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Global analysis of reef ecosystem services reveals synergies, trade-offs and bundles

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ABSTRACT

Millions of people around the world depend on the ecosystem services produced by rocky and coral reef ecosystems, including nutrition, aesthetic value, and coastal protection. Rocky and coral reefs also contribute to critical global and regional processes through the cycling of nitrogen, phosphorus, and carbon. The increased stress experienced by reefs in the Anthropocene threatens their ability to provide vital ecosystem services. This study investigates bundles of ecosystem services, ecosystem services that occur together, to identify trade-offs and synergies among services produced by coral reefs. To do this, we bring together estimates of seven ecosystem services: productivity, nitrogen cycling, phosphorus cycling, inorganic carbon cycling, aesthetic value, nutritional value, and coastal protection. We use correlations analysis to understand trade-offs and synergies between these seven ecosystem services and cluster analysis to identify clusters of reefs with distinct suites of ecosystem services, or ecosystem service bundles. Our analysis reveals (1) synergies and trade-offs among the seven ecosystem services, and (2) three distinct clusters of reefs, which differ on the basis of their overall and relative delivery of ecosystem services. Differences in service production among the clusters appear to be linked to differences in key ecological traits, including total reef fish biomass and species richness. Similar applications of ecosystem service bundles analysis in other marine and coastal systems could result in improved understanding of the spatial distributions and relationships between marine ecosystem services, which is a key input to marine policy.

1. Introduction

Rocky and coral reefs provide ecosystem services to millions of people around the world, including the provision of food from fishing and harvesting, protection from storms, and critical habitat for fish and other marine species that cycle nutrients and carbon (Burke and Spalding, 2022; Cinner et al., 2009; Moberg and Folke, 1999; Woodhead et al., 2019). Reef fish provide a vital source of nutrients and play a key role in overcoming malnutrition and food insecurity (Hicks et al., 2021, 2019). Due to numerous pressures, including increasing ocean temperature (Hughes et al., 2017), changing pH (Hughes et al., 2017), input of nutrients and pollutants into marine environments (D'Angelo and Wiedenmann, 2014), and fishing pressure (Eddy et al., 2021), rocky and coral reef ecosystems and the services they provide to coastal communities are under threat (Eddy et al., 2021). Ecosystem services generated by reefs are shaped by interactions between social and ecological systems (Woodhead et al., 2019). The increasing effects of globalization and climate change in the Anthropocene are accelerating bleaching (Hughes et al., 2018), loss of biodiversity and biomass (Hughes et al., 2017), and shifting ecological states (Eddy et al., 2021). Such changes, which contribute to degraded, low biomass, and low biodiverse reefs, affect the ability of reefs to continue providing vital ecosystem services (Aswani et al., 2018; Cinner et al., 2013, 2012). Urgent action is needed to address the pressures faced by reefs and protect the ecological functions that underpin ecosystem service provision (Darling et al., 2019; Woodhead et al., 2019). In this study, we investigate trade-offs and synergies among multiple ecosystem services produced by rocky and coral reefs, and explore the social-ecological conditions under which distinct bundles of services occur.

Ensuring the delivery of multiple services simultaneously is a key objective of ecosystem management (IPBES, 2019). Actions to increase the delivery of one service can lead to increases in other services (synergies) or declines (trade-offs). While the delivery of multiple ecosystem services at the same time and place is often desirable, not all ecosystem

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services increase in tandem with one another. Assessing the delivery of multiple ecosystem services across space can help to reveal which trade-offs occur and where (Raudsepp-Hearne et al., 2010; Rodríguez et al., 2006).

Quantification and mapping of ecosystem services is key to the utility and translation of the ecosystem services concept for environmental policy and decision-making (Daily and Matson, 2008; Rodríguez et al., 2006). Ecosystem service bundles analysis is one approach to quantify and map ecosystem services to understand their spatial distributions, what types of services tend to co-occur, and to identify synergies and trade-offs among services (Meacham et al., 2022; Raudsepp-Hearne et al., 2010; Spake et al., 2017). Synergies refer to services that are delivered simultaneously, while trade-offs may occur among services that typically do not co-occur in time and space, such as in cases where high delivery of one service coincides with low delivery of another (Raudsepp-Hearne et al., 2010). For example, in reefs, an increase in aesthetic value via the protection of visually-appealing reef fish may result in a decrease in nutritional value if the action causes a shift in reef fish population structure towards less nutrient-dense fish species. Such information may be useful in the design of management to optimize production of desired services. Additionally, an ecosystem service bundles approach can be used to understand clusters of sites with similar suites of ecosystem services and can help to identify priority sites for management. Despite the utility of ecosystem service bundles analysis for simplifying analysis and management of ecosystem services (Meacham et al., 2022), it has been predominantly used in terrestrial systems (e.g., Queiroz et al., 2015; Raudsepp-Hearne et al., 2010), with few examples of its use in marine and coastal systems (e.g., Lapointe et al., 2021; Rullens et al., 2019). Additional applications of ecosystem service bundles analysis in marine systems would respond to the documented need for spatially-explicit information on marine ecosystem services in order to support policy and decision-making for marine environments (Maes et al., 2012).

The ecosystem services concept is used to articulate how specific ecological functions and characteristics translate into the direct and indirect benefits people receive from nature, and as such, ecosystem services can be used to understand how differences in ecological function across space impact human wellbeing (Bennett et al., 2009). Understanding what proportion of the potential supply of an ecosystem service, or bundles of services, is actually used or realized, is also important (Burkhard et al., 2012; Goldenberg et al., 2017), since information on the supply and use of ecosystem services can guide management planning (Aziz and Van Cappellen, 2019). Burkhard et al. (2012) define the supply of an ecosystem service, or bundle of services, over a given time period as: "the capacity of a particular area to provide a specific bundle of ecosystem goods and services" and the use as "the sum of all ecosystem goods and services currently consumed or used in a particular area". The supply of an ecosystem service can also be thought of as a potential service, whereas the use represents the realized service. Previous ecosystem service bundles analyses have at times used indicators that correspond to a mix of potential and realized services (Meacham et al., 2022; Queiroz et al., 2015). Combining indicators for potential and realized services is sometimes necessary under conditions of limited data.

Many marine and coastal ecosystem services do not fit neatly within the existing ecosystem service classification systems, for example, The Millennium Ecosystem Assessment (Millennium Ecosystem Assessment, 2005), The Economics of Ecosystems and Biodiversity (TEEB, 2010), and the Common International Classification of Ecosystem Services (CICES) (Haines-Young and Potschin, 2017), which were largely developed to capture benefits arising from terrestrial systems (Hicks, 2011; Liquete et al., 2013). In response to this, Liquete and colleagues (2013) proposed an integrated classification of marine and coastal ecosystem services, which unites the most widely-used ecosystem service classification systems: MEA, Beaumont, TEEB, and CICES. In this study, we include seven ecosystem services derived from reefs which fall into the three main categories of marine and coastal ecosystem services proposed by Liquete and colleagues (2013): provisioning (productivity and nutritional value which fall under food provision); regulating and maintenance (nitrogen cycling and phosphorus cycling which fall under ocean nourishment, carbon cycling which falls under climate regulation, and coastal protection); and cultural services (aesthetic value).

