



Heat, human, hydrodynamic, and habitat drivers measured from space correlate with metrics of reef health across the South Pacific

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Abstract Diver assessments can reveal much about coral reef condition, but fieldwork is expensive and challenging. To address this limitation to effective reef assessment, we identified predictive relationships between diver measurements of reef condition collected at 650 stations across the South Pacific and a broad portfolio of socio-environmental drivers assembled from public-domain remote sensing data. Our models of coral cover, coral diversity, fish biomass, and fleshy macroalgae cover performed with relatively high accuracy (mean-squared prediction error, MSPE = 0.35–0.48), implying that the state of the art for public-domain remote sensing is already well poised to extrapolate diver measurements to unsurveyed reefs. Whereas sea surface

temperature, protected status, market gravity, and geomorphological zones retained high importance across all models, their ability to predict each diver measurement varied, highlighting the complex determinants of the different aspects of reef health. To quantify the performance of our approach for a variety of sampling scenarios, we constructed separate models for lagoonal reefs versus forereef stations, and for ‘archipelago,’ ‘region,’ and ‘basin’ spatial scales. Despite maintaining high accuracy (MSPE < 0.38), the socio-environmental drivers that delivered the best models varied between reef zones and spatial scale. While we demonstrated high accuracy in predicting metrics coral reef health, our findings caution against one-size-fits-all interpretation of the drivers, so we suggest testing remote sensing models across geomorphological zones and scale to understand systematic changes in the variables that drive reef condition. Our study paves the way for an amplified role of remote sensing to inform reef conservation at multiple scales.

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Introduction

Coral reef health is declining at an alarming rate (Hughes et al. 2017, 2018a; Stuart-Smith et al. 2018; Williams and Graham 2019). Mounting an effective response to this reef crisis benefits from the assessment of reefs via simple health indicators that can be swiftly measured by divers. The most common indicator of reef condition is the proportional cover of the seabed by live coral, which is fundamental to reef accretion and for maintenance of the three-dimensional structure that provides habitat for many species (Graham and Nash 2013; Perry et al. 2013). Consequently, the precipitous

demise of coral cover from a range of stressors including bleaching, disease, and declining water quality has been widely documented as a major concern (Gardner et al. 2003; Bruno and Selig 2007; De'ath et al. 2012). The diversity of coral species serves as a supplementary indicator of reef condition as high coral cover alone is not always indicative of a healthy reef. Rather, reefs can maintain relatively high cover while switching to dominance by a small number of species, like 'weedy' corals, dampening overall reef resilience (Keck et al. 2005; Purkis and Riegl 2005; Green et al. 2008; Hughes et al. 2012; Tanner 2017; Toth et al. 2019). Two additional widely used indicators are the biomass of reef-associated fish and macroalgal cover. Marine fisheries provide a major source of protein and economic opportunity, especially for small island developing states (Allison et al. 2009). Thus, overfishing not only threatens food and job security for those billions of people (Burke et al. 2011; Barange et al. 2014), but also has been linked to a decline in overall reef health (Newman et al. 2006; Mora et al. 2011), as reef fish serve important ecological roles. For example, herbivorous fish control macroalgal growth (Adjeroud et al. 2018) and limit shifts to macroalgae-dominated reefs, which are typical of degraded reef ecosystems (McManus and Polsenberg 2004; Mumby et al. 2007). Additionally, when the reef is overgrown with macroalgae, coral recruitment and survival are compromised (Graham et al. 2015). Healthy, undisturbed reefs are generally characterized by high values of hard coral cover, coral diversity, and fish biomass, coupled with low macroalgal cover (Sandin et al. 2008).

These four diver-measured indicators also underlie the most widely adopted reef monitoring programs, such as the Atlantic and Gulf Rapid Reef Assessment (AGRRA), Reef Check, the Healthy Reefs Initiative, NOAA's National Coral Reef Monitoring Program, the AIMS Long-term Monitoring Program, and the Global Coral Reef Monitoring Network (Halford and Thompson 1996; Wilkinson et al. 1997; Hodgson 1999; McField and Kramer 2007; Lang et al. 2010; Towle et al. 2021). They are also central to considerations of metrics of coral reef resilience (e.g., Obura and Grimsditch 2009; McClanahan et al. 2012; Maynard et al. 2015; Lam et al. 2017). The ability to map these indicators at large scales, bypassing the challenges of field surveys, would further promote their worth for implementing global reef management. Given the ecological importance and widespread use of reef indicators, we adopted live coral cover and coral diversity, fish biomass, and fleshy macroalgae cover for this study, and hereafter refer to them as our four 'ecosystem metrics.'

Our motivation for this work was predicated on the fact that it is logistically and financially impractical for large-scale monitoring of reefs to be solely built on data collected by divers. Remotely sensed imagery from a range of airborne sensors and satellites provides a key tool to observe

ecosystems at large scales (Hedley et al. 2016; Purkis 2018; Purkis and Chirayath 2022) and to extrapolate point data collected by divers across entire seascape. We consider our work timely considering the growing repositories of high-resolution remotely sensed data available for shallow marine ecosystems (Sbrocco and Barber 2013; Yeager et al. 2017; Gove et al. 2019; Asner et al. 2020, 2022; Smallhorn-West et al. 2020b; Roelfsema et al. 2021). We tested the hypothesis that systematic relationships existed between diver measurements of the four ecosystem metrics and public-domain remote sensing data. If these relationships could be modelled, a small number of diver surveys could potentially be extrapolated to unsampled locations, via open-source remote sensing, to create continuous and inexpensive maps of coral cover and coral diversity, fish biomass, and fleshy macroalgae cover for marine spatial planning at scale.

Our work builds forward from a rich portfolio of studies using remote sensing to model the biology of reefs. For instance, coral cover has been successfully correlated with remotely sensed variables (Zinke et al. 2018; Vercammen et al. 2019; Asner et al. 2020; Smallhorn-West et al. 2020a), as has coral diversity (Pittman et al. 2009; Knudby et al. 2013), reef fish richness and abundance (Purkis et al. 2008; Pittman and Brown 2011; Cinner et al. 2016; Harborne et al. 2018; Darling et al. 2019), and macroalgal cover (Kotta et al. 2013). Furthermore, coral cover modelled from remote sensing has already been used to guide designation of marine reserves in Tonga (Smallhorn-West et al. 2020c).

Most of these studies, however, have focused on a single property of the ecosystem. As a result, literature examples that use remote sensing to model multiple ecosystem metrics from the same set of satellite data are limited. One exception, however, is Jouffray et al. (2019) who modelled reef regimes, defined by varying benthic cover and fish biomass, and found that each regime was best predicted by different drivers. By extension, it is logical to assume that the drivers needed to successfully model a single ecosystem metric, such as coral cover, might also change across natural and anthropogenic gradients, and across spatial scale (Connolly et al. 2005; Williams et al. 2015a; Smith et al. 2016). It is well known, for instance, that a coral community situated in a restricted lagoon is ecologically different to one on an exposed forereef (Riegl et al. 2012; Maggioni et al. 2021). Ignoring this variability risks presenting managers with inappropriate models for reefs unique to their jurisdiction. Hence, there is a need to further examine the best approach for linking remote sensing to ecosystem metrics.

Here, we collate our field data collected with the Khaled bin Sultan Living Oceans Foundation, under the auspices of the Global Reef Expedition (hereafter 'KSLOF-GRE'), which possibly accomplished the most comprehensive survey of Earth's reefs so far achieved. We visited a global transect of > 1000 remote, shallow-water tropical reefs

distributed through the Atlantic, Pacific, and Indian Oceans, and their associated seas. Our expedition deployed standardized diver surveys to measure reef condition, coupled with habitat mapping from satellite and aircraft (Purkis et al. 2019). We only considered diver stations in a South Pacific subset of the global KSLOF-GRE field data to avoid convolving data from reefs in the Pacific with those from the Atlantic and Indian Oceans, which are ecologically different (e.g. Roff and Mumby 2012). However, our Pacific-wide study is sufficiently large (50 million km²) to comprise several bioregions and span pronounced gradients in marine biodiversity, anthropogenic stress, and climatological variability (Gove et al. 2013, 2016; Beger et al. 2020), giving us an opportunity to test the systematic variation of using remotely sensed variables to predict ecosystem condition.

Our first aim was to identify model efficacy and correlations between each of the reef assessments made in the field with remote sensing drivers through a regression-based modelling technique capable of extrapolating predictions to new areas. Rather than modelling metre-scale benthic and fish assemblages across a small reef area (e.g., a single atoll), our aim was to estimate reef condition across the South Pacific at the scale of satellite pixels from state-of-the-art remote sensing products. This means using relatively coarse data layers compared to traditional studies of assemblage structure. However, if successful, this research will be a prelude to broadly estimating reef health from orbit. Our second aim was to examine changes in drivers on reefs inside lagoons versus on forereefs and for field observations

aggregated at local versus basin-scales. Our motivation was to inform on the best practices of modelling reef condition and to examine whether interpretation of model relationships was applicable to new seascapes and regions outside of the Pacific.

