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CORAL REEF FUNCTIONAL ECOLOGY IN THE ANTHROPOCENE

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Coral reef ecosystem services in the Anthropocene

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Abstract

1. Coral reefs underpin a range of ecosystem goods and services that contribute to the well-being of millions of people. However, tropical coral reefs in the Anthropocene are likely to be functionally different from reefs in the past. In this perspective piece, we ask, what does the Anthropocene mean for the provision of ecosystem services from coral reefs?
2. First, we provide examples of the provisioning, regulating, cultural and supporting services underpinned by coral reef ecosystems. We conclude that coral reef ecosystem service research has lagged behind multidisciplinary advances in broader ecosystem services science, such as an explicit recognition that interactions between social and ecological systems underpin ecosystem services.
3. Second, drawing on tools from functional ecology, we outline how these social–ecological relationships can be incorporated into a mechanistic understanding of service provision and how this might be used to anticipate future changes in coral reef ecosystem services.
4. Finally, we explore the emergence of novel reef ecosystem services, for example from tropicalized coastlines, or through changing technological connections to coral reefs. Indeed, when services are conceived as coming from social–ecological system dynamics, novelty in services can emerge from elements of the interactions between people and the ecosystem.
5. This synthesis of the coral reef ecosystem services literature suggests the field is poorly prepared to understand the changing service provision anticipated in the Anthropocene. A new research agenda is needed that better connects reef functional ecology to ecosystem service provision. This research agenda should embrace more holistic approaches to ecosystem service research, recognizing them as co-produced by ecosystems and society. Importantly, the likelihood of novel ecosystem service configurations requires further conceptualization and empirical assessment. As with current ecosystem services, the loss or gain of services will not affect all people equally and must be understood in the context in which they occur. With the uncertainty surrounding the future of coral reefs in the

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Anthropocene, research exploring how the benefits to people change will be of great importance.

KEYWORDS
co-production, functional space, functions, novel ecosystems, service provider, social–ecological systems, traits, well-being

1 | INTRODUCTION

Under the pressure of global and local stressors, it is increasingly likely that tropical coral reefs of the future will be different from those documented in the recent past (Hughes et al., 2017). Stressors include marine heatwaves, ocean acidification, over-fishing, pollution and physical damage, which each interacts and selects for different response traits within the coral assemblage (Ban, Graham, & Connolly, 2014; Hughes et al., 2018). For example, some species of coral are more vulnerable to heat stress than others, resulting in differential mortality and recovery rates across coral taxa (Loya et al., 2001). In cases of severe heat stress, this can lead to altered community assemblages and a decline in functional diversity (Yadav, Alcoverro, & Arthur, 2018). Reef-associated fish species are also differentially affected by climate change, habitat alteration and other selective pressures like fishing (Wilson, Graham, Pratchett, Jones, & Polunin, 2006). It is likely that whilst some coral reefs will undergo regime shifts towards a different ecological state (Norström, Nyström, Lokrantz, & Folke, 2009), other reef ecosystems will continue to be dominated by calcifying organisms and will be characterized by a different set of structures and functions (Alvarez-Filip, Carricart-Ganivet, Horta-Puga, & Iglesias-Prieto, 2013). Understanding and predicting future configurations of reef organisms and the functions they provide is highly challenging, especially as these may be increasingly decoupled from underlying natural biophysical processes (Williams, Gove, Eynaud, Zgliczynski, & Sandin, 2015).

