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A review of ecosystem service supply in tropical marine ecosystems and its relationship to habitats in the Great Barrier Reef

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ABSTRACT

The benefits that people obtain from marine and coastal ecosystems are numerous and complex. Although marine ecosystem service approaches are increasing in prominence, relatively little is known about how marine ecosystem service provision relates to individual habitat types at the level at which they are typically considered in management and policy. To clarify and operationalise the links between tropical marine habitat types and ecosystem services, we undertook a literature review and a spatial mapping exercise. First, we systematically reviewed published studies of tropical marine ecosystem services, with the aim of describing the strengths and weaknesses of existing knowledge and directly linking identified ecosystem services to specific marine habitat types. Second, we tested whether we could use our new synthesis to connect ecosystem services to habitat types by mapping ecosystem service supply in a well-studied and iconic marine protected area, Australia's Great Barrier Reef Marine Park. The review showed that while some habitat types (particularly mangroves, seagrass and coral reefs) and their associated ecosystem services are well described, others (e.g. beaches, mudflats and surface waters) are far less explored. The mapping exercise showed that habitat mapping can provide a potentially useful interface between the types and locations of marine ecosystem services. Overall, tropical marine ecosystem services in our study area appear to be primarily clustered around coastlines and reefs and in close proximity to human populations. Our results highlight the potential value of ecosystem services approaches for informing management decisions that better connect ecological and human values in tropical marine environments.

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1. Introduction


Sustainable use of the planet's natural resources requires intense monitoring of supply and demand for ecosystem services (ES) to inform governance and management actions (Hein et al. 2020). Although ES approaches are increasing in prominence, there is a clear bias in their application towards terrestrial systems and high-income regions (e.g. Europe and the US) (Hattam et al. 2021). This has resulted in a 'blind spot' on ES assessments in marine environments (Lautenbach et al. 2019). In the tropics, this blind spot is particularly significant: marine ES are critical for the wellbeing and livelihoods of nearly a billion people (Sing Wong et al. 2022), with the loss and degradation of coastal ecosystems potentially affecting more than 1.3 billion people by 2050 (Lam et al. 2020).

Previous studies have recognised a number of important knowledge gaps in the ES literature on marine and coastal systems. First, more research is required into how ecosystem services are generated by different

habitat types (Carrasco De La Cruz 2021). Despite there being overlaps in ES supply across spatial scales, different habitat types may provide distinct ES. The lack of detail on specific connections between ES supply and individual habitat types in tropical marine environments makes it difficult to connect ES to the existing, habitat-based geographic data sets (e.g. benthic cover and bioregional maps) that are widely used to guide management plans.

Second, most marine ES research has been conducted in close proximity to coastlines. Limited research exists on the ES that the water column and open ocean provide (Stocker 2015). For instance, in their review of 145 papers, Liqueste et al. (2013) found that just 18% of articles focused on ES that are supplied by the open sea (Liqueste et al. 2013 in Carrasco De La Cruz 2021). The lack of ES valuations of the deep sea and open ocean is concerning given how important they are for the functioning of humanity (Carrasco De La Cruz 2021). When ES assessments

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focus on a limited range of habitat types, the overall value of an ecosystem or land/seascape can be greatly underestimated (Liquete et al. 2013).

Third, many coastal and marine areas in the tropics contain both high biodiversity and high human dependence on coastal ecosystem ES, but tropical waters are under-represented in ecosystem services research (Cumming et al. 2023). Compared to temperate marine and terrestrial systems information is lacking in certain aspects in tropical marine environments. For instance, human impacts in the tropics are often more difficult to illustrate and there is limited ES baseline data (Cumming et al. 2023). This makes tropical marine habitats and their potential for ES supply a high priority for further study (Cumming et al. 2023).

Not all ecosystem components and the services they provide found in the tropics have been studied through the lens of ecosystem services (Liquete et al. 2013). Therefore, our aim was to advance understanding of how ES are supplied by specific tropical marine habitat types. We also aimed to advance understanding of where ES are supplied by habitat types in a specific tropical location. In order to achieve these objectives, we undertook analysis that involved literature reviews and a spatial mapping component. First, we focused on systematically identifying published studies of tropical marine ES, understanding the strengths and weaknesses of existing knowledge, and trying to link the identified ES to specific marine habitat types. Next, we tried to connect ES to habitat types, focusing on mapping ES supply in a well-studied and iconic marine protected area, the Great Barrier Reef Marine Park (GBRMP) in Australia. The current state of the GBRMP under numerous threats has resulted in calls for the implementation of alternative management approaches like ES that more effectively highlight the independent relationship between people and nature. To our knowledge this is the first study that has attempted to systematically capture ES supply from individual habitat types in a tropical marine location. It thus offers both a valuable baseline for future tropical marine ES assessments and a starting point for future research on this topic.

2. Methods

Initially literature searches were conducted in Web of Science and Scopus to determine the ES classes that have been linked to tropical marine habitat types. Given the importance of ES in supporting tropical marine populations the number of peer reviewed research publications that have made links between habitat types and services was small. We dealt with this finding by adding a secondary and less exhaustive review focusing on marine and coastal habitat

types globally that have been connected to ES but not considered in a tropical context. For example, the extensive ocean surface layer and pelagic zone supply highly important functional ES on the GBRMP but have rarely been included in tropical ES assessments. The last step of our study involved mapping out the relationship between ES supply and habitat types on the GBRMP to show decision makers and future ES assessments how ecosystem services concepts can be operationalised in a tropical marine environment. The classification of habitat types used in this analysis was informed by a systematic review (Web of Science and Scopus searches) and the major habitat types identified in the 2019 Great Barrier Reef Outlook Report (GBR 2019).