Methods

Study area

To gather the field-measured ecosystem metrics necessary for this study, diver observations were made at 650 stations distributed across the South Pacific—Palau, the Solomon Islands, Cook Islands, New Caledonia, Fiji, Tonga, and French Polynesia (Fig. 1). Each station was comprised of a minimum of four replicate benthic and fish transects. Of our 650 stations, 250 were located on lagoonal reefs and 400 on forereefs. The field data were collected over four years. Through 2012 and 2013, four archipelagos in French Polynesia—Society, Austral, Tuamotu, and Gambier—were surveyed, delivering a total of 259 stations (Fig. 1g–j). Similarly accomplished in 2013 were the Cook Islands, Tonga, Fiji, and New Caledonia, delivering 30, 60, 70, and 75 diver stations, respectively (Fig. 1c–f). In 2014, the KSLOF-GRE surveyed 69 stations in the Solomon Islands (Fig. 1b), and in the following year, 87 stations were surveyed in Palau (Fig. 1a).

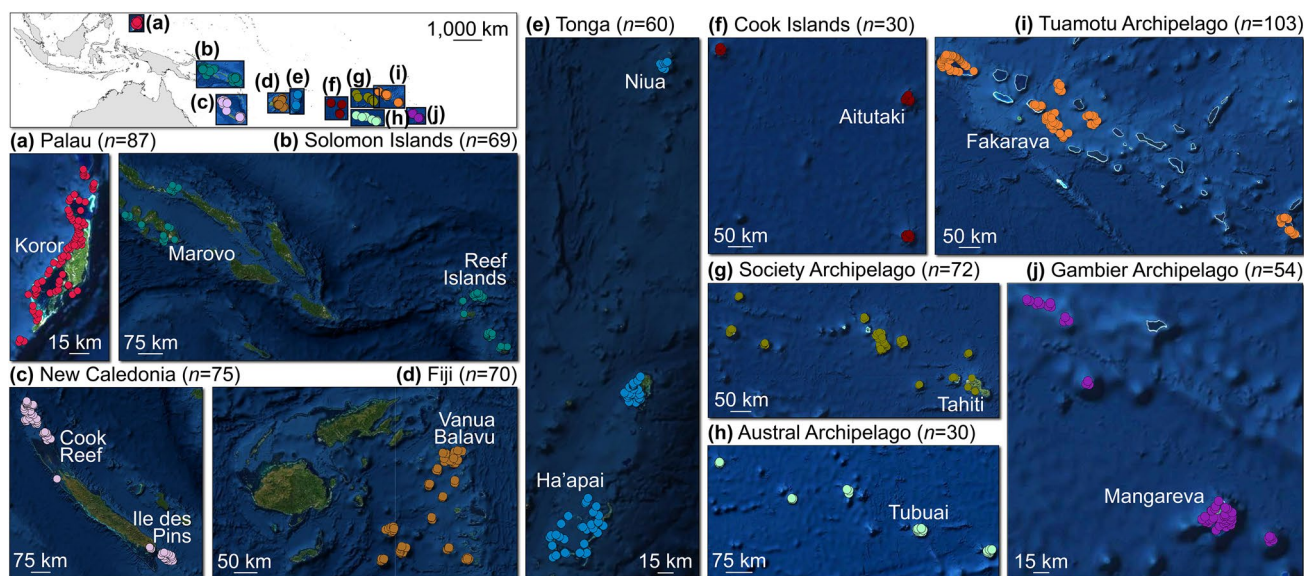


Fig. 1 Maps show the distribution of the 650 KSLOF-GRE field stations in each of seven South Pacific countries—**a** Palau, **b** the Solomon Islands, **c** New Caledonia, **d** Fiji, **e** Tonga, **f** the Cook Islands,

and the **g** Society, **h** Austral, **i** Tuamotu, and **j** Gambier French Polynesian archipelagos. Dive stations colour-coded by archipelago. These colours are maintained for all figures to ease cross-comparison

All our considered reefs had, to one extent or another, endured some form of disturbance prior to our visits. The reefs of French Polynesia, for instance, had suffered five mass bleaching events—1991, 1994, 1998, 2002, and 2007 (Mumby et al. 2001; Pratchett et al. 2013; Adjeroud et al. 2018). In addition to bleaching, the reefs of the Society and Austral Archipelagos had also been damaged by outbreaks of crown-of-thorn starfish between 2006 and 2009 (Kayal et al. 2012; Timmers et al. 2012; Yasuda et al. 2015). Cyclone Erica devastated New Caledonia in 2003 (Guillemot et al. 2010), and the reefs of Tonga were impacted by a tsunami in 2009 (Clark et al. 2011). Our east-to-west fieldwork from French Polynesia to the Solomon Islands was completed prior to the 2015–2017 mass coral bleaching which impacted reefs globally (Hughes et al. 2018a; Eakin et al. 2019) and Palau was completed in January 2015, a few months ahead of that pan-tropical bleaching event (Hughes et al. 2017). At the time that they were surveyed, none of our stations had experienced degree heating week values above the bleaching threshold since at least 2010.

Despite its expansive reefs and the economies built upon them, reef management at the scale of the South Pacific is modest. According to the Protected Planet database (www.protectedplanet.net), 8% of this area is designated as marine protected areas, hereafter ‘MPAs,’ and only 4% is designated as no-take fishing reserves. MPAs encompassing reefs in our considered countries were similarly scant. Of our 650 field stations, at the time they were surveyed, only 182 were situated within MPAs (disproportionately, 161 of those were in Palau and New Caledonia) and only 35 of the 182 stations were specified as no-take reserves. We considered the varied disturbance histories of our field stations and their disparate protected status as an important aspect of this study. These gradients allow the efficacy of our models to be tested for a wide range of disturbance and management conditions (e.g., widely varying coral cover and fish biomass), thereby maximizing the chance that our findings are relevant to other sites in the Pacific and beyond.

Ecosystem metrics from field data

At each of the 650 field stations, all four ecosystem metrics were derived from diver data extracted from four replicates of either 10-m-long benthic or 30-m-long fish transects at five water depths (< 8 m, 8–13 m, 14–18 m, 19–25 m, and > 25 m). For each benthic transect, divers quantified the percentage occupancy of live coral and macroalgae via point-intercept surveys. This technique required the surveyor to place a 10-m transect line on the seabed and record organisms and substrate type at every 10-cm mark for a total of 100 points per transect. However, in the rare cases where dive duration prevented a transect being completed, 1-m² photoquadrats were taken every metre along the transect and

these photographs were manually digitized to extract benthic cover. In these cases, 50 points were randomly overlaid on each photograph and benthic and substrate type were identified under the points. Regardless of survey technique, corals were identified to the level of genera and algae were classified into six functional groups (fleshy macroalgae, crustose coralline algae, erect coralline algae, sediment-dominated turf, turf, and cyanobacteria). We used all coral genera to represent our coral cover ecosystem metric. Of the six total functional groups of macroalgae recorded by the divers, we only used the percent cover of fleshy macroalgae for our second benthic ecosystem metric. Per transect, coral diversity was quantified using the Simpson’s diversity index, D , written as

$$D = 1 - \sum(n/N)^2 \quad (1)$$

where n is the total number of corals of a particular genus, and N is the total number of corals of all genera. Simpson’s index, like the Shannon-Wiener index, marries richness and evenness into a single metric (Simpson 1949). We opted for Simpson’s index because it gives more weight to dominant species, which more accurately represented our South Pacific dataset, where few coral species tended to dominate the benthos. Simpson’s diversity of coral genera served as our third benthic ecosystem metric.

Fish observations were also comprised of a minimum of four replicate belt transects at the five water depths. We surveyed reef fish assemblages following a visual census technique modified from English et al. (1997) conducted over a 15-min duration along 30-m-long, 2-m-wide belt transects. Cryptic fishes and fishes < 5 cm were excluded from the counts. Each fish was identified to the level of species, and size was visually estimated. Fish biomass was then computed using the formula

$$W = aLb \quad (2)$$

Here W is the weight of each fish in grams, L is the length of the fish in cm, and a and b are species-specific growth constants derived from the length-weight relationships (Bohnsack and Bannerot 1986; Kulbicki et al. 1993).

Replicate transects across the depths present at each station delivered a total dataset consisting of 4442 benthic transects and 4289 fish counts. To assimilate the field data into a form suitable for comparison with remote sensing drivers, the replicate transects were averaged within each depth class and then averaged across the depths at which they were collected to yield a single measurement of each ecosystem metric at the 650 diver stations. The purpose for averaging in this way was twofold. First, our drivers from remote sensing were limited by their coarse spatial resolutions varying from tens to hundreds of metres, with the result that each remote sensing pixel invariably spans a wide range of water depth.