Reef ecosystem functioning is connected to the well-being of millions of people who directly or indirectly benefit from tropical corals reefs (Moberg & Folke, 1999). These benefits, or ecosystem services, are often grouped under provisioning (defined as the products obtained from ecosystems), regulating (the benefits resulting from the regulation of ecosystem processes), cultural (encompassing cognitive and experiential benefits) and supporting services (services that underpin the provision of other services) (MEA, 2005). Despite over three decades of research into ecosystem services, we continue to have a poor understanding of how ecosystem structures and functions underpin the capacity of coral reefs to provide services. For example, declines in the structural complexity of reef habitat are often linked to changes in fish communities, with likely impacts on fishery services (Pratchett, Hoey, & Wilson, 2014). However, recent modelling and empirical research suggests that increases in herbivorous fish are able to maintain fishery yields under certain conditions (Robinson et al., 2019; Rogers, Blanchard, Mumby, & Arlinghaus, 2018). The links between ecological change and services may therefore be more complex than originally suggested (Daw et al., 2016).

The Anthropocene signifies a time in which human activities are the principal drivers of change across scales (Steffen, Grinevald, Crutzen, & McNeill, 2011). This presents a challenge for ecological research that must actively engage in understanding the human dimensions of coral reefs and the feedbacks between social and ecological systems (Williams et al., 2019). Understanding these relationships has important ramifications both for future well-being and future coral reef configurations. Against this backdrop, this paper asks the question: what does the Anthropocene mean for the provision of ecosystem services from coral reefs? First, we explore some of the conceptual advances in ecosystem services research outside of coral reef science. Second, we draw on approaches in functional ecology to propose a mechanistic basis for connecting between changes in reef functions and services. Finally, we reflect on whether novel reef ecosystems could also result in novel ecosystem services.

2 | ECOSYSTEM SERVICES FROM TOPICAL CORAL REEFS

Tropical coral reefs around the world underpin a wide range of services (Table 1; Moberg & Folke, 1999). Some of the most well-studied provisioning services include fisheries (e.g. Grafeld, Oleson, Teneva, & Kittinger, 2017), cultural services include recreation and tourism (Brander, Beukering, & Cesar, 2007), and regulating services include coastal protection (Ferrario et al., 2014). Other provisioning services include aquarium fish and building materials that come from reefs (Albert, Olds, Albert, Cruz-Trinidad, & Schwarz, 2015). Reefs also underpin a number of other important regulating services such as the generation of sand (Perry, Kench, O'Leary, Morgan, & Januchowski-Hartley, 2015) and the processing of nutrients (Archer, Stevens, Rossi, Matterson, & Layman, 2017). Many of these service groups are inter-related; for example, the presence of white sands generated by reef processes is closely linked to reef tourism (Spalding et al., 2017). Cultural services reflect the fact that coral reefs constitute unique spaces that are generative and supportive of human experience. As such, reefs underpin a diversity of livelihoods and associated identities (Cinner, 2014) and also provide opportunities for research and education (e.g. Motuhi, Mehiri, Payri, Barre, & Bach, 2016). Supporting services include important habitat and biodiversity services for the reef and adjoining ecosystems (Fisher et al., 2015; Gillis et al., 2014) that indirectly contribute to human