Table 1
List of ecosystem services assessed in this study, indicators, units, and data sources.

Ecosystem service	Indicator	Units	Data source
Productivity	Rate of reef fish biomass production per day, weighted by the total biomass	kg/day/total kg	Schiettekatte et al., 2022
Nitrogen cycling	Millimoles of nitrogen cycled per day by all reef fish	millimoles/day	Schiettekatte et al., 2022
Phosphorus cycling	Millimoles of phosphorus cycled per day by all reef fish	millimoles/day	Schiettekatte et al., 2022
Inorganic carbon cycling	Millimoles of inorganic carbon cycled per day by all reef fish	millimoles/day	Ghilardi et al., 2023
Aesthetic value	Model output of aesthetic value index	unitless index	Langlois et al., 2021
Nutritional value	Mean sum of percentage dietary references for six key micronutrients (calcium, iron, selenium, zinc, vitamin A, omega-3) per 100 g of fish wet weight	% daily value/100 g wet weight	Hicks et al., 2019
Coastal protection	Annual expected benefit from reefs for flood protection	$US millions	Mapping Ocean Wealth

In this paper, we combine estimates of six potential ecosystem services derived from rocky and coral reef fish surveys (productivity, nitrogen cycling, phosphorus cycling, carbon cycling, aesthetic value, and nutritional value), together with estimates for one realized ecosystem service derived from global models (coastal protection from storms), and apply a bundles analysis approach to these seven ecosystem services to understand: 1) what are the trade-offs and synergies among the ecosystem services generated by coral reefs; and 2) what are the social-ecological conditions under which distinct bundles of services occur? By taking an ecosystem service bundles approach, we analyze trade-offs, synergies and spatial distributions of services in rocky and coral reefs around the world. Our selection of these seven services allows us to investigate relationships among ecosystem services estimated through multiple methods, based on both ecological and socio-economic characteristics of rocky and coral reefs. By comparing ecosystem service bundles across a range of social-ecological co-variables, we identify possible drivers of bundles which may contribute to the production of certain suites of services in the world's temperate and tropical rocky and coral reefs. We also describe several possible implications of this work for future research and for spatially-explicit marine policy and management. Such information may serve as a foundation for future work that seeks to optimize the ecosystem services produced by reefs while meeting local and regional priorities.

2. Methods

2.1. Data and data preparation

We assessed seven ecosystem services in 224 reef sites located in 23 territories and 18 countries around the world (Table 1). The ecosystem services were selected based on the following criteria: 1) the services must have been identified in previous studies and/or by the REEF-FUTURES Consortium as important services provided by reefs, and 2)

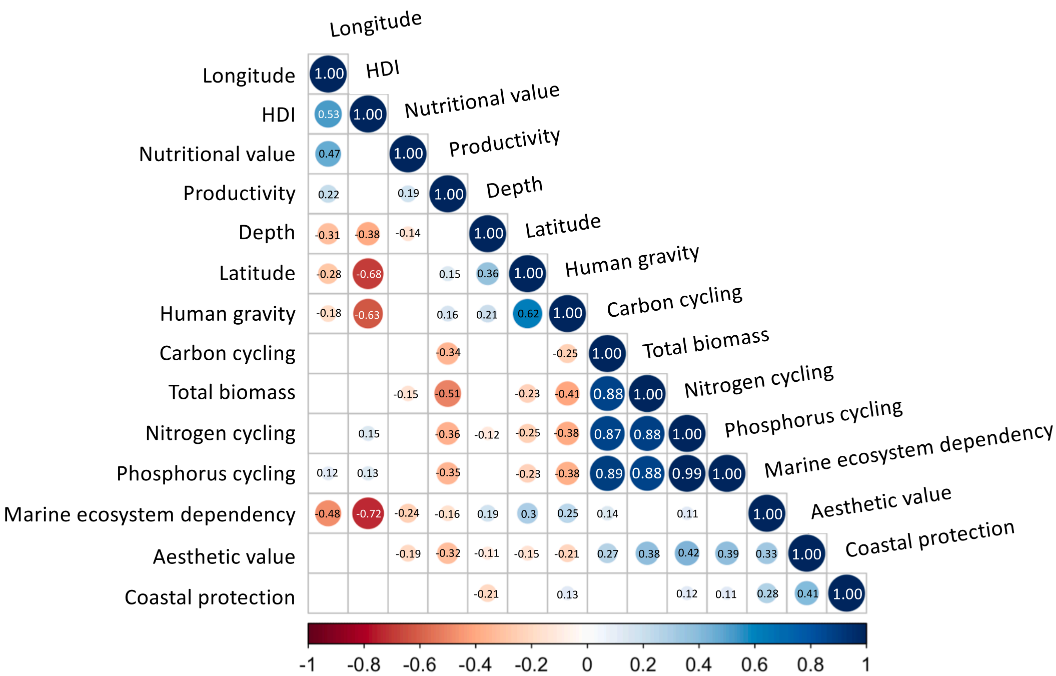

Fig. 1. Correlation matrix for pairs of ecosystem services and social-ecological co-variables. Positive correlations (synergies) are displayed in blue and negative correlations (trade-offs) are shown in red; the size and shade of the circle corresponds to the strength of the correlation. Non-significant correlations (p greater than 0.05) are left blank.

data on potential indicators for the service had to be available for reef sites or close to the reef sites in the Reef Life Survey database (https://reeflifesurvey.com/). The ecosystem services for which indicator data were sourced from members of the REEF-FUTURES Consortium included the following: productivity (Schiettekatte et al., 2022); nitrogen cycling (Schiettekatte et al., 2022); phosphorus cycling (Schiettekatte et al., 2022); inorganic carbon cycling (Ghilardi et al., 2023); aesthetic value (Langlois et al., 2022, 2021); and nutritional value (Hicks et al., 2019). Indicators for these six services were estimated based on reef fish community composition at Reef Life Survey transect sites and a database of 2 836 reef fish species (a list of species can be found in Appendix 1). Global reef fish survey data from the Reef Life Survey database represent a rich and spatially-explicit data source to estimate the supply of ecosystem services produced by rocky and coral reef fishes. Indicator data for the ecosystem service of coastal protection were sourced from Mapping Ocean Wealth (https://oceanwealth.org/). One indicator for each ecosystem service was selected (Table 1). Detailed methods for data collection of ecosystem service and co-variable indicators are provided in Appendix 2.