2.1. Theoretical framework

The ways in which habitat types co-produce benefits with people are documented in the System of Environmental Economic Accounting – Ecosystem Accounting (SEEA EA) (Hein et al. 2020; Comte et al. 2022). However, given the three-dimensional and dynamic nature of marine environments, the relationship between habitat types and ES supply is not completely understood. Apart from a few more obvious or charismatic habitat types, such as reefs and mangroves, detailed information about ES supply arising from tropical marine habitat types is difficult to find and its application to specific locations is lacking. There is also a tendency in the literature for ES to be considered in silos (e.g. with a singular focus on storm protection or carbon capture), leaving an obvious gap in the form of a lack of general synthesis of tropical marine ES across multiple habitat types and services.

The links between tropical ES supply and habitat types are multifaceted and complex. In this study we define this link as the direct and indirect benefits individual habitat types provide to human populations as recognized in the tropical marine ES literature. Outside of the tropics, habitats have been frequently used as marine ecosystem service providing unit with EUNIS (European Union Nature Information System), an example of a commonly used classification framework (Galparsoro et al. 2014). In the tropics, however there is an absence of a standardised classification system for habitat types. This study builds on the work of Hattam et al. (2021) as one of the few tropically focused marine ES studies that selects habitat types as a suitable measure of ES supply.

ES are co-produced by people and nature through a dynamic social-ecological interaction that involves both the production of goods and services by ecosystems and the human values and received benefits that make elements of ecosystems valuable or beneficial to

people. Co-production refers to the ways in which human values and needs shape the flow of benefits people obtain from natural systems (Bruley et al. 2021). For example, the co-production of firewood by a social-ecological system has an ecological element of tree growth and senescence; and a human element by which wood is valued as a fuel for use in cooking food. In a society in which energy for cooking and warmth is provided by other sources, firewood provisioning is no longer an ecosystem service. For clarity, we use the term ‘ES supply’ to describe the primarily ecosystem-based part of the supply-demand co-production interaction.

The Common International Classification of Ecosystem Services (CICES) provides a well-structured, detailed typology of ES, and has a long, widespread use in marine research (Haines-Young and Potschin-Young 2018). We categorised ecosystem services using the hierarchical CICES classification scheme to create a standardised typology (Appendix 1) for the different marine and coastal ecosystem services discussed in the 49 included publications. CICES splits ecosystem services into three broad categories: provisioning services, regulating and maintenance services, and cultural services. Provisioning services include all the nutritional/non-nutritional materials and energy that are obtained from biotic and abiotic outputs (Haines-Young and Potschin 2012). Regulating and maintenance ES are produced when biotic and abiotic factors moderate the environment in ways that benefit people’s safety and health (Haines-Young and Potschin 2012). Lastly, cultural ecosystem services include all the non-material outputs by which ecosystems influence people (Haines-Young and Potschin 2012). Some ES fell in the abiotic ecosystem outputs category of the CICES classification (e.g. mineral substances used for nutrition). Most ES discussed in the literature fell into the biotic output categories, and so all other ES were classified into the broader categories of provisioning, regulating and maintenance, and cultural Ecosystem services and then into relevant sub-categories. After classifying each ES, we recorded the number of papers that referred to each service category.

2.2. Tropical marine literature

We used the Web of Science and Scopus databases to undertake a systematic literature review. We ran a topic search (which included the title, abstract, author keywords and keywords plus) in English, on the terms ‘ecosystem services’ OR ‘ecosystem service’ AND ‘marine’ OR ‘coastal’ OR ‘ocean’ AND ‘tropical OR inter-tropical’ AND/OR ‘review’. The identified papers were published between 2000 and 2022. This methodology identified 91 research papers, which we reviewed to identify lists of ecosystem services and/or

those which connected tropical marine habitat types to ES. Seventy-one papers were filtered out and consequently not used in the review (Figure 1). We then analysed the remaining twenty papers.

2.3. Secondary literature searches

Screening of explicitly tropical marine ES identified a range of ES that were primarily derived from mangrove, reef, and seagrass habitat types. These three habitat types were subsequently used as part of the geospatial analysis. Based on wider reading, several ES (e.g. food provision, nutrient cycling and carbon storage) that significantly benefit human populations in the GBRMP did not appear to be adequately represented. We therefore conducted additional searches to ensure the inclusion of marine ecosystem services that have been identified from other habitat types but were not mentioned in detail in papers focusing on tropical marine environments. For the secondary literature searches we used the Web of Science database. As we did not use the word ‘tropical’ (i.e. we included results from all marine and coastal areas) a significant number of results was generated and (keeping in mind that this was not the primary focus of the review) we did not need to further broaden the search using Scopus. The additional searches helped to ensure that the overall value and distribution of ES provided by our study system (the GBRMP) were not severely underestimated (Liquete et al. 2013).

The additional searches identified another 226 publications, from which 84 appeared suitable for more detailed screening and another 29 were added to the final dataset. Screening for marine and coastal studies added four habitat types that were discussed sparingly or not at all in the original 91 publications (the Web of Science and Scopus searches described in section 2.2): (1) beaches; (2) the seafloor; (3) the pelagic zone; and (4) the ocean surface layer. Beaches offer many ES (e.g. recreation, sites of symbolic significance, food provision and coastal protection; Harris and Defeo (2022)). Seafloor and pelagic habitat types are particularly important for commercial and recreational fisheries as well as thermodynamics and nutrient cycling (Thrush and Dayton 2002; Block et al. 2011). The ocean surface layer plays several important regulating roles in moderating the ambient environment (e.g. transfer of nutrients, trapping and transfer of heat, and carbon storage; Wohlers et al. 2009; Li et al. 2023). These habitat types were included for their global importance in tropical marine environments. Some more specific and geographically limited habitat types (e.g. *Halimeda*/macroalgae banks on the GBRMP) may be important providers of ES in certain tropical locations, but we decided to keep the level of our search