TABLE 1 Examples of ecosystem services drawn from tropical coral reefs

MEA category[a]	Ecosystem service	Definition[b]	Examples
Supporting (underpins the provision of all other services)	Biodiversity benefit	Describes the services and benefits gained from having a diverse reef ecosystem that underpins other services and benefits	Tropical coral reefs are one of the most biodiverse ecosystems containing approximately 830,000 species world-wide (Fisher et al., 2015) The diversity of reefs contributes to the maintenance of a genetic library (Moberg & Folke, 1999)
	Habitat	Describes the services and benefits gained from having a reef ecosystem that provides key habitat	Corals engineer the environment, interacting with and creating suitable conditions for other tropical nearshore ecosystems (Gillis et al., 2014) The structural complexity of reefs provides important refugia for species (Graham & Nash, 2013) Reefs provide habitat for species at different life stages (Ortiz & Tissot, 2012)
Regulating (regulates the environment)	Coastal protection	Describes the services and benefits gained from reefs providing coastal protection from waves and extreme weather events	Coral reefs dissipate 97% of the energy that would otherwise hit shorelines. This shoreline protection benefits 197 million people who live below 10 m elevation and within 50 km of reefs (Ferrario et al., 2014) Across reef coastlines, reefs reduce annual expected damages from storms by more than $4 billion (Beck et al., 2018)
	Water quality and biogeochemical cycling	Describes the services and benefits gained from the cycling of nutrients and other material on reefs	Coral mucus acts as an energy carrier between reefs and other nearshore environments (Wild et al., 2004), whilst sponges play an important role in transferring energy and nutrients between trophic levels (De Goeij et al., 2013) Decades of land reclamation in Seychelles has influenced water quality and coral reef fishers identify the role of biotic and abiotic processes around reefs in helping to disperse sediment loads (Hicks, Stoeckl, Cinner, & Robinson, 2014)
Provisioning (goods and services from nature)	Fishery	Describes the services and benefits gained from fishing on reefs	Fish provide vital nutrition to many coastal communities (Golden et al., 2016). From 2009 to 2013, the nearshore fishery in Hawaii provided 7.7 million meals annually (Grafeld et al., 2017) Fisheries products from reef environments include a range of taxa that are used for subsistence and cash income (Albert et al., 2015) Coral reef fisheries provide diverse livelihood opportunities. More than a quarter of small-scale fishers fish primarily on coral reef ecosystems (Teh, Teh, & Sumaila, 2013). Reef fishers get enjoyment, a sense of personal and cultural identity, prestige and a lifestyle from fishing (Cinner, 2014)
	Materials	Describes the services and benefits gained from the use of materials, other than comestibles, from reefs	In the Solomon Islands, sand and coral is harvested for use in construction, land reclamation and betel nut consumption (Albert et al., 2015) 1,471 species of fish, 140 species of coral and more than 500 species of non-coral invertebrates are harvested from reefs world-wide for use in the aquarium and curio trade (Wabnitz, Taylor, Green, & Razak, 2003)
Cultural (cognitive and experiential benefits)	Cultural	Describes the services and benefits gained from reefs as generative and supportive of human experience	Coral reefs can underpin the discovery of compounds with high biotechnological potential (Motuhi et al., 2016) Reef tourism is calculated to be worth *ca.* US $35.8 billion dollars globally per annum (international and domestic visitors). This includes on-reef tourism (e.g. diving, snorkelling and glass bottom-boat tours) and indirect contributions from reefs to tourism (e.g. calm waters, beaches, views, seafood and their use in advertising) (Spalding et al., 2017)[c] In Hawaii, the gathering and sharing of fish encompasses a range of cultural values including subsistence values (physical and cultural), activity values, knowledge values and social cohesion (Grafeld et al., 2017)

[a]This is the Millennium Ecosystem Assessment (MEA) category that the service is most often classified against but this may vary on a case by case basis. For example, coastal protection could be considered a regulating and supporting service depending on the time-scale and immediacy of impact it has on people (MEA, 2005). [b]These definitions are intended to be broad enough to capture the diversity of ways in which an ecosystem services framing can be applied to the interactions between human well-being and coral reef ecosystems. Specific approaches may adopt a more restricted definition. [c]The distinction between recreation and tourism is not often made in the literature, but generally, tourism refers to the activities of often stayover visitors and recreation refers to the activities of local residents (Laurans et al., 2013).

well-being, but are challenging to capture in terms of their independent service value (Hicks, 2011).