The second motivation for averaging the field data across depth was to build an approach that would be applicable to new field locations, which avoids rendering this model obsolete. Field data from other sources are likely collected following different protocols (e.g., AGRRA surveys exclude our two depth classes > 19 m), which will yield sparse, missing, or surplus depths compared to the field surveys that we used to construct our models. We deemed this averaging technique to be more robust and relevant for predicting ecosystem metrics in other ocean basins for future use.

Socio-environmental drivers from remote sensing data

We derived 45 ‘socio-environmental drivers’ from public-domain remote sensing products, 28 of which we kept after removing drivers due to multicollinearity (Table 1). To the best of our knowledge, our original list of 45 socio-environmental drivers is exhaustive in terms of the open-source remote sensing data that are globally available and potentially relevant to coral reef health. While retaining all 45 variables did not change model performance, our motivation for discarding correlated variables was to ensure that they did not hinder the ranking of relative driver importance in each model, thereby simplifying interpretation of results. Continuous variables were assessed for multicollinearity with a correlation matrix and selected for removal based on predetermined thresholds ($VIF > 7$ and/or $R^2 > 0.8$; Supplementary Fig. 1). Assessing multicollinearity among categorical variables was completed by running chi-square (χ^2) tests between each pair of variables and removing those which had test statistics exceeding the χ^2 critical value of $p > 0.05$. We also ran Kruskal-Wallis tests on pairs of categorical and continuous variables and removed those which were significantly correlated, as denoted by p values > 0.05 .

To aid in the interpretation of our final list of 28 socio-environmental drivers, we split them into four convenient categories—those related to heat stress (3 ‘Heat’ drivers), human pressure (9 ‘Human’), the hydrodynamic regime surrounding the reef (3 ‘Hydrodynamic’), and the physical properties of the reef itself, including the distribution of habitat and geomorphology (13 ‘Habitat/physical’ drivers). For the sake of brevity, the derivation of the 28 drivers is detailed in Supplementary Material, along with an explanation of our assessment of multicollinearity. Using the 28 drivers, we aimed to predict our four ecosystem metrics (field measurements of coral, fish, and fleshy macroalgae) when assembled into a regression-based modelling framework.

Random forest modelling of ecosystem metrics

Random forests are nonparametric models composed of many regression trees that are used to predict the value of a single response variable from multiple predictors (Breiman

2001). These models are considered equal, if not superior, to competing classification and regression models, such as boosted regression trees and generalized linear modelling (De’ath and Fabricius 2000). The accuracy of random forest models does not suffer when they are presented with many predictor variables, as assembled by this study. We picked random forests over tree-boosting methods for two reasons. First, because random forests take advantage of bootstrapping to avoid overfitting and improve model stability (Ishwaran and Lu 2019), whereas boosted trees are grown sequentially without resampling. Also, boosting requires fine-tuning of many different model parameters, which can be complicated for ecological data with small sample sizes. The second reason why we choose random forests is that they implicitly account for spatial autocorrelation within the predictor and response variables by bootstrapping. As further insurance against spatial autocorrelation, however, we used Moran’s I to test for spatial dependency of all four ecosystem metrics. We built our random forest models using R package ‘randomForestSRC’ (v. 2.14.0). Normalization is unnecessary for random forest modelling, and therefore, no prior transformations were performed on the socio-environmental drivers.

Each model of the four ecosystem metrics was trained on a random split of 80% of the 650 field stations, while the remaining 20% were reserved for validation. Observed versus predicted values were plotted against a 1:1 identity line, and the mean squared prediction error (MSPE) was computed by

$$\text{MSPE} = \text{avg}[\Sigma(O-P)^2] \quad (3)$$

where O is the observed value from the field data and P is the value predicted by the random forest. MSPE is a common goodness-of-fit measure for regression models because it quantifies the model residuals where lower MSPE values represent lower predictive error.

One further output from the random forest models was the relative variable importance (VIMP), which was computed via permutation of bootstrapped samples during forest building. Per-model VIMP lists were used to evaluate which combinations of the 28 socio-environmental drivers possessed predictive power over each of the four ecosystem metrics. A driver was deemed important for a given model if it accounted for > 50% of the relative VIMP. Following the lead of Pittman and Brown (2011), Harborne et al. (2018), Jouffray et al. (2019), and Smallhorn-West et al. (2020a), we considered the partial dependence plots (PDPs) for the socio-environmental drivers that exceeded the 50% VIMP threshold. The PDPs were used to visualize the marginal effect of drivers on random forest predictions for each ecosystem metric, and the PDP y-axis describes an averaged effect to the model predictions. We classified the effects for

Table 1 The 28 socio-environmental drivers used as independent variables for random forest modelling of coral, fish, and macroalgae, were grouped into the four H's: Heat ($n=3$), Human ($n=9$), Hydro-dynamic ($n=3$), and Habitat/physical ($n=13$). Details of drivers given in Supplementary Material

Category	Socio-environmental driver	Description ¹	Scale, source ²
Heat	Max. degree heating weeks	Maximum heat stress accumulated over time	5 km, NOAA
	Mean sea surface temperature	Average °C from time-series data	1 km, NASA
	Max. sea surface temperature	Maximum °C from time-series data	1 km, NASA
Human	Dollar value	Dollar value of reefs to tourism sector	1 km, TNC
	Human population density	Number of humans within 20 km	1 km, LandScan
	Human pressure	Number of humans per reef area within 20 km	1 km, LandScan
	Marine protected area coverage	Coverage by marine protected areas in each country	Country, WDPA
	Market gravity	Intensity of human impacts as a function of human population and reef accessibility	10 km, Cinner et al. (2018)
	Protected status	Protected area established, or not, at time of survey	Station, WDPA
	Socioeconomic development	First principal component from population, age, population growth, birth/death rate, urban population, life expectancy, GDP, GDP growth rate, GDP per capita, and unemployment rate	Country, World Bank and World Factbook
	Terrestrial protected area coverage	Coverage by terrestrial protected areas in each country	Country, WDPA
	Tourism	Annual visitation to reef	1 km, TNC
Hydrodynamic	Wind exposure	Leeward, windward, or intermediate	25 km, KSLOF
	Storms	Frequency and intensity of storms passing by reef since 1980	11 km, NOAA
	Max. wind-induced wave exposure	Mechanical energy based on fetch, wind speed, and wind direction	25 km, NASA
Habitat/physical	In situ bathymetry	Average water depth of field station as measured by divers	Station, KSLOF
	Distance to land	Euclidean distance to nearest land	0.025 km, OSM
	Distance to pass	Euclidean distance to nearest pass	0.025 km, OSM
	Lagoon	Inside or outside lagoon	Station, KSLOF
	Land area	Area of land within 20 km	0.25 km, OSM
	Max. island elevation	Highest point of island or atoll in metres	Atoll, DEM
	Millennium Coral Reef Mapping Project (L2)	Reef geomorphology at Level 2	30 m, MCRMP
	Millennium Coral Reef Mapping Project (L3)	Reef geomorphology at Level 3	30 m, MCRMP
	Millennium Coral Reef Mapping Project (L4)	Reef geomorphology at Level 4	30 m, MCRMP
	Mean net primary productivity	Average net primary productivity modelled from photosynthetically available radiation, temperature, and chlorophyll a concentration	5 km, Yeager et al. (2017)
	Max. net primary productivity	Maximum net primary productivity modelled from photosynthetically available radiation, temperature, and chlorophyll a concentration	5 km, Yeager et al. (2017)
	Reef area	Area of reef within 20 km	30 m, WCMC
	Reef extent	Linear extent of continuous reef tract in kilometres	30 m, WCMC

Driver description¹: *GDP* gross domestic product

Data sources²: *NOAA* National Oceanic and Atmospheric Administration, *NASA* National Aeronautics and Space Administration, *TNC* The Nature Conservancy, *WDPA* World Database on Protected Areas, *KSLOF* Khaled bin Sultan Living Oceans Foundation, *OSM* OpenStreetMap, *DEM* Digital Elevation Model, *MCRMP* Millennium Coral Reef Mapping Project, *WCMC* World Conservation Monitoring Centre

continuous drivers as either positive (+), negative (−), or complex (C), with the latter defined as a blend of positive and negative relationships within the parameter space.

Modelling all 650 South Pacific stations showed the statistical relationship between diver-measured ecosystem metrics and remotely sensed socio-environmental drivers to

biomass, and fleshy macroalgae cover were 0.35, 0.24, 0.20, and 0.22, respectively, suggesting that there was little autocorrelation and data dispersion was close to random (z scores with associated p values < 0.01).