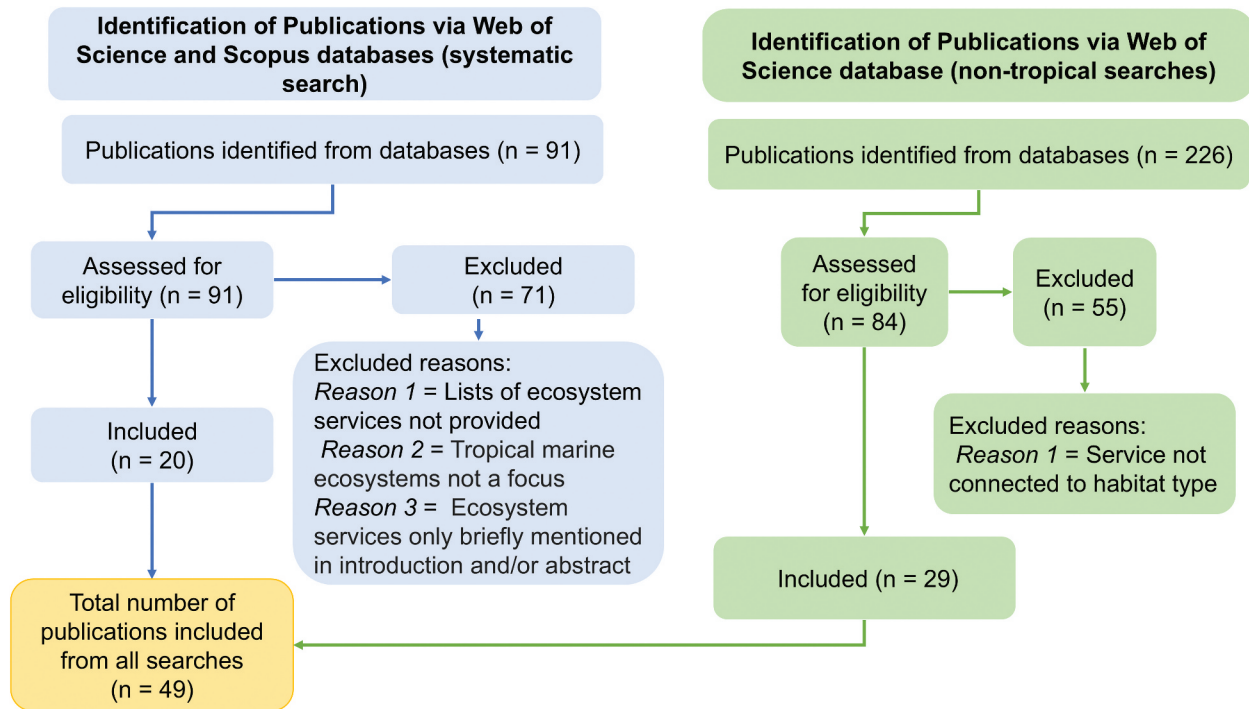


Figure 1. Flow diagram illustrating how the literature review was carried out. Flow diagram template follows PRISMA (preferred reporting items for systematic reviews) (Page et al. 2021). Blue boxes are for the original review on tropical systems that was carried out with the key words ‘ecosystem services or ecosystem service’ and ‘marine or ‘coastal’ or ‘ocean’ and ‘inter-tropical or ‘tropical’ and ‘review’. The green boxes are for the less exhaustive searches that were carried out to ensure that ‘missing’ marine ecosystem services identified from other habitat types but not mentioned in detail in tropical papers were included. Orange box represents all studies included for this study.

relatively general so that it would remain relevant to a wider range of locations.

We checked for additional publications within these types using four separate topic searches in Web of Science. Searches were not limited by year, and we removed papers that did not connect the chosen habitat type to an ecosystem service (Figure 1). We included searches for (1) beach habitat types, using ‘beach’, ‘habitat’ and ‘ecosystem services’ (‘beach’ generated numerous results (122) and hence other relevant terms like ‘sandy shore’ were not used here); (2) seafloor habitat types, using ‘seafloor’, ‘ecosystem services’ and ‘habitat’ (‘benthic’ primarily focused on coral, which was covered previously); (3) pelagic habitat types, using ‘pelagic zone’ and ‘ecosystem services’; and (4) surface layer habitat types, using ‘ocean surface layer’ and ‘ecosystem services’. ‘habitat’ was not used for pelagic and surface layer habitat types as it generated too few results. The lack of known connections between individual habitat types and ES supply informed the decision to include a small number of terms for each search. Once the search terms had been set, we alternated between screening the most cited and the most recent papers for studies that connected the chosen habitat type to an ecosystem service until no new types of ES were identified. For the ocean surface layer, which few studies explicitly connected to ES, we had to interpret ES from the literature.

The results of the second set of literature searches were used to illustrate how ES assessments of ecosystem services can be operationalised in a tropical environment in conjunction with data obtained from reef, seagrass and mangrove in the first systematic review (i.e. the results of these habitat types were used to supplement our geospatial analysis, Figure 4). Since the focus of this paper was tropical, the review results section and the discussion uses (only) the first Web of Science and Scopus search; and the presentation of results for this section is for the tropically focused literature review.

2.4. Linking marine and coastal ES to habitat types

This section of the analysis focused specifically on Australia’s GBRMP. We connected marine and coastal ES to habitat types by cross-referencing the list of ES produced in the first step of our analysis against existing habitat maps. We used existing information from the GBRMP, including publications identified through the literature review as well as the 2014 and 2019 Great Barrier Reef Outlook Reports (GBRMPA 2014, 2019), to determine which accepted habitat types occur within the study area and how they are aligned with particular ES. Each habitat type could be associated with one or more ES.

2.5. Visualising ES through habitat maps

We created a 2 × 2 km vector grid file ('fishnet') that spanned the extent of the GBRMP and extracted information about existing habitat types into each cell using ArcGIS Pro (Version 3.0.0) and R software. The resulting file contained information on geomorphic area coverages, benthic area coverages, coastal features, and bathymetry (Table 1).