Moberg and Folke (1999)'s paper is one of the earliest efforts to identify and categorize ecological goods and services from coral reefs, and connected coral reef science to the then growing interest in ecosystem services. Their approach embodied an ecological perspective on the services provided by coral reef ecosystems and highlighted the challenges of connecting biological complexity and the provision of goods and services. Since then, our understanding of reef structures and functions in the context of environmental change has increased, whilst reef condition has continued to decline (Hughes et al., 2017). Despite this, the types of services identified from reefs have arguably changed very little. In contrast, the broader field of ecosystem services research has evolved, with wider engagements across disciplines and knowledge systems, and richer conceptualizations of how nature provides benefits to people (e.g. MEA, 2005; TEEB, 2010; Díaz et al., 2015). For example, ecosystem service approaches have engaged more broadly with the social sciences and are adopting a more critical approach to the relationships between services and different groups of people (Chan et al., 2012). For instance, recent work in Spanish wetland ecosystems shows that not all stakeholders benefit equally from ecosystem services, and that variables such as formal education, gender, and rural versus urban livelihoods can be key factors influencing the access of individuals or groups to ecosystem services (Felipe-Lucia et al., 2015; Martin-Lopez et al., 2012). Furthermore, science–policy arenas such as the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES)—and specifically its thematic assessment of pollinators, pollination and food production—are piloting approaches to bring indigenous and local knowledge into assessments (Tengö et al., 2017).

In parallel to wider disciplinary engagement, the form in which services are conceptualized has also developed. Many approaches assume a linear relationship, with services flowing from ecosystems to people (Haines-Young & Potschin, 2010). These often recognize that services are inherently social and ecological but ultimately focus on one or other aspects of this relationship. However, people actively modify ecosystems to influence the delivery of services. Aquaculture, for example, is primarily adopted in marine and coastal systems to enhance food production, but can also be used to support the delivery of other services such as restoring biogenic habitat (Froehlich, Gentry, & Halpern, 2017). Moreover, people and cultures are shaped by ecosystems (Caillon, Cullman, Verschuuren, & Sterling, 2017). For instance, activities that can take place in marine and coastal environments such as shellfish harvesting form an integral part of place attachment that is connected to personal experiences, social relationships, heritage values, ecological knowledge and local identity (Poe, Donatuto, & Satterfield, 2016). Recent approaches to assessing ecosystem services are now more explicitly engaging with the fact that services are the result of interactions between people and ecosystems (Fischer & Eastwood, 2016), which is increasingly important in the context of a human-dominated planet. An approach that captures the interactions between social and ecological systems can be applied to understand how ecological changes are received by different people (Hamann et al., 2018) and how human actions, in relation to changing services, feedback onto the ecosystem (Reyers et al., 2013). If predicted changes in reef ecosystem functioning affect the perception of services, then an approach that recognizes services as co-produced from social and ecological systems could provide analytical tools for connecting changing ecosystems, changing services and future reef functions. Few studies to date, however, have fully explored what the co-production of services on reefs would look like.

Ecosystem services research continues to develop, with active discussion ongoing as to its future direction (Braat, 2018; Díaz et al., 2018; Peterson et al., 2018). Similarly, in coral reef ecosystem services research there is no one conceptual or methodological leading edge. Publications from 2018 encompassed work on changes in ecosystem service provision (Reguero, Beck, Agostini, Kramer, & Hancock, 2018), economic assessments of services (Robles-Zavala & Reynoso, 2018), patterns and preferences across service beneficiaries (Lau, Hicks, Gurney, & Cinner, 2018) and the use of services for management prioritization (Pittman, Poti, Jeffrey, Kracker, & Mabrouk, 2018). Drawing on the advances of wider ecosystem services science could help identify gaps and future research opportunities. Moreover, as future reef community assemblages are unlikely to be the same as those seen in recent times (Graham, Cinner, Norstrom, & Nystrom, 2014), the relationships between ecosystem structures, functions and services will likely change, requiring a more mechanistic understanding of these processes, and likely more anticipative management (Rogers et al., 2015).