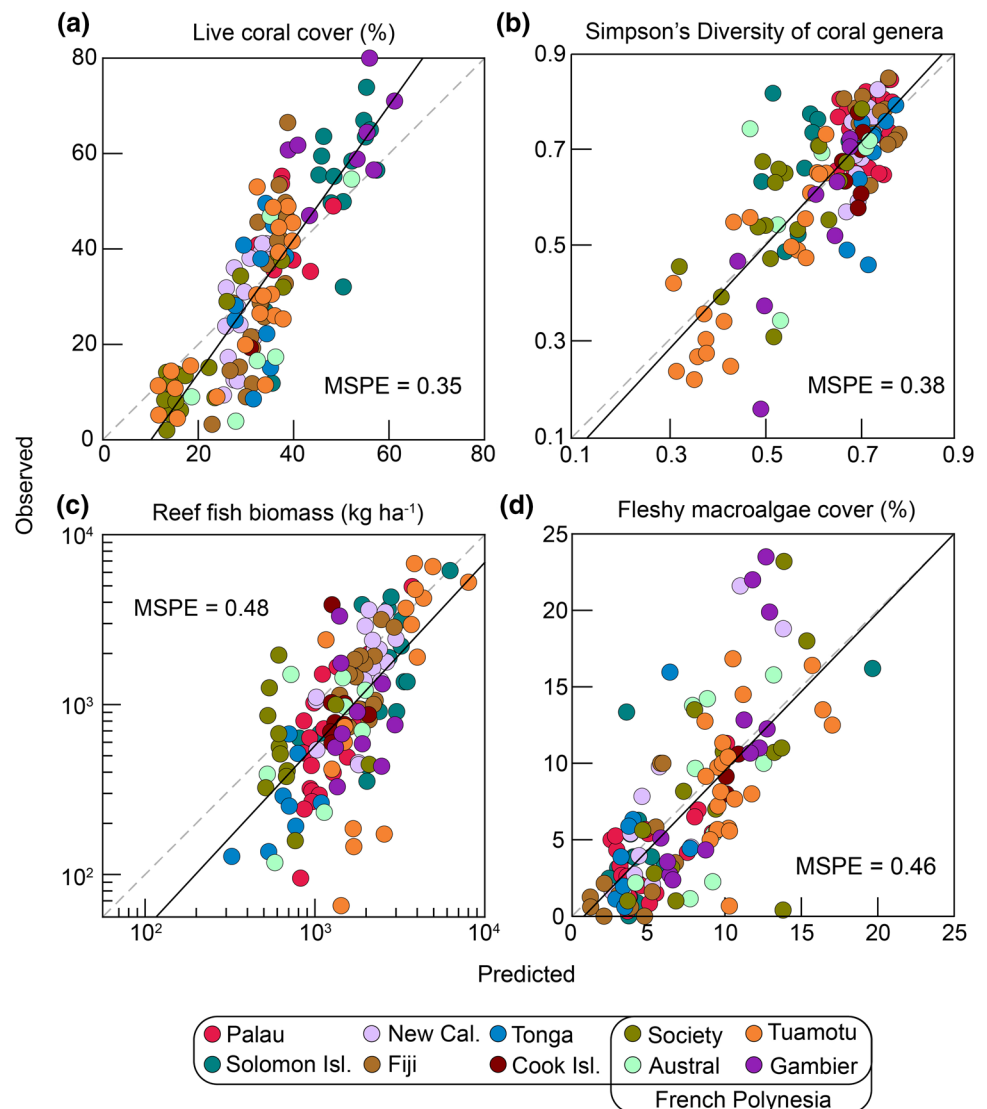
Correlation plots of predicted versus observed values showed that the random forests made meaningful predictions of all four ecosystem metrics (Fig. 3). The model for coral cover (MSPE = 0.35) performed the best, followed by coral diversity (MSPE = 0.38), then fleshy macroalgae cover (MSPE = 0.46), and finally fish biomass (MSPE = 0.48). All four models performed with high accuracy at certain ranges, however, especially for macroalgae and fish biomass, deviated at the extremes of those ranges. Whereas the difference between observed and predicted values for live coral cover and coral diversity was generally constant across the full ranges of the models (Fig. 3a, b), values measured in the field of reef fish biomass $< 10^2$ kg ha⁻¹ tended to be overpredicted by the random forest (Fig. 3c). For the low

biomass points predicted in this model, Tuamotu (French Polynesia), an archipelago with highly variable fish biomass (Fig. 2d), was particularly affected. The model of fleshy macroalgae cover, by contrast, performed well in its lower range, but tended to underpredict cases of fleshy macroalgae cover $> 10\%$ (Fig. 3d).

Relationships exist between ecosystem metrics and their environment

For coral cover, seven socio-environmental drivers exceeded the threshold of 50% VIMP and were considered relevant predictors (Fig. 4a). Coral cover appeared particularly sensitive to MPA coverage from the ‘Human’ category, such that higher coral cover was found in countries with larger MPAs (Fig. 5a). In the ‘Heat’ grouping, the important correlates were degree heating weeks (DHW), and mean and maximum sea surface temperature (SST). The model showed

Fig. 3 Correlation plots of random forest model predictions versus field-observed values for **a** coral cover, **b** coral diversity, **c** reef fish biomass, and **d** fleshy macroalgae cover. Model performance was evaluated mean-squared prediction error (MSPE). Points colour-coded by country. Dashed grey lines represent a 1:1 fit, while solid black lines represent least square regressions of the relationships. All models can predict the field-measured values with meaningful accuracy, though that for fish biomass tends to overpredict low values and that for macroalgae underpredicts high values



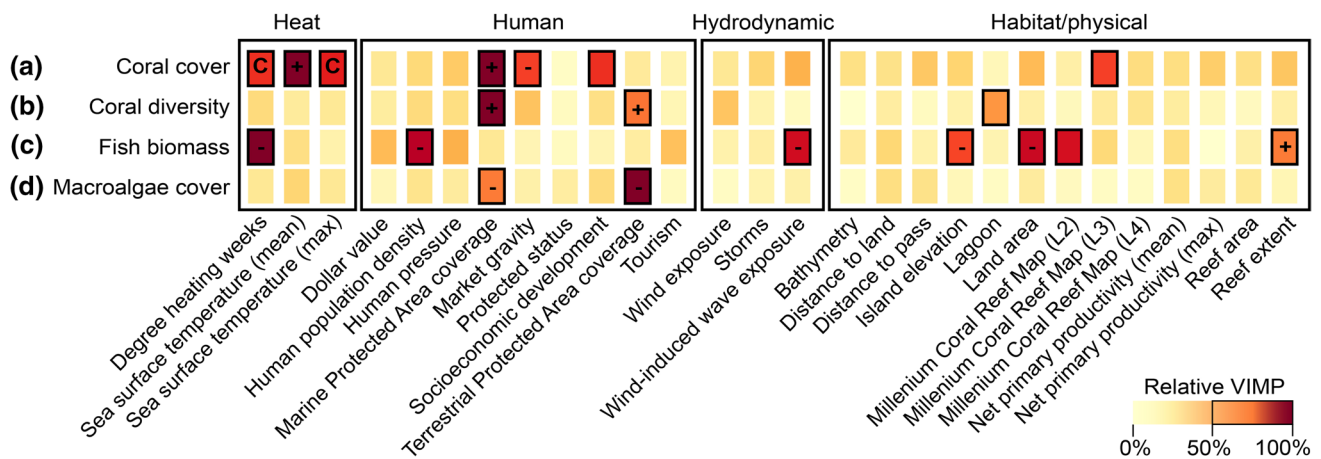


Fig. 4 Heatmap of relative variable importance (VIMP) for the 28 socio-environmental drivers for the models of **a** coral cover, **b** Simpson's Diversity of coral genera, **c** reef fish biomass, and **d** fleshy macroalgae cover. Drivers are grouped as they pertain to the 'Heat,' 'Human,' 'Hydrodynamic,' and 'Habitat/physical' properties of our diver stations. Black boxes identify drivers with >50% relative

VIMP, and their positive (+), negative (-), or complex (C) effects on the ecosystem metrics are denoted within these boxes. Drivers with >50% relative VIMP for coral cover and reef fish biomass models are greater in number and span more socio-environmental categories than the other two ecosystem metric models

coral cover decreasing with mean and maximum SST and DHW; then, coral cover increased at the upper range of SST values (Fig. 5b, c, e, respectively). Within the 'Human' category, market gravity and the socioeconomic development score were also important in the model. Lower coral cover in our dataset was predicted by high socioeconomic development scores (Fig. 5d). Here, high scores were associated with high birth rates and GDP growth (Supplementary Fig. 2). High values for market gravity were correlated with low coral cover (Fig. 5f). From the 'Habitat' category, Millennium Coral Reef Mapping Project (MCRMP) Level 3 driver exceeded the 50% VIMP threshold. Coral cover was particularly affected if the station was classified as 'ocean exposed fringing,' or the three MCRMP Level 3 classifications associated with atolls ('atoll lagoon,' 'atoll patch,' and 'atoll rim'; Fig. 5g). No 'Hydrodynamic' drivers exceeded the 50% VIMP criteria for modelling coral cover.