We calculated benthic cover in and near to reefs by extracting the number of 5 × 5 m grid cells in The Allen Coral Atlas (Lyons et al. 2020; ACA 2022) that fall within each 2 × 2 km grid. To convert extracted values (pixel numbers) to km², each value was multiplied by 25 to convert to m² and divided by 1,000,000 to give Ha. The ACA categories that were included in this study were reef slope, reef crest, outer reef flat, inner reef flat, back reef slope, coral and or algae, sheltered reef slope, sand, rock, rubble and microalgal mats. These categories were chosen as they most closely aligned with the findings from the literature search. The geomorphic categories (reef slope, reef crest, outer reef flat, inner reef flat, back reef slope, coral and or algae and sheltered reef slope) were grouped together and averaged to form a broad overall habitat type for reef. Similarly, the benthic habitat categories (sand, rock, rubble and microalgal mats) were grouped together to form an overall habitat type for seafloor.

We used bathymetry data to define the surface layer habitat as any grid cell that did not possess the habitat types reefs, seafloor, seagrass, and mangroves and had a depth of greater than 1 metre. The pelagic zone was defined as occurring at a depth of 2 metres or greater. For beaches there was no available shapefile of adequate resolution across the GBRMP, so we excluded beaches from the visualisation exercise.

Following area conversions, based on the presence or/absence of ES, ES were added together to obtain the total number for each cell in the column. The Excel data were then imported back into ArcGIS Pro for visualisation.

3. Results

3.1. Tropical literature review results

Our first systematic Web of Science and Scopus review identified 23 ES arising from tropical marine ecosystem habitat types, which is 27.3% of the total ES in CICES v5.1. There were clear biases towards certain service classes (Figure 2). Regulation and maintenance ES were discussed most frequently ($n = 56$) in the selected studies (Appendix 3). This was followed by provisioning ES ($n = 22$) and cultural ES ($n = 19$). Most studies that have reviewed tropical marine provisioning ES have focused on food provisioning ($n = 7$) and income generation from wild capture fisheries ($n = 7$). The most described regulation and maintenance service class was coastal protection ($n = 10$). This was followed by the role of habitat in providing species refuge/nursery sites ($n = 8$). For cultural ES, most studies focused on income generation from tourism ($n = 4$) and recreation ($n = 3$).

The number of papers explicitly making a connection between tropical marine habitat types and ES was highest for the broad biogenic habitat types of reefs, mangroves, and seagrass (Figure 3). Mangroves were identified most often as sources of tropical marine ES ($n = 44$), followed by seagrass ($n = 35$), coral reefs ($n = 27$) and other reefs ($n = 18$).

Overall, we found a relatively weak connection in the tropical, marine and coastal literature between marine and coastal habitat types and ES, with few studies considering multiple ES produced by the same habitat type or exploring finer sub-divisions in service supply within broadly-defined habitat categories. For example, there was little to no consideration of habitat age, stage or condition as influences on ES. Reef habitat, for instance, may show high or low structural diversity or fish productivity, with quite different levels of service supply (Morais et al. 2023); but most ES analyses treat reef as a single generic habitat type. We also found that the majority of studies focused on ES supply from just one habitat

Table 1. The different shapefiles used to map habitat types across the GBRMP. All of these data sets are publicly available. A full list of all assumed links between habitat types and ES is provided in Appendix 2.

Original Shapefile Name	Source	Description
Great Barrier Reef Marine Park Boundary	GBRMPA web portal	Boundary of the Great Barrier Reef Marine Park
Great Barrier Reef Features	GBRMPA web portal	Map of polygon outlines of all reefs and islands in the GBRMP
Cairns Plan of Management (POM) Locations	GBRMPA web portal	Dataset that shows where the Cairns Area plan of management (POM) is located spatially
Coral reef benthic classes and geomorphic zones	Allen Coral Atlas (Lyons et al. 2020)	Description of seafloor habitat at 5 × 5 m resolution within boundaries of Great Barrier Reef Features (see above)
Queensland coastal wetlands data set 1987-1997	eAtlas version of DEEDI (2010) wetlands data set	1:100,000 coastal wetland vegetation mapping for the Queensland coastline including mangrove communities, salt pans and saline grasslands. See https://eatlas.org.au/data/uuid/7548432f-36d3-4333-a3c5-49a7b0c311cf . (checked 22-3-23)
Queensland seagrass meadows data set	Carter et al. (2021)	Seagrass meadows, shapefile in polygon format obtained from eAtlas. See https://eatlas.org.au/media/3559 . (checked 22-3-23)
Bathymetry (ocean floor depth) data set	Beaman (2010)	Interpolated bathymetry data for the Great Barrier Reef at 100 m resolution. Available at https://eatlas.org.au/data/uuid/200aba6b-6fb6-443e-b84b-86b0bbdb53ac (checked 22-3-23).