3 | A MECHANISTIC APPROACH TO SERVICE PROVISION

Trait-based approaches are increasingly used to understand the mechanistic basis of ecosystem service provision (Harrison et al., 2014). Functional traits are broadly defined as measurable characteristics of an organism that contribute to ecosystem functioning (McGill, Enquist, Weiher, & Westoby, 2006). The presence or absence of different traits can determine differential responses to disturbances (Haddad et al., 2008). For example, the shape and size of corals determine their risk of dislodgement during storms (Madin & Connolly, 2006). Where there is overlap between traits that contribute to specific functions and traits that respond to disturbances, it is possible to map out relationships between drivers of change and ecosystem functions (Suding et al., 2008). This has recently been extended to include relationships between disturbances, functions and services (Hevia et al., 2017). However, few studies have explicitly connected this to coral reef services and a more systematic approach to trait identification is needed for this to be achieved (Carturan, Parrott, & Pither, 2018). We propose that expanding this mechanistic approach to reflect the co-production of ecosystem services could provide a useful tool to understand the impact of ongoing and future disturbances to reef ecosystem services.

If services are co-produced between ecological and social systems, then the ecological units that underpin services, known as service providers, should be defined in relation to the needs, wants and aspirations of beneficiaries (Luck et al., 2009). Identifying service providers as distinct from wider ecosystem functioning resonates with previous findings that proxies of ecological condition and proxies of ecosystem service provision from reefs do not always overlap (Mumby et al., 2008). Specific characteristics (i.e. traits) of service providers determine the relationships between providers and the services that they underpin. Importantly, service providers could be a population of a species, multispecies groups, functional groups, communities and habitats (Luck et al., 2009). Moreover, if services are born out of interactions within coral reef social–ecological systems (Reyers et al., 2013), it follows that the traits of service providers can also be defined based on societal needs and preferences (Goodness, Andersson, Anderson, & Elmqvist, 2016). A working example of this comes from Seychelles where underwater visual census of fish biomass indicates that an increase in herbivores is sustaining fisheries yield two decades after a mass coral bleaching event. Fishery data however indicate that although catches were maintained, they became more spatially and temporally variable linked to habitat associations when resources are patchy (Robinson et al., 2019). This potentially exposes fishers and markets to greater uncertainty. By acknowledging the traits of service providers that are relevant to service beneficiaries (here the identity, biomass and predictability of the reef fish assemblage; Rogers, 2019), a more holistic understanding of how disturbance impacts services may be captured.

Trait-based approaches have been growing in popularity in functional ecology research as acquiring high resolution data on species' functional roles remains challenging (Bellwood, Streit, Brandl, & Tebbett, 2019). Similarly therefore, methods that adopt a trait-based approach can be applied to develop a mechanistic understanding of the links between disturbances and service provision. For example, tools such as a multivariate functional space could be applied to understand the mechanisms through which disturbances act on ecosystem services. A functional space is defined as "a multidimensional space, where the axes are functional traits along which species are placed according to their functional trait values" (p.167, Mouillot, Graham, Villeger, Mason, & Bellwood, 2013). A similar multidimensional space, where the axes are the traits of service providers along which ecosystem services are placed, could be used to map the response of services to disturbances (Figure 1). Axes may also represent synthetic traits that through ordination techniques summarize the relative contribution of multiple traits that underpin service provision.

In identifying traits of service providers that are socially and ecologically significant, it may be possible to determine relevant thresholds below which a reef's potential to provide services is lost (Figure 1). For example, Shideler and Pierce (2016) found that divers who visited Florida during *Epinephelus itajara* (Atlantic goliath grouper) spawning season had a strong preference for goliath grouper sightings and that abundance had a positive effect on divers' willingness to pay to see them. Goliath groupers are a protected species in Florida, and the value of goliath grouper to dive tourism operators is likely to diminish if goliath grouper numbers decrease (Shideler & Pierce, 2016). The threshold value below which this ecosystem service is no longer provided is set by the expectations of the tourists. A service could therefore be lost from an ecosystem even if the service provider, here the local population of goliath groupers, persists. Of course, population abundance is also important in the functional role of many species but defining thresholds that reflect the co-production of ecosystem services can highlight when a service may be affected by a disturbance, before or after other tangible shifts in ecosystem functioning.