In the coral diversity model, MPA and terrestrial protected area (TPA) coverage in the 'Human' category and the lagoon driver from 'Habitat' were the three drivers that exceeded 50% VIMP (Fig. 4b). A minor increase in protected area coverage, both MPA and TPA, correlated with instances of higher coral diversity (Fig. 6a, b), and coral diversity was lower within lagoons than outside of them (Fig. 6c).

The seven drivers that surpassed the 50% VIMP threshold for the model of fish biomass covered all four of our categories—a single driver represented each of the 'Heat,' 'Human,' and 'Hydrodynamic' categories, which were DHW, human population density, and wave exposure, respectively (Fig. 4c). The remaining four drivers from the 'Habitat' category were land area, island elevation,

reef extent, and MCRMP Level 2. Fish biomass exhibited a negative relationship with each of the first four continuous drivers, so that biomass was predicted to be lowest with higher DHW, human population, land area, and wave energy (Fig. 7a–d). In the case of MCRMP Level 2, fish biomass was higher on reefs classified as 'oceanic atolls' and lower for the remaining classifications (Fig. 7e). Fish biomass was low around islands with high elevation and high on reefs with long linear extents (Fig. 7f, g).

Finally, only two socio-environmental drivers—MPA and TPA coverage—both within the 'Human' category exceeded the 50% VIMP threshold for our fleshy macroalgae model (Fig. 4d). The reefs situated in South Pacific countries with little to no MPA and TPA had higher fleshy macroalgae cover and algal cover steeply declined with even a small addition of protected area (Fig. 8a, b).

Coral cover can be accurately modelled across geomorphological zones and across scale

We applied random forests to model the cover of live coral for 400 forereef and 250 lagoonal stations (Fig. 9). The accuracy for these two models was not significantly different to that achieved by modelling the entire Pacific-wide dataset, without splitting by reef geomorphology. The MSPE of the 'forereef' model was 0.37 and the 'lagoonal' model MSPE was 0.34, as compared to MSPE of 0.35 when all the data were considered as a single set. Despite consistent accuracy, the VIMP lists differed for the models created for the forereef stations versus those in the lagoon. The seven drivers with >50% VIMP for the forereef model of coral cover (Fig. 9a) were mean SST and DHW from the 'Heat'

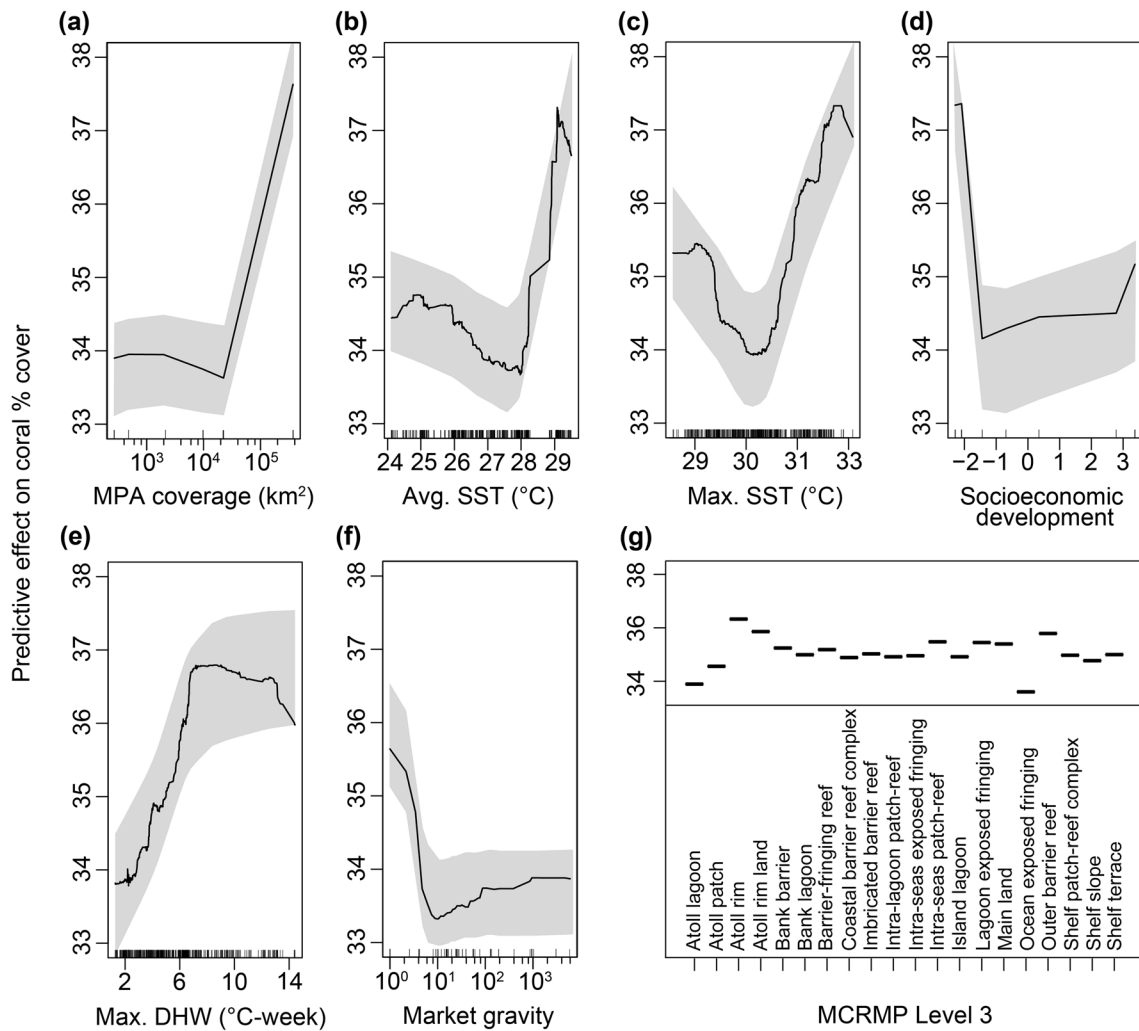
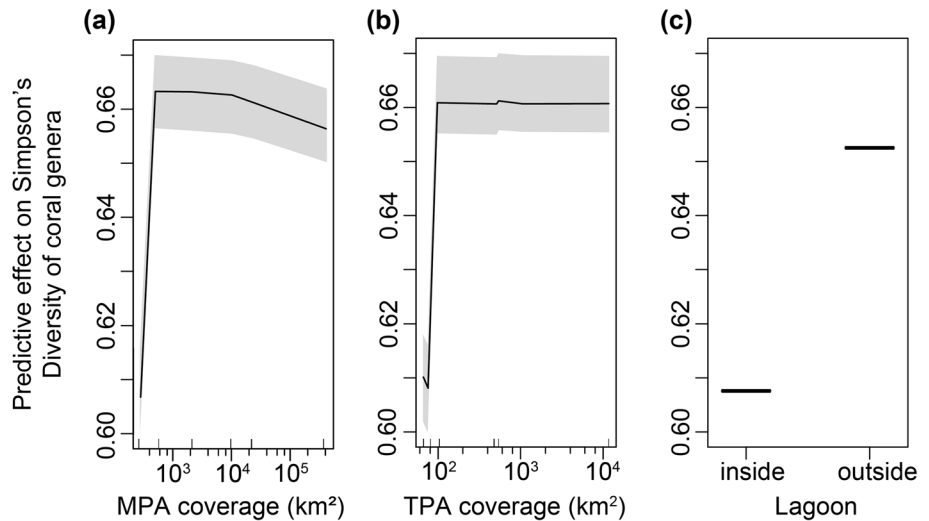


Fig. 5 Partial dependence plots **a** through **g** for the seven socio-environmental drivers with >50% variable importance from the random forest model of coral cover. SST=sea surface temperature, DHW=degree heating weeks, and MCRMP=Millennium Coral

Reef Mapping Project classifications. Tick marks on the x-axis show distribution of observations along the range of each driver. 95% confidence intervals around the predicted effects depicted in grey

Fig. 6 Partial dependence plots **a** through **c** for the three socio-environmental drivers with >50% variable importance from the random forest model of Simpson's diversity of coral genera. MPA=marine protected area and TPA=terrestrial protected area. Tick marks on the x-axis show distribution of observations along the range of each driver. 95% confidence intervals around the predicted effects depicted in grey