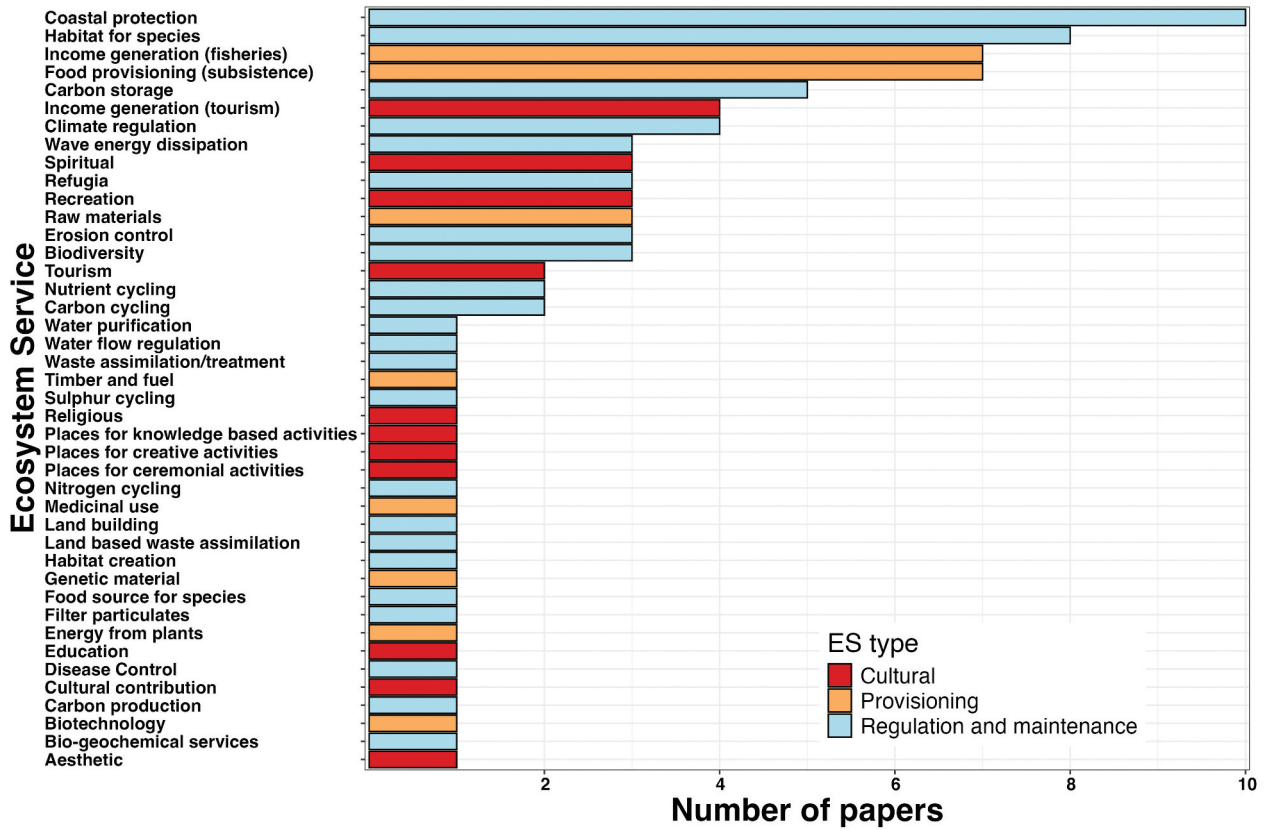


Figure 2. Counts of the number of tropical marine papers that referred to different service classes. These are the exact terms used in the literature. Service classes broken into provisioning, regulation and maintenance and cultural categories.

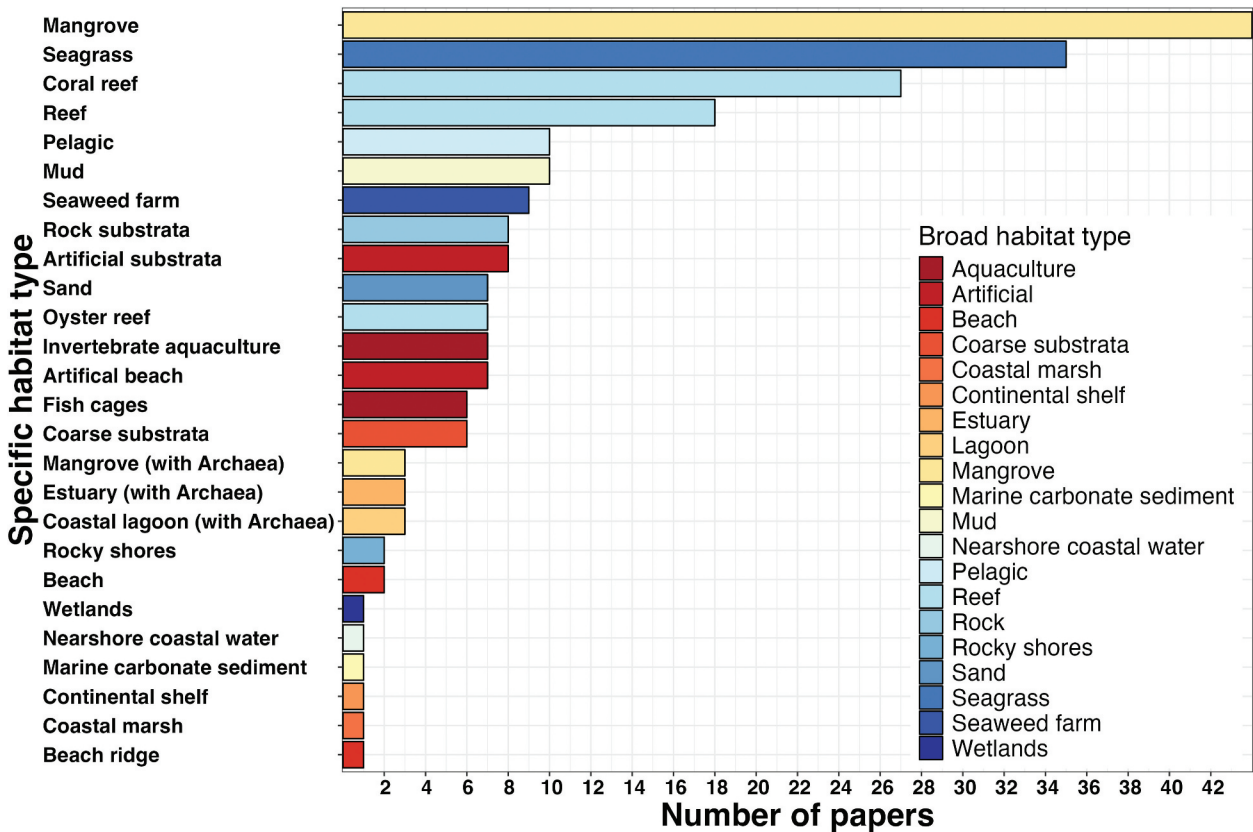


Figure 3. Counts of the number of times an ecosystem service class was connected to a specific habitat type within the papers assembled during the tropical marine literature review. Bars with the same colour scheme belong to the same broad habitat type (e.g. light blue bars represent habitat types that could fit into the broad habitat type of Reef).

type and linked a small number of services to an individual habitat. There has been limited discussion in the marine literature about how different habitat types can supply the same groups or bundles of ES.