The selected ecosystem service indicators were screened prior to analysis to ensure that all variables were normally distributed. The nitrogen cycling, phosphorus cycling, inorganic carbon cycling, and coastal protection indicators were log10 transformed to achieve a normal distribution. Normalizing the indicator data prior to cluster analysis ensures that the distance measure accords equal weight to each variable within the clustering.

As a first step in data preparation, data on the six ecosystem services sourced from the REEF-FUTURES Consortium (productivity, nitrogen cycling, phosphorus cycling, inorganic carbon cycling, aesthetic value, and nutritional value) were merged based on reef site ID. From 7 000 + reef sites within the Reef Life Survey database for which the REEF-FUTURES Consortium estimated ecosystem services, only reef survey sites which had estimates for all six ecosystem services within the REEF-FUTURES database were used, totalling 1 827 reef sites. Reef sites represent locations of Reef Life Survey subtidal transect surveys. Then, these data were imported into QGIS as point vector data based on geographic coordinates associated with each reef site (QGIS.org, 2022). The coastal protection dataset from Mapping Ocean Wealth was also imported as point vector data based on geographic coordinates associated with each reef site within the corresponding dataset. This dataset has 2 529 points representing reef sites around the world. Since the Mapping Ocean Wealth and REEF-FUTURES datasets are two spatially-distinct point shapefiles, the two datasets were then combined via spatial join using the "Join attributes by nearest" tool from the QGIS Processing Toolbox. The resulting vector point shapefile contained 1 827 rows, one for each of the REEF-FUTURES sites, with an additional column added for coastal protection. Next, to filter the dataset to include only those reef sites within 50 km of the coastal protection data points, we used the "Distance to the nearest hub (points)" tool from the QGIS Processing Toolbox. The resulting distance measurements were used to filter out those coastal protection sites more than 50 km away from the reef site. The total number of reef sites used in our analyses included only those reef sites within 50 km of a site with data on annual expected benefit from reefs for flood protection. The 50 km cutoff was chosen as a compromise between a reasonable distance over which a reef may provide wave attenuation (thus, coastal protection from the worst effects of storms) and a distance that would still include as many reef sites as possible. After filtering and removing sites with null values for any of the ecosystem service estimates, there were a total of 224 reef sites on which we performed ecosystem service bundles analysis.

In addition, the variables latitude, longitude, depth, species richness, total biomass of reef fish, marine ecosystem dependency, Human Development Index (HDI), and human gravity associated with each reef site were also investigated as social-ecological co-variables, which may be relevant for understanding differences in ecosystem service values among reefs. A full description of these variables and data collection of the indicators is provided in Appendix 2.

2.2. *Analyses: Trade-offs and synergies*

Correlation analysis was performed on each pair of variables to determine synergies and trade-offs among ecosystem services. Since our

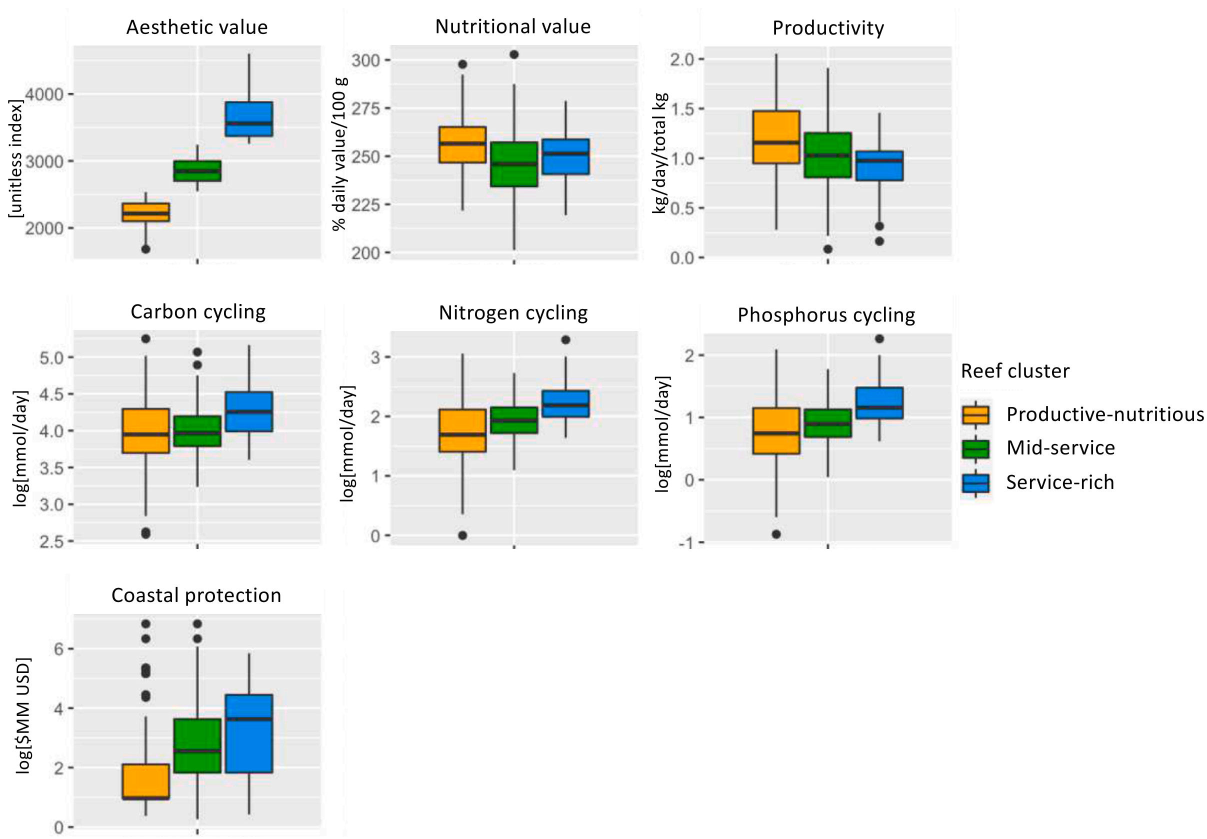

Fig. 2. Box and whisker plots showing values of seven ecosystem services across the three clusters. Colors correspond to clusters; Productive-nutritious reefs are shown in gold, Mid-service reefs in green, and Service-rich reefs in blue. The upper limit of each box represents the upper quartile (75th percentile) and the lower limit presents the lower quartile (25th percentile), with the horizontal line through the middle of each box showing the median. The vertical lines above and below each box represent the minimum and maximum values and black dots represent potential outliers in the data (i.e., values lower than Q1 − 1.5 × (Q3 - Q1) or higher than Q3 + 1.5 × (Q3 - Q1)).

analysis included several log-transformed variables, correlations were analyzed using the Spearman non-parametric correlation test with the corrplot package in R (Wei and Simko, 2021). Spearman rank correlation enables the estimation of association between both transformed and non-transformed variables because the variables' ranks do not change with log transformation (Crawford, 2006).