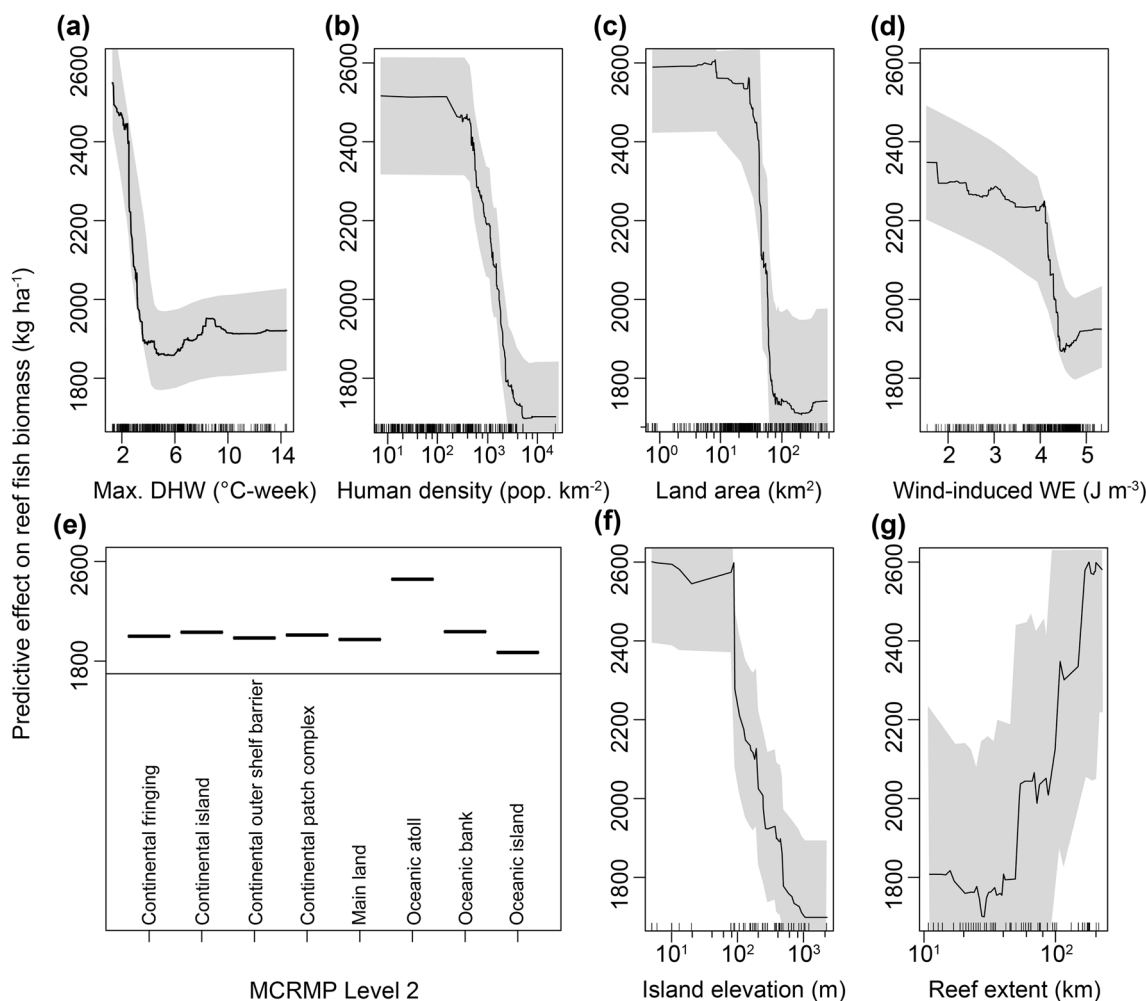


Fig. 7 Partial dependence plots **a** through **g** for the seven socio-environmental drivers with >50% variable importance from the random forest model of reef fish biomass. DHW = degree heating weeks, MCRMP = Millennium Coral Reef Mapping Project classifications.

Tick marks on the x-axis show distribution of observations along the range of each driver. 95% confidence intervals around the predicted effects depicted in grey

category, population density, MPA coverage, and market gravity from ‘Human,’ and distance to pass and MCRMP Level 3 from ‘Habitat.’ The only three drivers that exceeded our VIMP threshold for the lagoonal model, meanwhile, were MPA coverage, socioeconomic development, and distance to the nearest pass (Fig. 9b).

When modelling live coral cover across spatial scales, 650 dive stations in the South Pacific represented the full basin-scale model, 144 stations in Solomon Islands and New Caledonia, 160 in Fiji, Tonga, and the Cook Islands, and 259 in French Polynesia comprised our three region-scale models, and the final archipelago-scale included 103 stations situated in the French Polynesian archipelago of Tuamotu (Fig. 10a). Running the model for coral cover at these three granularities delivered prediction accuracies which, just as for the geomorphological splits, did not qualitatively vary (Fig. 10b). The MSPE was 0.31 for the archipelago-scale,

and region-scale MSPE was 0.37, 0.38, and 0.30, respectively, from west to east, compared to MSPE of 0.35 from the full basin-scale model.

Whereas model error was stable across scale, the VIMP lists varied between the three granularities (Fig. 10c). The > 50% VIMP list for the archipelago-scale model was composed of four drivers—DHW from ‘Heat,’ wind exposure from ‘Hydrodynamic,’ and MCRMP Level 3 and Level 4 from the ‘Habitat/physical’ category. The archipelago-scale model was the only example without an important ‘Human’ driver.

The three region-scale models resulted in different sets of important drivers. Those for modelling Solomon Islands and New Caledonia were all three ‘Heat’ variables, human pressure and storms from the ‘Human’ and ‘Hydrodynamic’ categories, and island elevation and the MCRMP Level 4 classification from ‘Habitat/physical.’ This was the only

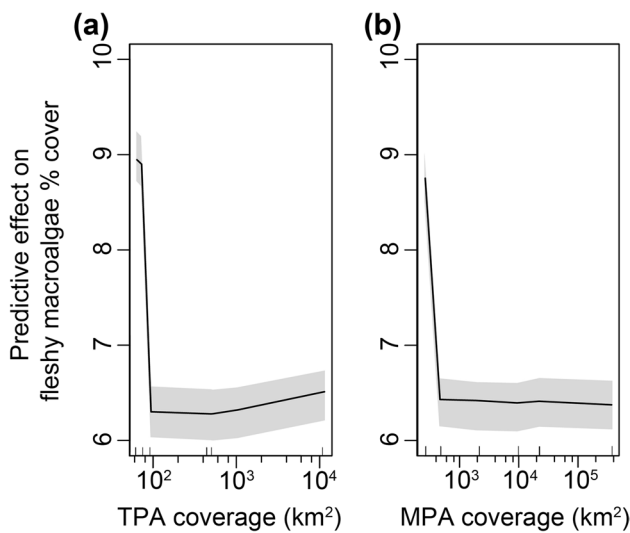


Fig. 8 Partial dependence plots **a** through **b** for the two socio-environmental drivers with > 50% variable importance from the random forest model of fleshy macroalgae cover. MPA=marine protected area and TPA=terrestrial protected area. Tick marks on the *x*-axis show the distribution of observations along the range of each driver. 95% confidence intervals around the predicted effects depicted in grey

region-scale model without market gravity as an important driver. The model of coral cover in French Polynesia resulted in the shortest VIMP list. Those four drivers were almost the same as those for the basin-scale scale, the only difference being the exclusion of max SST, DHW, and socioeconomic development. Both the French Polynesia and basin-scale models did not have any ‘Hydrodynamic’ drivers. Mean net primary productivity and MCRMP Level 3 were two additional important drivers in French Polynesia. Modelling across Fiji, Tonga, and the Cook Islands produced six drivers above the 50% VIMP threshold. These were DHW from

‘Heat,’ market gravity from ‘Human,’ two ‘Hydrodynamic’ drivers wind exposure and storm impact, and island elevation and reef extent from the ‘Habitat/physical’ category. This was the only model without an important MCRMP driver.

Discussion

Understanding which satellite-derived variables can predict different ecosystem metrics is an important step towards modelling reef health from orbit. To meet this objective, the KSLOF-GRE generated an unprecedented dataset of standardized in situ measurements for four metrics of reef condition—coral cover and diversity, fish biomass, and fleshy macroalgae cover. We discovered that each of these metrics could be effectively modelled across the South Pacific with remote sensing products that are already globally available. This key result suggests that large-scale extrapolation of field data is feasible for reef health indicators to support assessment and management across entire seascapes.

All the models were similarly effective. Protected area coverage, market gravity, geomorphological classifications, and temperature were among the key drivers for all four ecosystem metrics, though the best combinations of drivers varied between each model. Most notably, there were very few drivers (2–3) with high variable importances (VIMPs) for the models of coral diversity and macroalgae, as compared to the other two models, which each had seven important drivers. Though this suggests that fewer remotely sensed variables are needed to model coral diversity and macroalgal cover, it also potentially reflects the fact that the variables that we included were mostly guided by studies for coral cover and fish biomass, since few examples exist for modelling coral diversity and even less so for macroalgae.