3.2. Secondary coastal and marine results

While the focus of the results section is on the Web of Science and Scopus review, it is nevertheless interesting to note that similar findings were observed for literature searches conducted on marine and coastal areas (i.e. including both tropical and temperate marine regions). Regulation and maintenance services were discussed most frequently ($n = 38$) and the ES classes of tourism ($n = 2$), food provisioning ($n = 3$) and the role of habitats in providing refuge for species ($n = 6$) were mentioned in the literature.

3.3. Visualising ES through habitat maps

Our review of the international literature suggests that ES supplied by marine and coastal habitat types on the GBRMP are concentrated around reefs and coastlines (Figure 4 and Appendix 3, Figure A3). The highest number of ES ($n = 27$) occurred in locations (grid cells) where seagrass, mangrove, reef, and seafloor habitat types occurred in close proximity (Figure 4). This was followed by grid cells where reef, mangrove and seafloor habitat types occurred ($n = 25$). The lowest number ($n = 3$) of ES were concentrated in open water areas (in pelagic and surface layer habitat types; Figure 4). Diversity of ES was also higher closer to shore. For instance, ES discussed in the pelagic zone and the surface layer habitat types were primarily those of regulation and maintenance. Some provisioning ES were also mentioned at greater distances from shore.

4. Discussion

To our knowledge this is the first study that has attempted to systematically capture ES supply from individual habitat types in a large, tropical marine protected area. The literature review coupled with the habitat mapping component show that ES supply from tropical marine systems, where data and synthetic analyses have been significantly lacking compared to temperate environments (Townsend et al. 2018, Lautenbach et al. 2019, Hattam et al. 2021), is clustered around coastlines and offshore structural habitats such as reefs and cays. Our analysis provides a potentially useful reference point and approach for future ES assessments that focus on tropical marine ecosystems, as well as illustrating research gaps in tropical settings that may limit our capacity to operationalise ES measurement.

4.1. Tropical marine ES, habitat types and mapping

From the literature on ES in tropical marine environments, we identified 23 ES classes produced by the broad biogenic habitat types of reefs, mangroves and seagrass. Consideration of published studies from the marine environment outside the tropics yielded another five ES classes (Appendix 1). Our results suggest that the tropical ES that were commonly represented in the literature were generally those that can be more easily quantified in monetary terms, such as those in the CICES service classes of coastal protection, recreation and income generation from tourism and food provisioning (Milcu et al. 2013; Fish et al. 2016). Surprisingly few studies considered the importance of the surface layer and pelagic zone for ES supply; beaches appear to be another largely overlooked habitat type in studies of ES supply in tropical systems.

The exercise of trying to link coastal and marine ES to habitat types and then map out and visualise them showed very clearly that the highest supply of ES was located around coastlines and reefs, often in close proximity to people. This may reflect the general bias in the literature towards ES assessments along the coastline, but it is also strongly reflective of ease of access as an influence on ecosystem use (Chaplin-Kramer et al. 2022). Our results suggest that although the habitat mapping approach has considerable potential for identifying the locations of ES, several important conceptual and practical gaps need to be addressed before convincing ES maps can be produced for tropical marine locations such as the GBRMP. Some of the more challenging questions for ES characterisation and mapping that arose from our review include that of how best to connect cultural ES to habitat types; how to integrate spatially dispersed ES, such as regulation and maintenance ES that occur patchily over broad extents, into ES mapping exercises; how to represent the supply of ES that depend on the interactions between different habitat types, such as the dependence of some reef fish on mangroves for the survival of their juvenile stages; and how to incorporate environmental and ecological dynamics, such as seasonality in ES supply related to breeding and animal migrations, into assessments.

4.2. Tropical ES supply and links to habitat types

A focus on food supply for provisioning ES was expected given the significant direct benefits that food resources provide coastal populations (Mumby et al. 2008). Tropical reefs, despite their relatively small area, currently account for as much as 10% of fish consumed by people around the globe (Lough 2008; Shin et al. 2022). In temperate marine