2.3. Analyses: Bundles

Cluster analysis was used to identify groups of reefs with similar sets of ecosystem services, or ecosystem service bundle types, where trade-offs and synergies between ecosystem services were consistent. Clusters in the ecosystem service data were identified and analyzed using cluster analysis by K-means with the R package Cluster (Maechler et al., 2021). The optimum number of clusters was estimated based on a statistical test of fit for different levels of clustering using the function NbClust() from the R package NbClust (Charrad et al., 2014). The method selected was k-means with Euclidean distance. Results were visualized using the function fviz_nbclust() from the R package factoextra (Kassambara and Mundt, 2020). The final number of clusters was selected based on a combination of the results of cluster analysis and practical considerations to ensure the utility of the bundles analysis results. Practical considerations included the significance of differences in ecosystem services among clusters and the relative numbers of reef sites assigned to each cluster, or bundle. Reef clusters were mapped in QGIS to visualize spatial distributions of reef sites across the clusters. Tukey multiple pairwise comparisons were performed for each ecosystem service indicator to quantify differences between and among clusters. Summary statistics for each cluster were compiled using the R package dplyr (Wickham et al., 2021). Figures were created using the R package ggplot2 (Wickham, 2016).

2.4. Differences among reef clusters

To analyze quantitative differences among clusters in the co-variables latitude, longitude, depth, species richness, total biomass, Marine Ecosystem Dependency, Human Development Index, and human gravity, Tukey multiple pairwise comparisons were performed.

3. Results

3.1. Analyses: Trade-offs and synergies

We found strong positive pairwise correlations (or synergies) between nitrogen cycling, phosphorus cycling, and total inorganic carbon cycling (Fig. 1). We also found positive pairwise correlations between aesthetic value and each of the three cycling services: nitrogen cycling, phosphorus cycling, and inorganic carbon cycling. We also found positive correlations between coastal protection and aesthetic value; and weak positive correlation between coastal protection and each of nitrogen and phosphorus cycling. Additionally, we found a weak but significant correlation between nutritional value and productivity. We

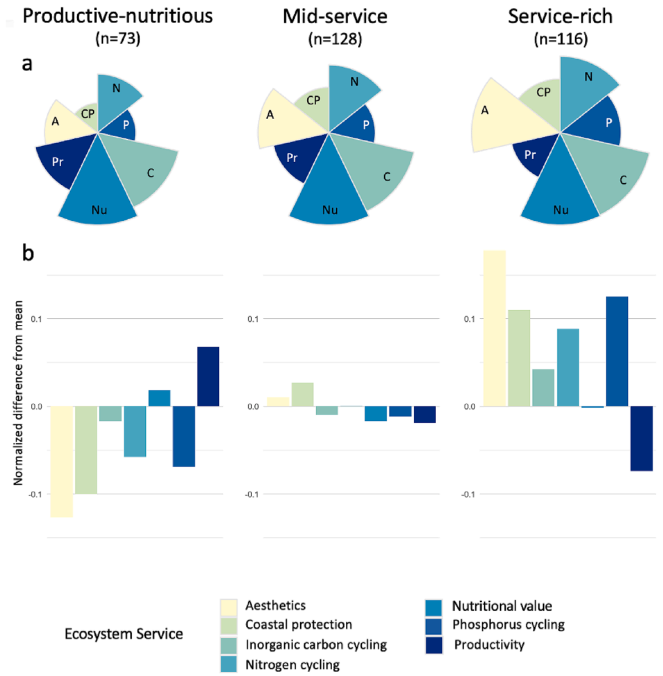

Fig. 3. Ecosystem services by reef cluster. (a) Petal diagrams for each reef show the relative values of ecosystem services in the three clusters where the petal length represents the value of each service relative to the maximum value for that service across all reef sites. Symbols in the petals correspond to each of the following: aesthetics (A); coastal protection (CP); Inorganic carbon cycling (C); Nitrogen cycling (N); Nutritional value (Nu); Phosphorus cycling (P); Productivity (Pr). (b) For each cluster, the normalized difference from the mean of ecosystem service values for all reefs are shown.

found negative correlations (or tradeoffs) between productivity and each of the following: aesthetic value, nitrogen cycling, phosphorus cycling, and inorganic carbon cycling.

3.2. Analysis: Bundles

Cluster analysis identified either two or three as the optimum number of clusters for our data. Based on these results, together with practical considerations, we decided to study the results when our dataset is partitioned into three clusters of reef ecosystem service bundles.

Selecting three clusters generated distinct suites of ecosystem services (Fig. 2; Fig. 3). Values for individual ecosystem services differed among the clusters, with aesthetic value being the ecosystem service that differed most among the three clusters (Fig. 2). Each clusters' ecosystem service bundles profile differed from that of the other two clusters (Fig. 3). Based on their ecosystem service bundles profiles, we assigned descriptive names to each cluster; we refer to cluster 1 reefs as Productive-nutritious reefs, cluster 2 as Mid-service reefs, and cluster 3 as Service-rich reefs. Service-rich reefs dominated in Aceh, Indonesia and in the Red Sea; Mid-service reefs dominate off the coast of Tanzania, the Hawaiian Islands, and in the Ningaloo Reef in northwestern Australia; a mix of Productive-nutritious and Mid-service reefs were found in the Caribbean Sea and on both coasts of Central America; a mix of Service-rich and Mid-service reefs were found in the South Pacific Ocean; and a mix of all three types are found in Maluku, Indonesia and the Great Barrier Reef in eastern Australia (Fig. 4).

The results of Tukey multiple pairwise comparisons revealed that there were significant differences across all three clusters for three of the seven ecosystem services: nitrogen cycling; aesthetic value; and coastal protection (Fig. 5). Values for phosphorus cycling and inorganic carbon cycling differed significantly between Productive-nutritious and Service-rich reefs and between Mid-service and Service-rich reefs, but did not differ significantly between Productive-nutritious and Mid-service reefs. On the other hand, values for nutritional value and productivity differed significantly between Productive-nutritious and Mid-service reefs and between Productive-nutritious and Service-rich reefs, but did not differ significantly between Mid-service and Service-rich reefs. Performing the analyses on two clusters, rather than three, produced similar results (Figure S1-S3; Table S1).