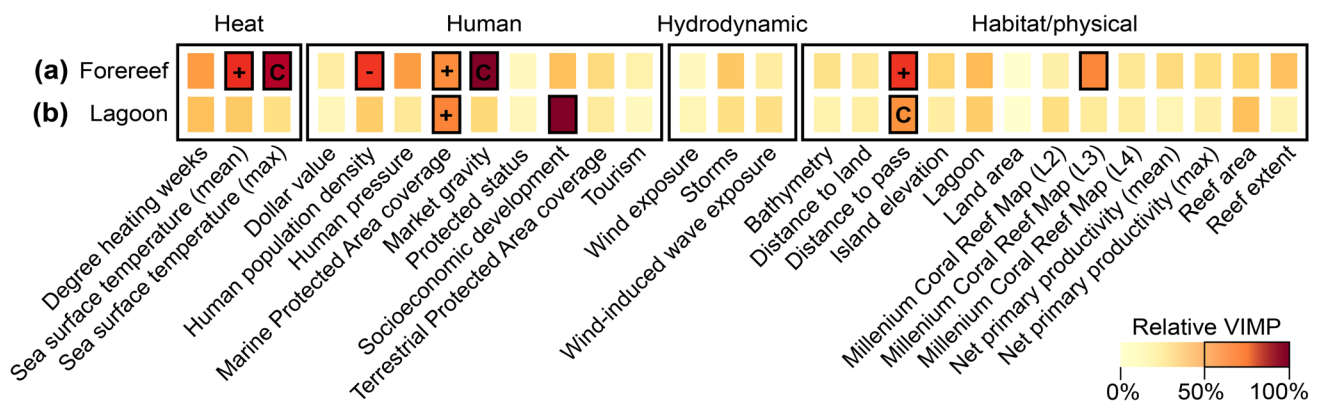


Fig. 9 Random forest models of live coral cover were deployed for stations **a** on the forereef (*n*=400) and **b** inside the lagoons (*n*=250). Drivers with > 50% VIMP denoted by black boxes, and the form of their predictive effect on coral cover were signified as positive ‘+,’

negative ‘-,’ and complex ‘C.’ The coral cover model for the forereef resulted in seven drivers with > 50% VIMP, whereas the lagoon model resulted in only three important drivers

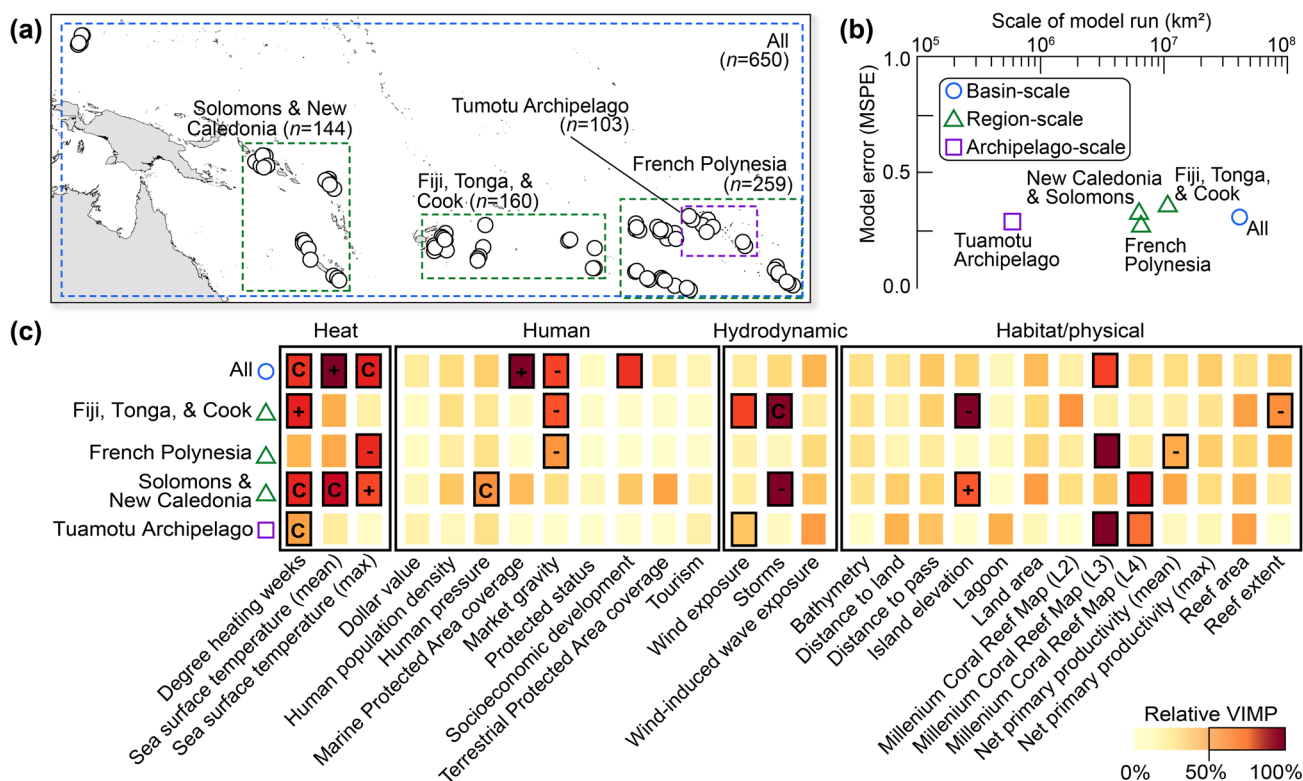


Fig. 10 Random forest models of live coral cover were deployed at three granularities **a**: basin scale (entirety of Pacific KSLOF-GRE stations), region scale (Solomon Islands and New Caledonia [$n=144$], Fiji, Tonga, and Cook Islands [$n=160$], and French Polynesia [$n=259$]), and archipelago scale (Tuamotu Archipelago [$n=103$]). The three granularities are coloured blue, green, and purple, respectively, from largest to smallest. Model performance across these three scales **b** was evaluated by mean-squared prediction error

(MSPE). Driver variable importance (VIMP) was organized on the **c** heatmap, where drivers with $>50\%$ VIMP were denoted via black boxes, and the form of their predictive effect on coral cover was signified as positive '+', negative '-', and complex 'C.' The predictive power of the random forests was virtually unchanged between model scales, while drivers that exceeded the VIMP threshold changed considerably

For instance, one of the few successful algal studies relied on sediment characteristics in the Baltic Sea (Kotta et al. 2013) and another study gathered detailed morphometric data (slope, rugosity, etc.) to model coral diversity in Puerto Rico (Pittman et al. 2009). Although those studies carry important lessons for our macroalgae and coral diversity models, these predictors do not exist for our study sites, nor would their use have been consistent with our aim to solely use open-source, globally available remote sensing data.

We acknowledge that our drivers are by no means an exhaustive list of all the important determinants of reef health. Nonetheless, we show that several drivers have predictive power over the considered ecosystem metrics. First, we inferred that establishing protected areas, regardless of size, conveyed a measurable positive effect on the ecosystem—coral cover and diversity was higher and macroalgal cover lower because of management goals, such as protecting grazing fish populations within MPAs (Mumby et al. 2007; Lester et al. 2009; McCook et al. 2010) and reducing land-based runoff from TPAs (Klein et al. 2012; Brown et al.

2017). Like Harborne et al. (2018), who considered fish, our models did not identify the simple presence/absence of protection at a station to be an important driver. Instead, we found per-country MPA and TPA cover to be relevant, suggesting that being positioned inside of a protected area is not as important as belonging to a country that prioritizes creating them, even if the protected areas are small. It is easier for local communities to enforce small MPAs, therefore increasing their success (Aswani and Hamilton 2004). Furthermore, well-managed MPAs are known for their 'spillover' effect, in which the benefits extend beyond the physical boundaries of the MPA (Di Lorenzo et al. 2020; Lenihan et al. 2021).

Other important drivers in our models were market gravity and human population density, which have been shown to proxy fishing pressure and other stressors (Stallings 2009; Brewer et al. 2012; Cinner et al. 2013, 2018; Williams et al. 2015b; Ford et al. 2020). In our dataset, coral cover and fish biomass exponentially declined with increasing market gravity and human density, supporting conventional wisdom that human pressures deteriorate reef condition from

activities ranging from fishing to coastal development. Human population density, rather than market gravity, was a better predictor of fish biomass in our models, contrary to the pattern Cinner et al. (2018) reported. Upon closer examination of the market gravity variable, this may be because gravity values in the Pacific do not have enough inter-station variability (they are typically low across the region) for our models to converge on any meaningful relationships. This highlights the idea that variables were not always excluded by the random forests because they were unimportant, but instead because of an incongruity between model scale or setting, and the range of values for that variable. It is also important to note the caveat that Heenan et al. (2016) highlighted for market gravity in the Pacific. The authors identified cases where market gravity did not describe fishing pressure because fish were being sold informally, and that some fisheries were dominated by shore-based rather than boat-based fishing.