Service providers can also encompass a wide range of ecological groups. For example, different taxonomic groups and processes are responsible for sand generation from reefs (Perry et al., 2015). The loss therefore of one calcifying species or even family may have little effect on the overall provisioning of this service. Defining a threshold at which disturbances affect the capacity of reefs to generate sand is therefore challenging. In cases like this, certain services may continue to be underpinned by even highly disturbed or degraded reefs, particularly when considering that alternate benthic states also support relevant service providers (Fulton et al., 2019). These examples illustrate that relationships between ecological change and services are highly nonlinear (Daw et al., 2016), which is significant when anticipating future changes in services and peoples' response. An example at the local reef scale might include fish feeding, used to enhance tourism services, but which can result in changes in fish behaviour and distribution (De Paula, Schiavetti, Sampaio, & Calderon, 2018). However, it is increasingly important that changes in ecosystem services are considered within an inter-connected planet, as changes in local service provision may result in an increased reliance on service providers elsewhere, with the potential for knock-on effects (Pascual et al., 2017). For instance, demand for *Holothuria* sp. (sea cucumbers), largely driven by Asian luxury seafood markets, leads to dramatic changes in fisheries in Mexico with the arrival of new fishers, new livelihood opportunities, and changes in resource use and institutional power dynamics (Kaplan-Hallam, Bennett, & Satterfield, 2017).

Gathering evidence for traits that are socially and ecologically relevant to service provision will require a broad transdisciplinary approach. Returning to the goliath grouper example in Florida, divers have a predominantly positive interaction with this species whereas recreational fishers may have negative perceptions that groupers are over-predating other reef species (Shideler & Pierce, 2016). The relationships between goliath grouper abundance and the provisioning of two recreational services could therefore be very different. Moreover, ecosystem services are highly context dependent (Andersson et al., 2015). Looking at the social–ecological context in which services are co-produced can help identify socially and ecologically relevant traits of service providers (Table 2). Lastly, it is understood that the traits of service providers may be connected in

