharing agreements. The authors do not have permission to distribute these data without explicit consent from its contributors. A complete list of all data sets and respective contributors is available in Supporting Information. The environmental data used to model coral cover are freely available and can be accessed here: http://www.bio-oracle.org. A copy of the spatial data file containing our model predictions is available here: https://osf.io/us3g6/?view_only=c22a64e35ad940fa9a7b0144e9217212.

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BIOSKETCH

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SUPPORTING INFORMATION

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

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