Of the three clusters, Productive-nutritious reefs had the lowest mean values for nitrogen cycling, aesthetic value, and coastal protection, and the highest mean productivity and nutritional value (Table 2). On average, Productive-nutritious reefs' nutritional value was 4.5% higher than that of Mid-service reefs and 2.4% higher than that of Service-rich reefs. Productive-nutritious reefs also had the lowest mean value for phosphorus cycling and inorganic carbon cycling among the three clusters, although these were not significantly different from Mid-service reefs. Service-rich reefs had the highest mean values for nitrogen cycling, phosphorus cycling, inorganic carbon cycling, aesthetic value, and coastal protection among the three clusters. Mid-service reefs had mean values for all services that were between those of Productive-nutritious reefs and Service-rich reefs, except for nutritional value, which was the lowest for Mid-service reefs, although this did not differ significantly from the mean nutritional value of Service-rich reefs.

3.3. Differences among reef clusters

The three clusters varied significantly in their total biomass and species richness, but not in depth (Fig. 6). Latitude differed between Productive-nutritious reefs (more northerly) and Mid-service reefs (more southerly) but not between the other cluster combinations. Longitude differed between Productive-nutritious and Mid-service reefs and Mid-service and Service-rich reefs, but not between Productive-nutritious reefs and Service-rich reefs. There were significant differences in Marine Ecosystem Dependency across all three clusters with Service-rich reefs having the highest Marine Ecosystem Dependency, followed by Productive-nutritious and intermediate reefs. Human Development Index differed between Productive-nutritious (higher index) and Service-rich reefs (lower index) but not between the other cluster pairs. There was no significant difference in human gravity between any of the cluster pairs. We found a negative correlation between productivity, which is weighted by biomass, and total biomass (Fig. 1). This means that high biomass sites in fact had low productivity, or rate of new growth of biomass compared to total biomass.

4. Discussion

Our analysis of a global set of rocky and coral reef ecosystem service bundles revealed three clusters of reefs: Productive-nutritious reefs; Mid-service reefs; and Service-rich reefs. Many of the differences in these reefs' ecosystem service profiles appear to be linked to distinct ecological characteristics among the clusters, especially reef fish biomass and species richness. Productive-nutritious reefs had low biomass and species richness, but high levels of productivity and low levels of most other ecosystem services, which is consistent with degraded or overfished reef systems (McClanahan, 2022). Such reefs also had higher nutritional value per 100 g of fish, indicating that in such reefs, the reef fish are more nutritionally-dense, although overall reef fish biomass is lower. Temperate fish species have lower micronutrient concentrations than tropical fish species (Maire et al., 2021), and Productive-nutritious reefs tended to be more northerly than Mid-service reefs. However, there was no significant difference in latitude between Productive-nutritious reefs and Service-rich reefs, so the latitude of the reef clusters does not clearly explain observed differences in nutritional value. Since micronutrient density differs among reef fish species (Hicks et al., 2021; Maire et al., 2021), it is likely that differences in nutritional value among the clusters are linked to distinct compositions of reef fish communities.

Mid-service reefs offered potential ecosystem service values that

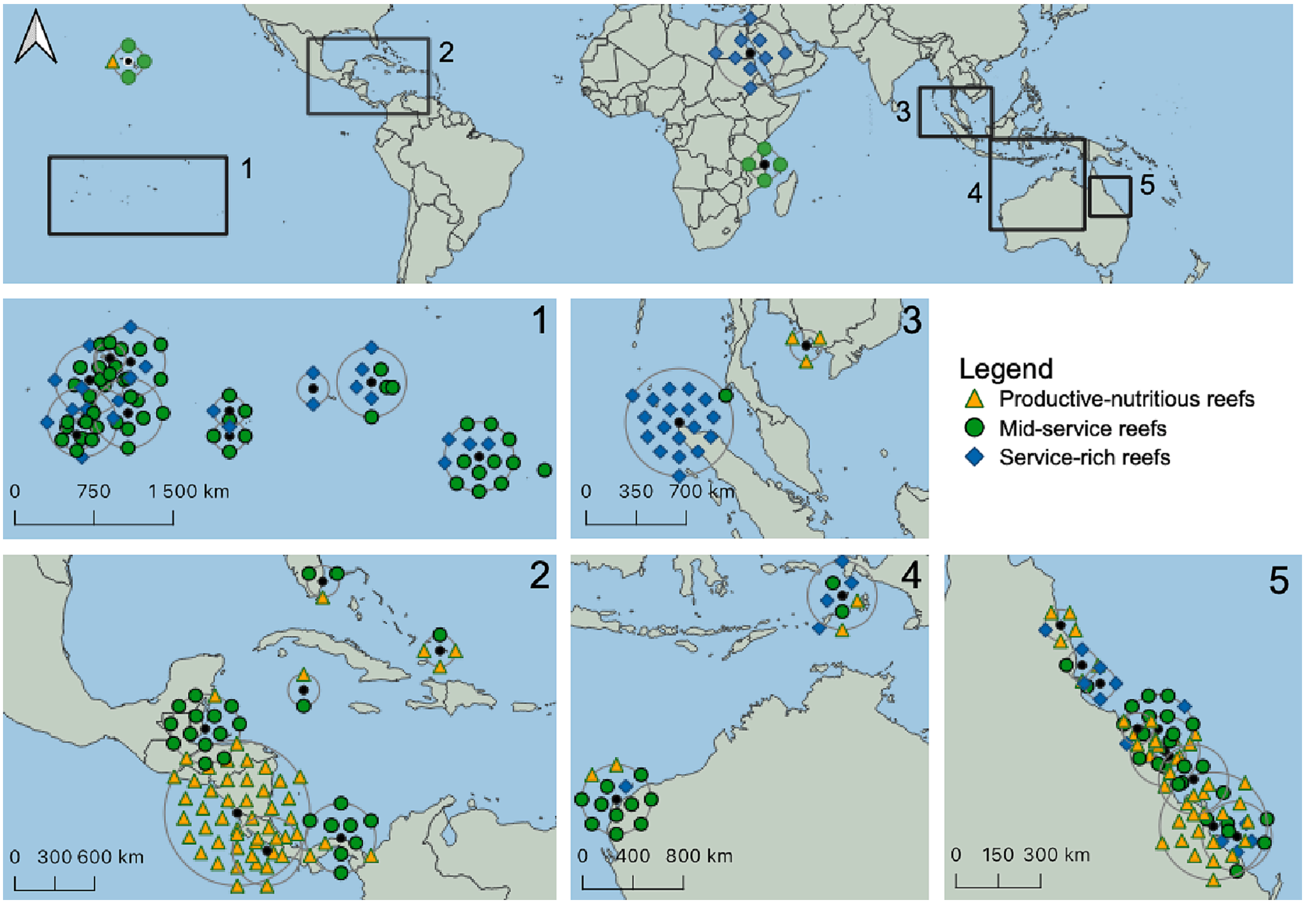

Fig. 4. Map of reef sites by cluster with five reef regions in focus. Shapes and colors correspond to each of the three reef clusters; Productive-nutritious reefs (n = 73) are shown with gold triangles, Mid-service reefs (n = 128) with green circles, and Service-rich reefs (n = 116) with blue diamonds. Where multiple reef sites overlap in this map view, they are shown in concentric circles around a central point (small black circle), indicating the actual location of the reef sites.