We also note that the MCRMP classifications (Andréfouët et al. 2006) emerged as important drivers, implying that ecosystem metrics stratify by reef geomorphology locally, regionally, and across the Pacific. In particular, the finer-resolution geomorphological classification (MCRMP Level 4) was important in our smallest archipelago-scale coral model, where coral cover was lowest in MCRMP classes ‘atoll lagoon’ and ‘ocean exposed fringing,’ as also observed by Riegl et al. (2012). Meanwhile, the broadest MCRMP geomorphology classification (Level 2) indicated high importance for the basin-scale model of fish, where biomass was highest in atolls, possibly because this MCRMP class coincided with reefs farther away from human populations. The atolls considered by our study also tended to have low island elevations, which are shown to have high fish abundances, possibly due to the opportunity for a greater number of habitats to develop in the large lagoons that atolls without high islands yield (Heenan et al. 2016; Ford et al. 2020). Harborne et al. (2018) also found geomorphology to be among the top predictors of fish biomass in Micronesia. Recent reef ecosystem models have not considered fine-scale geomorphology and instead use broad map classes (Williams et al. 2015b; Cinner et al. 2018; Ford et al. 2020). Ours is one of the first studies to include detailed geomorphologic classes when predicting reef health, through multiple layers of MCRMP data, and highlights the benefit of including geomorphology when modelling ecosystem metrics.

Thousands of studies have documented that increasing temperature kills corals through bleaching, and indeed this underpins the global reef crisis (Veron et al. 2009b; Hughes et al. 2018a). In our dataset, the relationship between SST and coral cover did not initially appear to adhere to this pattern; coral cover declined with increasing temperature, as would be anticipated, until an average SST of 28 °C and maximum SST of 30 °C, at which point coral cover rapidly

increased with increasing temperature. Careful examination of these relationships reveals, however, that it was constructed from two clusters of data from two different temperature and biodiversity regimes. Palau and the Solomon Islands are both situated about 8° N and S from the equator, where they experience high SSTs (> 29 °C) and belong to the Coral Triangle, a biodiversity hotspot, harbouring higher coral cover relative to other regions (Veron et al. 2009a). Considering Palau and the Solomon Islands in isolation, both clusters of field stations displayed the anticipated relationship of decreasing coral cover with increasing temperature, and the overall relationship therefore is consistent with hotter temperatures leading to coral mortality. Work by Williams et al. (2015a) emphasizes that this relationship should not be assumed. Counterintuitively, for unpopulated islands in the Pacific, the authors found temperature and coral cover to be positively correlated, for instance. Populated islands, however, showed no significant relationship, consistent with the notion presented by Ford et al. (2020) that human impacts can disrupt well-established relationships between coral cover and the environment.

Similarly counterintuitive was the positive relationship in our dataset between coral cover and DHW—a measure of accumulated heat stress—until about 8 °C-weeks, when coral cover began to decline. Eakin et al. (2010) and Liu et al. (2014), who produced the DHW product, identified 8 °C-weeks to be the tipping point at which corals experience mass mortality, and our results support that designation. DHW also appeared as the top driver of fish biomass. Although a direct relationship between DHW and fish has not yet been described (but see Stuart-Smith et al. 2018), increasing DHW causes a decline in coral cover and, indirectly, a decline in fish biomass (Jones et al. 2004; Russ et al. 2021).

Predicting coral cover across geomorphological zones and spatial scales indicated that a variation in important drivers not only existed between metrics, but also between lagoonal reefs and forereefs, and over changing spatial scales. It might not have been expected that a one-size-fits-all model would exist for reef condition, given that reef assemblages along geomorphologic zones are generally distinct from one another (Williams et al. 2013; Edmunds and Leichter 2016; Adjeroud et al. 2019; Moustaka et al. 2019) and because large-scale gradients are expected to become less important in small-scale models (Brown et al. 2013). However, the extent of this difference has rarely been quantified and therefore clear guidance to conservation practitioners is lacking.

Coral cover on the forereef was influenced by a greater number of drivers (7) than cover in lagoons, which was only correlated with three drivers operating on local scales (the per-country socioeconomic development score and MPA coverage, and distance to the nearest reef pass). The physical restriction of atoll lagoons naturally predisposes them

to hotter, less oxygenated, and more acidic waters (McCabe et al. 2010; Camp et al. 2017), which have been shown to promote resilient reefs built by less diverse coral assemblages than those on forereefs (Adjeroud et al. 2000). Additionally, our distance to pass driver was designed to proxy the degree of connectivity between the open ocean and the lagoon. As such, it is not surprising that this driver is important in the prediction of coral diversity, since, when connectivity is high, nutrients from the lagoon can be distributed to the forereef, thereby promoting diversity (Williams et al. 2018). Our models reflect these characteristics. In the full model, inside versus outside the lagoon was a top driver of coral diversity, and neither of the important drivers for the model of lagoonal coral cover were related to anthropogenic or environmental stress. In fact, this was the sole coral cover model without a 'Heat' driver from our entire study, including the five models across spatial scales.

Though temperature was a key correlate in all our multiscale coral cover models, the remaining drivers varied in importance across all scales. Our region-scale model, for instance, which encompassed field observations from Fiji, Tonga, and the Cook Islands, was the only model lacking one of the MCRMP drivers. In this case, however, the random forest substituted MCRMP with the reef extent driver, which is an accepted proxy of geomorphology (Andréfouët et al. 2006; Li et al. 2020). The finest resolution MCRMP classification (Level 4) was important at the archipelago- and smaller region-scale model of the Solomon Islands and New Caledonia, while the intermediate MCRMP (Level 3) was important at all scales. MPA coverage and socioeconomic development were only important predictors of coral cover in our basin-scale model, likely explained by the fact that this pair of drivers is represented by a single value per country. Their lack of inter-country variation masks any locally driven relationships to coral cover. Also absent in our archipelago-scale model were any important drivers from the 'Human' category. Although human activity (e.g., coastal development, tourism, fishing) may not be affecting the Tuamotu Archipelago in the same way as it affects coral cover at region-to-basin scales, anthropogenic disturbance has subjected these atolls to drastic shoreline changes that disturb surrounding reefs (Duvat et al. 2017). Our results confirm that the random forests are responding to gradients of scale within the drivers. Hence, even when modelling a single ecosystem metric, the drivers in the random forest change depending on whether the model is run at local versus large scale.

The change in the form of our models across geomorphological zones and spatial scales implies that care must be taken when extrapolating field data to larger scales. In general, we show that such extrapolation is reasonable within a country and within reef zones, or across reef zones if field data are available for each and zone is included as a driver

(e.g. forereef and lagoonal reef). However, extrapolating between countries or regions without additional field data may be problematic and emphasizes the need to spatially stratify in situ surveys across the area of interest. Similarly, we cannot necessarily conclude that the models we built will translate to other locations, or across other socio-environmental gradients that we have not considered in this study, even if the reefs are relatively similar. This prediction could be tested, though, by using our models to extrapolate to new sites and comparing the prediction accuracy to real-world observations.

We consider our work to be prescient regarding the recent momentum behind the global-scale appraisal of reefs from satellite, such as the KSLOF-GRE (Purkis et al. 2019), the Allen Coral Atlas (Lyons et al. 2020; Roelfsema et al. 2020, 2021), as well as recent technological advances from NASA which apply fluid lensing to image reefs at millimetre resolution (Chirayath and Earle 2016; Chirayath and Instrella 2019; Chirayath and Li 2019). These new high-resolution maps will give us the opportunity to assemble drivers that had to be omitted from our models. One such example is rugosity, a known correlate of reef fish abundance and diversity (Purkis et al. 2008; Pittman and Brown 2011; Darling et al. 2017; Foo et al. 2021; Asner et al. 2021). These new mapping initiatives will provide rugosity, along with other drivers, and should therefore improve the prediction of reef fish and potentially other ecosystem metrics, too.

Our study is a prelude to producing global-scale maps of ecosystem metrics from remote sensing. Since the four metrics that we modelled are commonly used in the field to quantify reef health, they might be similarly combined in map form to build towards a global reef health product. Managers could use such a map to direct conservation interventions aimed at restoring coral cover and fish biomass (targeting areas with low cover and biomass), protecting areas with high coral cover and fish biomass, increasing the diversity of coral, and controlling macroalgal growth (addressing key influences such as low grazing fish biomass or improving water quality). A temporal sequence of such maps would also function as an important tool for long-term monitoring reef health and the efficacy of management interventions. We hope that our study will lead to these types of improved management outcomes and evidence-based marine spatial planning, including more effective multinational marine reserves.

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Declarations

Competing interests The authors declare no competing interests.

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