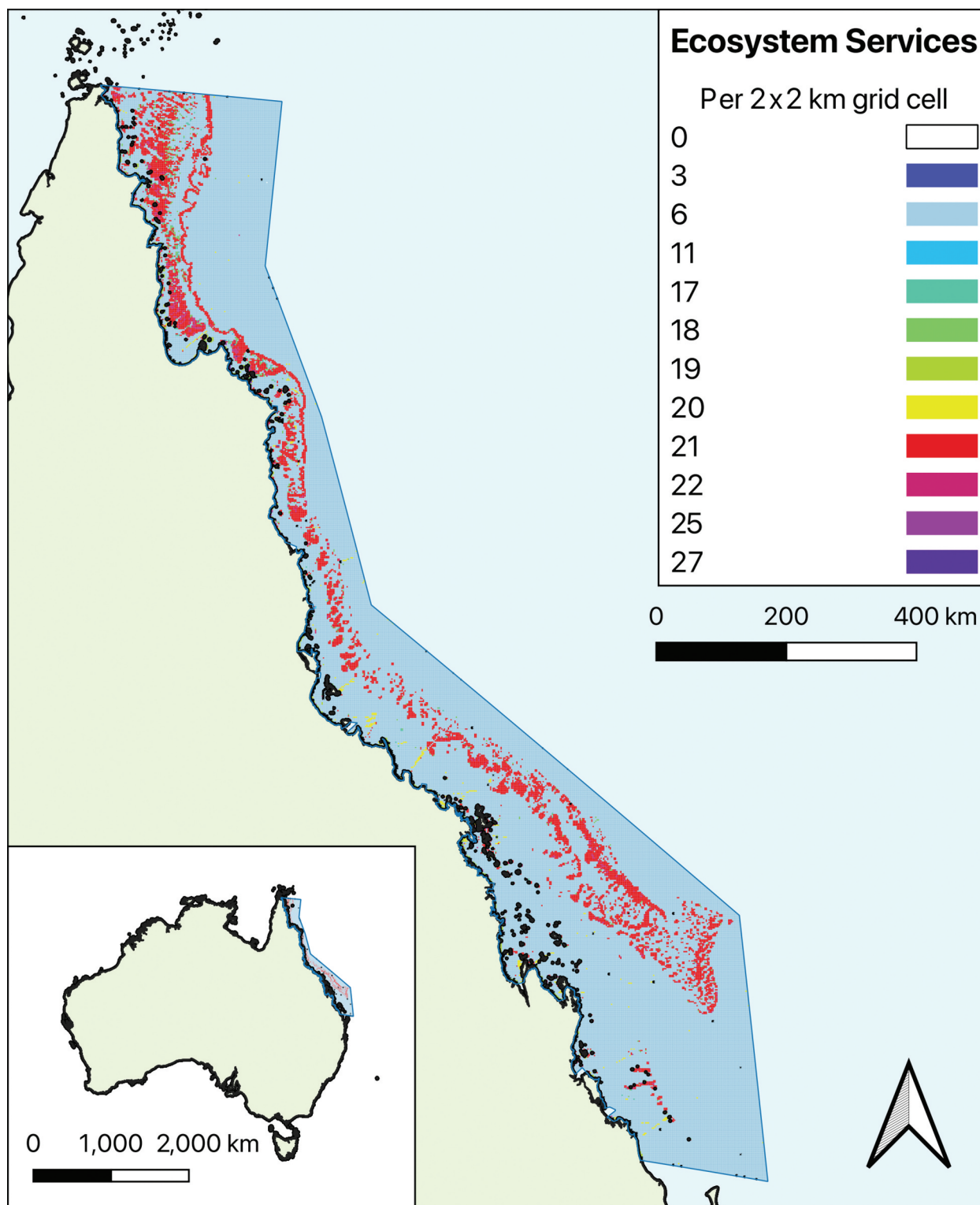


Figure 4. Total number of ecosystem services supplied by each 2×2 km grid cell in the Great Barrier Reef Marine Park. This map shows how (1) assigning ecosystem services to habitat types and then (2) mapping a literature-derived inventory of services by habitat type can provide a spatially explicit overview of ecosystem service provision in a large marine protected area. Colours indicate the number of services provided by each grid cell. Note that some numbers are missing in the legend because grid cells only possessed certain numbers of services: 0, 3, 6, 11, 17, 18, 19, 20, 21, 22, 25, 27. The major habitat types included are reefs, seagrass, mangroves, the seafloor, the pelagic zone and the ocean surface layer. Habitat type choices were based on the results of the literature review and the classification of major habitat types in the 2019 Great Barrier Reef outlook report (GBR 2019).

environments, food provision (primarily fisheries) has been the most analysed provisioning service (Liquete et al. 2013). Most other provisioning ES classes (e.g. the extraction of mineral resources from tropical marine systems) do not possess such clear

indicators of value and hence are largely overlooked in both the research and management space.

Several reviewed studies identified the wide range of material and energetic outputs provided to people by reefs, seagrass, and mangroves. For instance,

Hernández-Delgado (2015) discussed the value of reefs in providing food to coastal communities as well as providing raw materials for the cosmetic industry. The many provisioning ecosystem ES provided by mangroves include fuel, wood and timber (Worthington et al. 2020). Studies that analysed service supply at finer spatial scales (e.g. habitat type in relation to distance from shore) found that certain provisioning ES only occur in particular habitat types. For example, the harvesting of wild oyster populations is an important source of income for tropical communities in shallow coastal and estuarine waters (Richardson et al. 2022).

The considerable emphasis in the published literature on coastal protection was not surprising given the vulnerability of tropical coastal ecosystems to anthropogenic climate change and rises in sea surface levels (Barbier et al. 2011; Brooks et al. 2020; Steinberg et al. 2020) and the number of indicators in place to value this service. For instance, research has assessed the replacement costs associated with the building of artificial breakwater structures to value the coastal protection service afforded to people by mangroves (Pascal et al. 2016). Several other regulation and maintenance ES have also been discussed in the literature; for instance, Hyndes et al. (2018) explored the role of seagrass in primary production. However, service classes such as primary production are difficult to conceptualise and have historically been characterised as supporting/intermediate ES in other ES frameworks as they support a range of other services. Our findings imply a need for a diverse range of stakeholders to agree on better ways in which to measure and include regulation and maintenance services that do not possess clear indicators of value.

Our literature review also highlighted the important contribution of reefs and seagrass towards regulation and maintenance services in tropical marine environments. For example, coral reefs can play an important role in element cycling (Dsikowitzky et al. 2019). Similarly, seagrass provides numerous regulation and maintenance ES (Ugarelli et al. 2017). The biological and morphological composition of seagrass mean that seagrass habitat types not only play an important role in coastal protection, but also effectively reduce exposure to bacterial pathogens through the presence of phytochemicals (Ugarelli et al. 2017). There is again a gap, however, in understanding variance in regulation and maintenance service delivery at finer spatial scales (e.g. differences between inshore seagrass and deep-water seagrass). This information would more effectively provide us with knowledge on the strength of regulation and maintenance service supply across a spatial gradient.

Tropical marine ecosystems provide significant opportunities for tourism activities and recreation

(Popova et al. 2019; Hattam et al. 2021). Studies that discussed cultural ES highlighted the importance of tropical reef-related tourism as a foreign currency earner for many nations around the world (Wolff et al. 2023). The cultural service of recreation was commonly considered in relation to leisure activities on the beach (Wolff et al. 2023). As people become concentrated in coastal areas, it is expected that there will be increased trade-offs between recreation and other ES (Harris and Defeo 2022). For instance, with more people participating in recreational activities along shorelines we could see increased pressure on the coastal protection capacities of beach and dune systems.