were between those of Service-rich and Productive-nutritious reefs. Service-rich reefs had high biomass and species richness and delivered high levels of most services. Differences among clusters may be related to total biomass and species richness and composition of reef fish communities across sites, since nitrogen cycling, phosphorus cycling, inorganic carbon cycling, aesthetic value, and nutritional values differ among reef fish species (Ghilardi et al., 2023; Hicks et al., 2019; Langlois et al., 2022, 2021; Schiettekatte et al., 2022; Tribot et al., 2019). Lower overall reef fish biomass at Productive-nutritious reefs and Mid-service reefs, relative to Service-rich reefs, explains their lower levels of nitrogen, phosphorus, and inorganic carbon cycling. The indicators for these three services were calculated as the sum daily nitrogen, phosphorus, and inorganic carbon, respectively, excreted by all reef fish observed at each reef site, thus it is unsurprising that clusters with lower total biomass would have lower values of cycling services, compared to clusters with higher total biomass. Aesthetic value, the ecosystem service that differed most among reef clusters, is linked to the species richness and composition of the reef fish community at each site. The model that generated the aesthetic value estimations used in our analyses is based on previous studies which used human image evaluation and deep learning algorithms to study the aesthetics of reefs (Langlois et al., 2021). The studies found, and the model reflects, that the perceived aesthetic value of reefs is driven by the species diversity and composition of reef fish assemblages (Langlois et al., 2021; Tribot et al., 2019). Since our study uses aesthetic value from this model, and based on our finding that aesthetic value differs significantly among the three clusters, we conclude that ecological characteristics are likely key drivers of the bundles.

To be effective, reef management must be context specific. The reef clusters we present provide a starting point for identifying which interventions will be most appropriate for a given reef context. Productive-nutritious reefs, with lower coastal protection than the other reef clusters, may require interventions that limit the physical degradation of reefs. Even small declines in the height of reefs would allow higher waves to reach the shore, resulting in less coastal protection (Spalding et al., 2016). The preservation of coral structure may help to maintain or increase coastal protection at Productive-nutritious reef sites. Although the two other clusters have relatively higher coastal protection, such interventions would likely benefit them as well. Mid-service reefs may require interventions to ensure a diverse food system, since nutritional value was lowest in these reefs. Additionally, since human gravity was high at these sites, measures to reduce anthropogenic pressures on the reefs may help to maintain service production in the future. Service-rich reefs were high biomass and high biodiversity sites located in areas with high Marine Ecosystem Dependency, but they offered a lower density of potential nutritional value. The negative correlation we found between Marine Ecosystem Dependency and nutritional value suggests that, in places with higher Marine Ecosystem Dependency, reef fish contain a lower density of vital micronutrients. Given the role of reef fish as a key source of nutrition in many coastal communities (Hicks et al., 2019), it will be important to protect marine biodiversity, which underpins the ecological functions responsible for the provision of nutritional value, in the regions around these reefs (Mace et al., 2012). Importantly, this study includes the total biomass of reef fish and does not consider how much of that biomass is targeted by fisheries. Expanding analyses to account for how much of the total reef fish biomass is available to and accessed by people for food will be key to an improved understanding of the nutritional contribution of the reef clusters to coastal communities.

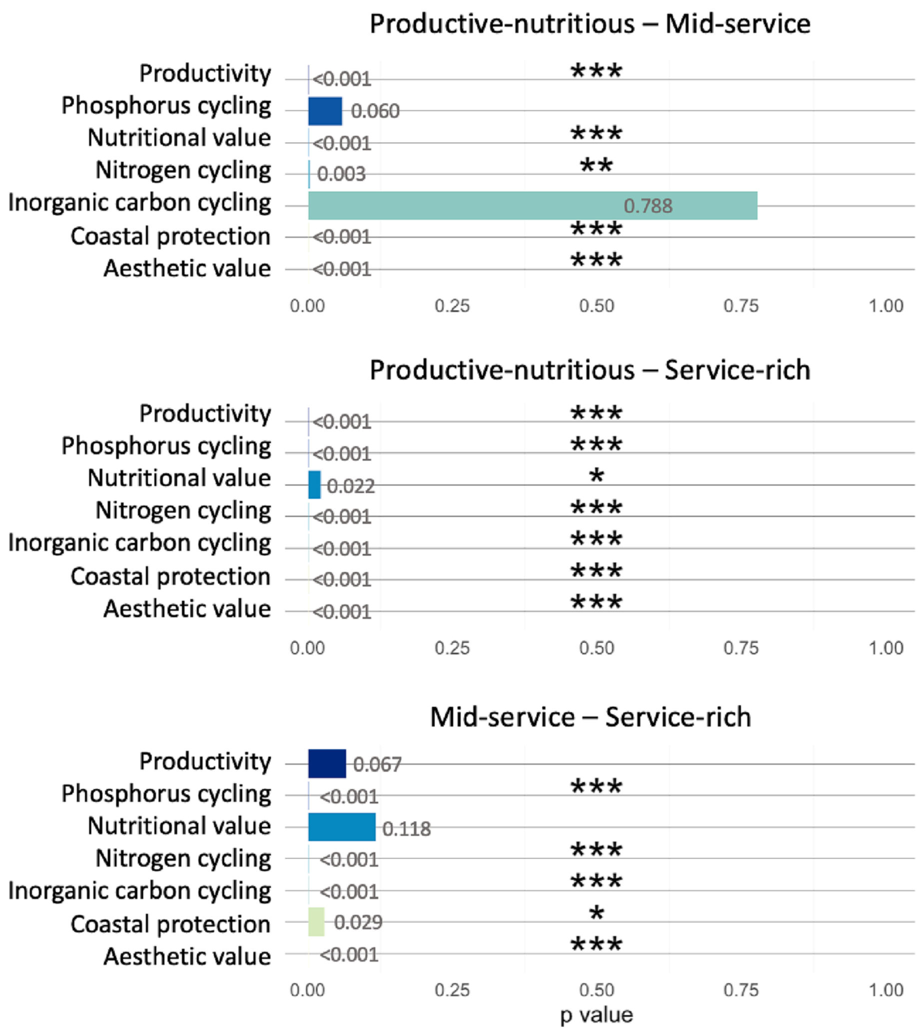

Fig. 5. Results of Tukey multiple pairwise comparisons showing p-values and significance of differences in ecosystem service values across each pair of clusters. Asterisks denote statistically significant differences in ecosystem service values for the cluster pair (* for p values < 0.5, ** for p values < 0.01, *** for p values < 0.001).