While discussions of cultural ES often focused on tourism and recreation, there were also brief discussions of other less commensurable service classes (e.g. Hernández-Delgado 2015; Hattam et al. 2021). For instance, Hattam et al. (2021) mentioned the potential of certain areas to serve as places of ceremony and education. However, overall, there was limited information in the literature on cultural ES classes. Greater recognition of the cultural differences and identities that underpin people's relationships with nature, as proposed in the Nature's Contributions to People framework (Martin et al. 2016; Pascual et al. 2017), might improve our ability to map cultural ES. By making different cultural identities visible to decision makers it should be possible to identify the types of shared values that are important for the creation of sustainable human environment interactions (Pascual et al. 2017). A different conservation framing might be useful in determining whether habitat mapping offers an appropriate way to describe cultural ES supply; when only select service classes are included in ES studies, the worth of the system in question can be under-estimated (Liquete et al. 2013).

The majority of papers that we reviewed investigated links to ES through one habitat type. For instance, Paiva et al. (2023) reviewed the impacts of marine carbonate mining and the associated impacts on the supply of raw materials; and Risandi et al. (2023) studied the ES of coastal protection afforded by seagrass in Indonesia. The few studies (e.g. Dsikowitzky et al. 2019; Hattam et al. 2021; Wolff et al. 2023) that considered multiple ES supply across different habitat types acknowledge that there are interdependencies between services across space (Hattam et al. 2021). ES that were commonly mentioned together across habitats (mostly for reefs, seagrass and mangroves) were food provisioning, income generation (provisioning), coastal protection, habitat for species, recreation and tourism (mostly supplied by reefs). This finding suggests the presence of ES bundles, which may be useful in future studies

for identifying common ES trade-offs and synergies (Kermagoret et al. 2019).

4.3. Challenges in mapping tropical marine ES

The practical exercise of trying to map habitat types that we had identified as relevant for ES supply highlighted three locally specific problems that are likely to have parallels in other marine locations, particularly given that the GBRMP provides a relatively data-rich context in which to work. First, appropriate habitat maps at comparable scales were unavailable for many ES. For example, the only fully extensive spatial data for mangroves was outdated, being based on the Queensland coastal wetlands data set at a scale of 1:100,000 and spanning 1987–1997 (DEEDI 2010). There were more recent maps for mangrove distributions along the GBRMP, but their extents were often incomplete or not easily accessible. By contrast, the broad-scale, standardised Allen Coral Atlas benthic cover data set was very useful for illustrating ES at the habitat level on the GBRMP; but these data describe habitat type without additional information such as habitat condition. There is a connection between the condition of ecosystems and the ES they provide (La Notte et al. 2022). Information such as habitat condition would be needed to move beyond presence/absence of an ES to describe how much of the service is produced. A lack of appropriate habitat maps was particularly relevant for cultural ES, where several elements of the marine environment that are culturally significant (e.g. beaches, sites of historical value, habitat types of Indigenous significance) have not been consistently mapped over the extent of the GBRMP. Despite efforts to centralise GBRMP data in a few locations for ease of access, we also encountered typical problems with different versions, different data servers and challenges in tracking down some data sets. For example, The Great Barrier Reef Marine Park Authority's Reef Knowledge System website (created August 2022a) provides copious amounts of spatial data information (GBRMPA 2022b) and offers a central point for obtaining information on ES at the habitat level on the GBRMP. At the same time, however, the Australian Bureau of Statistics' National Ocean Account has released (29/11/22) a wide range of information on ES including data about the extent and density of mangroves (ABS 2022); and information on commercial fishing activities and fisheries is held separately in a different database.

A second locally specific problem likely to have parallels in other contexts was that available data layers tended to focus on obvious biophysical characteristics such as vegetation or coral cover; few maps were available that interpreted the relevance of combinations of these features for other organisms that

provide particular ES, for example through mapping dugong habitat or locations favoured by recreational fishers.

A third problem was that most maps were relatively static; there was little or no material available that could be used to integrate animal movements, seasonality, or oceanic currents and tides into habitat maps. For example, some parts of the GBRMP are particularly important for migratory species such as birds and lobsters, but the information that would be needed to map and incorporate these seasonally important habitat types into ES maps is often diffuse and difficult to locate.

We did not attempt to relate ES supply to actual human usage of ES, although some ancillary data exist that could be used for this purpose (Cumming and Dobbs 2019). The actual benefits derived from ES will change along a gradient from inshore to offshore, with differences in access resulting in offshore ES potentially being less used (and hence, providing less 'service') (Chaplin-Kramer et al. 2022). In this context it is nonetheless interesting that the majority of ES are produced at the interface of the land and the sea, where they are more accessible to people than offshore ecosystems.

4.4. Future research priorities

Our analysis provides a strong starting point for ES supply from tropical marine habitat types, but many gaps and weaknesses were identified through this exercise. The framework used here identified a particularly large gap in marine ES research in relation to incommensurable ES classes (e.g. cultural ES and certain regulation and maintenance ES). The incorporation of multiple strands of evidence (e.g. traditional ecological knowledge, biophysical metrics and stakeholder perceptions) and the use of different ES frameworks could be used to build a greater understanding of the contribution that less tangible service classes make to human populations (Harris and Defeo 2022).

Advancing research on ES supply from tropical marine habitat types will also rely on the creation of more sophisticated ways in which to map ES. In order to move beyond presence/absence of ES, factors such as seasonality, animal migration patterns and habitat quality need to be included in habitat data layers. With more detailed information on factors such as habitat quality and ES bundles, it would be possible to explore and include ES information in spatially explicit analysis that is used to guide management (e.g. in the form of marine spatial planning or the establishment of different use zones on the GBRMP).

5. Conclusion

Using the GBRMP as a case study, we showed how a spatially explicit overview of ES supply created from published literature and existing geospatial data can provide a direct and explicit connection between management units ('habitats') and benefits to people. Given that the sustainable management of marine protected areas relies on maintaining both ecological and human values, our findings highlight the benefit of incorporating ES approaches in management decisions as a way of connecting these values and understanding their relationships to each other. The inclusion of measures of habitat quality into analyses of ES supply emerged as a particularly important priority for future research. Understanding the geography of ES co-production will be critical for future efforts to prioritise and conserve ES (Castro et al. 2014). Once refined, this approach has the potential to guide and facilitate the sustainable governance and management of ES in tropical marine environments.

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