A diverse food system in these areas will also help ensure that those with the highest dependence on seafood have access to alternate sources of nutrition (Hicks et al., 2021). Regardless of the reef cluster, interventions which focus on managing social-ecological relationships are likely to be ineffective if climate change is not first addressed, since achieving emissions reductions targets is key to sustaining the ecosystem services produced by reefs (Eddy et al., 2021).

Assessing mismatches between supply and use of ecosystem services may be used by reef management to increase benefits by highlighting areas to improve access and ecosystem use efficiency. Mapping global proxies of potential ecosystem services, as we have done here, provides a useful starting point to highlight regions of biological and social importance which could benefit from further investigation (Naidoo et al., 2008), even when service use is not quantified or known. Spatial mismatches between supply and use of ecosystem services may create governance challenges, as service-providing areas – areas where services are produced – may be distanced from service-benefiting areas – areas where services are used or consumed (Syrbe and Grunewald, 2017). Such challenges are heightened when the scale of management does not match the scale at which ecosystems are produced, or when there exist trade-offs between services that are managed at different scales (Raudsepp-Hearne and Peterson, 2016). Spatial distributions of potential and realized ecosystem services can help to inform policy making around natural resource governance (Aziz and Van Cappellen, 2019), particularly when the scale(s) at which services are managed are known and considered (Raudsepp-Hearne and Peterson, 2016). However, data at comparable scales and resolutions for realized and potential ecosystem services are often lacking (Elmhagen et al., 2015), and such lack of consistency in data availability represents a key gap that must be addressed for future work to provide meaningful ecosystem service assessment (de Groot et al., 2010; Goldenberg et al., 2017).

This analysis includes six potential (or supply-side) services and one realized (or use-side) service. Potential services represent the total supply of ecosystem services from ecological functions, which may or may not translate into benefit to humans based on factors such as use and access (Turner et al., 2013). Realized ecosystem services, on the other hand, represent direct benefits to people (Goldenberg et al., 2017). The mix of potential and realized services included in our study means that interpreting our results requires a consideration of how social-ecological interactions shape the production of coral reef ecosystem services (Meacham et al., 2022), as assessments of potential and realized services do not consider how people's demand, access, and interventions can alter the use of ecosystem services by multiple beneficiaries. This work provides a starting point for further work to inform reef management at a global scale, however, more information will be needed to make specific recommendations that will be appropriate across the broad and varied context of the world's reefs. Expanding upon this work to include additional ecosystem services, particularly cultural services,

Table 2
Mean and standard deviation in ecosystem service values for each of three clusters.

Ecosystem service	Productive-nutritious (n = 73)	Mid-service (n = 128)	Service-rich (n = 116)
Nitrogen cycling (log10 millimoles/day)	Mean = 1.76 SD = 0.564	Mean = 1.95 SD = 0.343	Mean = 2.24 SD = 0.360
Phosphorus cycling (log10 millimoles/day)	Mean = 0.792 SD = 0.548	Mean = 0.921 SD = 0.357	Mean = 1.23 SD = 0.364
Inorganic carbon cycling (log10 millimoles/day)	Mean = 3.97 SD = 0.503	Mean = 4.00 SD = 0.337	Mean = 4.28 SD = 0.365
Nutritional value (% daily value/100 g fish wet weight)	Mean = 256 SD = 13.5	Mean = 245 SD = 17.4	Mean = 250 SD = 14.7
Productivity (kg/day/total kg)	Mean = 1.20 SD = 0.367	Mean = 1.02 SD = 0.367	Mean = 0.91 SD = 0.259
Aesthetic value (unitless index)	Mean = 2224 SD = 188	Mean = 2854 SD = 189	Mean = 3627 SD = 316
Coastal protection (log10 $US millions)	Mean = 1.85 SD = 1.50	Mean = 2.71 SD = 1.32	Mean = 3.28 SD = 1.82

as well as social, economic, and political information about reef sites will enable the development of policy recommendations that are more appropriate to the specific contexts of reefs, the ecosystem services the produce, and the beneficiaries who rely on them. Future work may also opt to include multiple types of marine habitats, since reefs often exist alongside other habitats, including mangroves and sandy seafloors, which also contribute valuable benefits. Including a range of habitat types would generate better understanding of how ecosystem service production and the relationships among services vary across multiple types of marine ecosystems.

In analyses or assessments of ecosystem services, indicators or proxies are often used to provide quantitative measures of ecosystem services when the service itself cannot be directly measured (Meacham et al., 2022). In some cases, there are multiple possible indicators for an ecosystem service, and the selection of indicators has consequences for how the results may be interpreted (Meacham et al., 2022). Our analysis used micronutrient density as the indicator for nutritional value, rather than total micronutrient supply, which is a function of both micronutrient density and the total availability of fish. Our decision to use nutritional density, rather than total supply, enabled us to compare across reef sites with very different total biomass, and ultimately revealed a trade-off between total biomass and nutritional density, which is an important consideration for understanding how reefs contribute to meeting the needs of stakeholders. A future study may investigate how total nutritional supply varies across multiple types of reefs.

Ecosystem service bundles analysis is a flexible method that uses data for multiple ecosystem service indicators at comparable spatial scales to produce information about relationships among services and spatial patterns of service production. However, data availability, scale of resolution, and spatial coverage remain important challenges. In our study, we faced a trade-off between the number of ecosystem services and the number of reef sites that could be included in the bundles analysis. Ecosystem service bundles analysis requires comparable data for ecosystem service indicators across all sites, thus, filtering the sites to include only those for which there was data for all seven ecosystem services was a necessary step. The datasets we used each contained a different number of reef sites; thus, the inclusion of additional ecosystem services came at the cost of fewer reef sites in the final analyses. While six out of seven ecosystem service indicators were modelled for the sites in the RLS database, coastal protection was derived from Mapping Ocean Wealth, whose spatial coverage is distinct from that of RLS. Filtering the reef sites to include only those with data for all ecosystem services resulted in the exclusion of sites which did not have data from both databases. The RLS database reef sites are locations where subtidal data collection efforts have taken place, thus, these may be sites which are more accessible by boat and perhaps close to human settlements. It is possible that filtering the sites in this way may have introduced bias by limiting the reef sites to those closer to human-built infrastructure, and increasing the representation of sites with the potential for human use and access to the reefs. However, this is an assumption. The small number of countries (18) with sufficient data coverage to be included in our study may limit the applicability of our results at a global scale. Future data collection and research efforts to improve data coverage across more countries for these ecosystem services would enable more robust analyses and confirm whether the reef clusters we identify are representative of all major reef regions around the world.

Additionally, since the reef sites from RLS and Mapping Ocean Wealth did not have perfect spatial match, we filtered them using a 50 km radius. This number represents a compromise that enabled us to include coastal protection values as close as possible to the reef sites in our analysis, while keeping the number of sites after filtering as large and globally distributed as possible. However, it should be noted that the 50 km distance we used to assign coastal protection data from Mapping Ocean Wealth to the RLS reef sites is larger than the distance over which reefs are typically considered to provide coastal storm protection. In a previous study modelling coastal protection from reefs, coasts were considered to have "low protection" from waves if they were further than 2 km away from a reef (Burke and Spalding, 2022). The 2-km distance represents the "maximum effect distance" for coral reefs used in The Natural Capital Project's InVest models (Chaplin-Kramer et al., 2019). However, as is the case with many ocean datasets, spatial overlap between the sites from different datasets was limited. In fact, we found only one RLS site with all six RLS ecosystem service values that was < 2 km of a Mapping Ocean Wealth data point for coastal protection. Therefore, filtering sites following the work of Burke and Spalding (2022) would have required a complete omission of the coastal protection ecosystem service from analysis. We acknowledge that this is a limitation of our study, and should be considered when interpreting the results.

Data on a wider range of ecosystem services would also allow us to assess whether the patterns of ecosystem service production we find are supported for a larger number of ecosystem services, and reveal additional trade-offs and synergies among services which may be important for marine policy. Social-ecological data at finer spatial resolutions would also enable more reliable assessment of the drivers of ecosystem service bundles. A fuller understanding of the social-ecological interactions producing particular bundles of ecosystem services requires identifying the spatial distributions of realized services to a set of key beneficiaries. However, achieving such a goal has a high data demand. An intermediate goal could be a fuller assessment of the social-ecological interactions of multiple actors on reefs, using available proxy data.

This study provides new knowledge on synergies, trade-offs, and spatial distributions of reef ecosystem service bundles at a global scale. The three reef clusters we identify reveal differences both in terms of the ecosystem services they generate and their social-ecological characteristics. Differences in service production among the clusters appear to be linked to differences across in key ecological traits, including total reef fish biomass and species richness. Building on this work to link ecosystem service bundles to policy and management will require placing the results of this study in the broader context of reef social-ecological systems and their spatiotemporal dynamics. Changes in

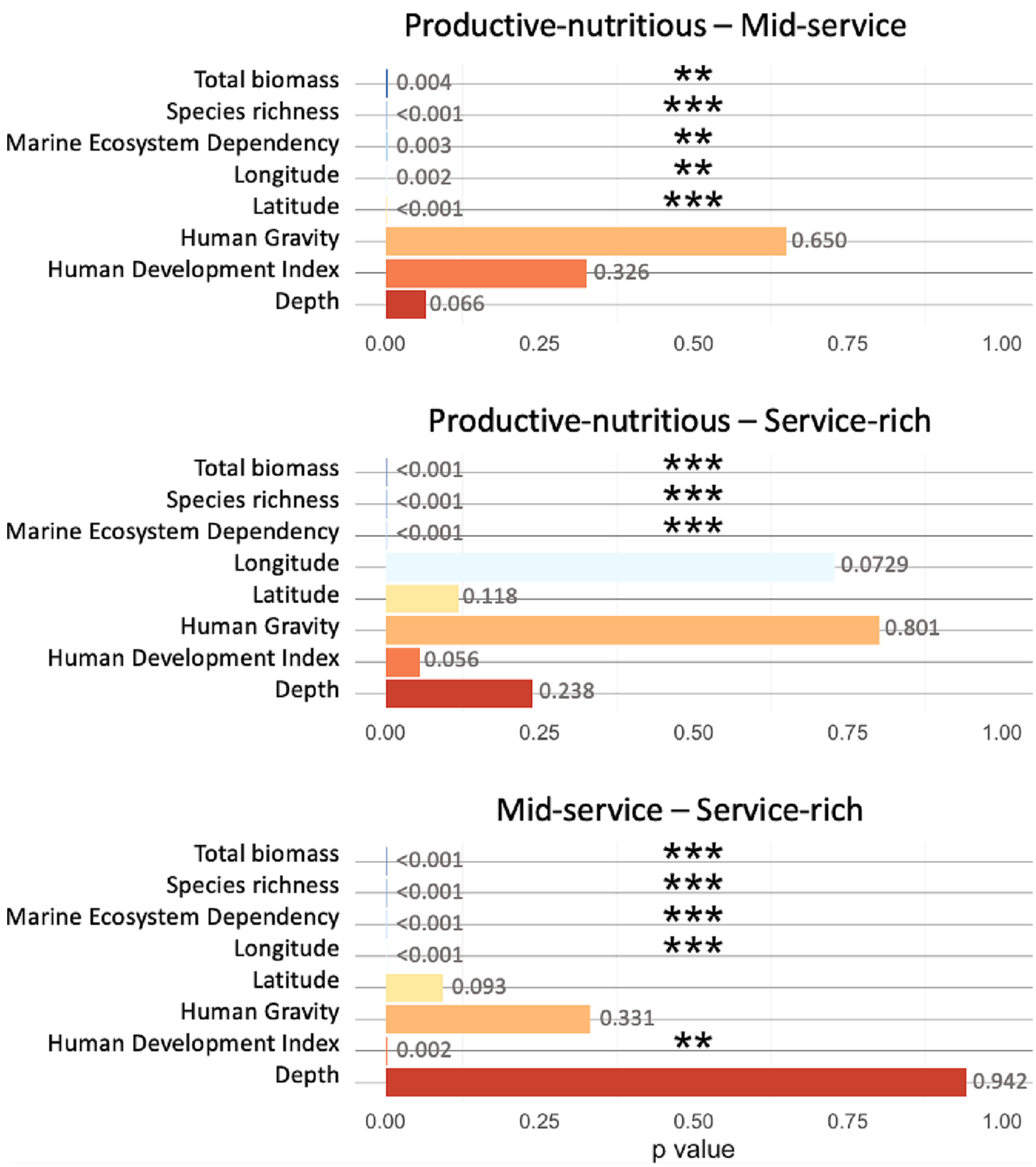

Fig. 6. Results of Tukey multiple pairwise comparisons showing p-values and significance of differences in social-ecological variables across each pair of clusters. Asterisks denote statistically significant differences in ecosystem service values for the cluster pair (* for p values < 0.5, ** for p values < 0.01, *** for p values < 0.001).

marine social-ecological systems affect ecosystem service supply and use, and alter the delivery of services to coastal stakeholders (Lapointe et al., 2021). Thus, the appropriate course of management action for each reef cluster will require careful consideration of the social-ecological context, the spatial scale of management, and the priorities of local communities and regions. Similar applications of ecosystem service bundles analysis in other marine and coastal systems could result in improved understanding of the spatial distributions of marine ecosystem services, which is a key input to marine policy (Maes et al., 2012). When performed at finer spatial scales and with a deeper understanding of the social-ecological context in which services are produced and used, the bundles analysis approach that we demonstrate here could be used to inform marine management that optimizes the production of desired ecosystem services.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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