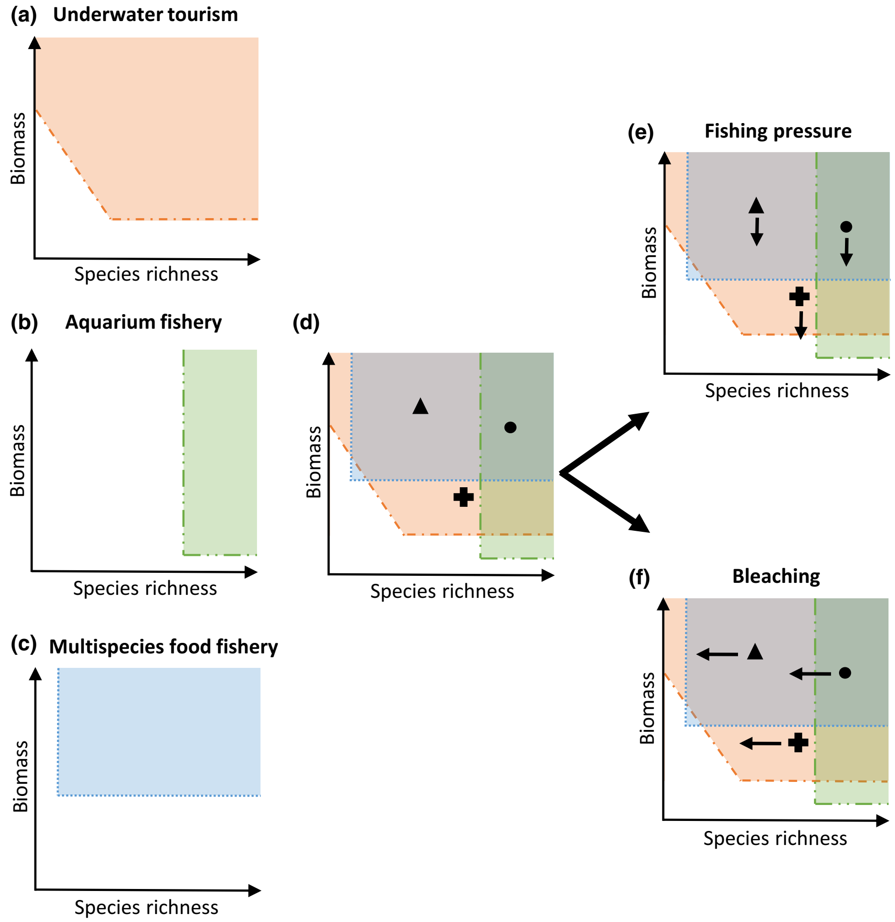

FIGURE 1 Visualizing changes in the capacity of coral reefs to underpin three ecosystem services: (a) to (f) are multidimensional spaces with axes representative of biomass and species richness (traits) of the reef fish community (service provider) that are significant in the provisioning of three ecosystem services from coral reefs: underwater tourism, an aquarium fishery and a multispecies food fishery. Panels (a) to (c) indicate the area above which trait values are sufficient to underpin the three ecosystem services. These areas could be determined by the ecology (e.g. number of fish available to a fishery) or society (e.g. levels of fish species richness and abundance that result in aesthetically pleasing reefs for dive tourism); (d) indicates the potential of three different coral reefs to underpin services: ▲represents a site with the potential to underpin a multispecies food fishery and underwater tourism. ✚ could underpin underwater tourism services, and ● has the potential to underpin all three ecosystem services; (e) and (f) outline the possible effects of disturbances on traits underpinning service provision and the capacity of the reef sites to provide services. In (e), fishing pressure at all three sites has a negative effect on biomass and under this scenario ✚ is unable to support underwater tourism services. In (f), bleaching at all three sites has a negative effect on species richness. Under this scenario, the potential for ● to underpin an aquarium fishery is lost. The use of multivariate spaces to visualize ecosystem service potential from reefs can show when reefs may be close to losing or gaining the ability to underpin different services

multiple ways to multiple services (Hevia et al., 2017), and that there are important interactions to consider between services (Bennett, Peterson, & Gordon, 2009). Most ecosystem service studies focus on one or two services, but a mechanistic understanding of multiservice provision will be important for monitoring and managing future changes (De Groot, Jax, & Harrison, 2016).

4 | NOVEL ECOSYSTEM SERVICES

Questions remain as to whether reefs are able to sustain current ecosystem services into the future (particularly under high degradation; Table 2). However, as environment and society continue to change in the Anthropocene, novel ecosystem services may emerge from coral reef social–ecological systems. We propose that novel ecosystem services from coral reefs could originate from changes in social and ecological systems, as well as from changes in the interactions from which services are drawn. Novelty could therefore occur at different points in the co-production of services.

Changes in the underlying ecology of reefs will likely result in new or different configurations of service providers. For example, the tropicalization of temperate areas is occurring in many locations, where corals and tropical fishes are establishing populations at the expense of temperate rocky reef organisms (Vergés et al., 2019). This could lead to the presence of novel service provider combinations that may change the services drawn from an area. In Japan, where

TABLE 2 Identifying traits of service providers and possible outcomes for coral reef ecosystem services in the Anthropocene. Identifying traits of service providers that are relevant to the social–ecological context in which services are co-produced can provide a more nuanced mechanistic understanding of how coral reef ecosystem services respond to disturbances. Examples provided on changes in coral reef ecosystem services are based on moderate (with some patches live coral cover intact) and severe levels of reef degradation (no remaining live coral cover)

Ecosystem service (MEA category)	Examples of traits likely to underpin service provision	Importance of social–ecological context	Ecosystem service changes in the Anthropocene
Fishery (Provisioning)	Species composition and suitability of gear (Hicks & McClanahan, 2012) Biomass and accessibility of target species (Robinson et al., 2019) Nutritional value of locally available species (Golden et al., 2016)	Specific traits will be highly dependent on local diversity, the capacity of local fisheries and the needs and choices of consumers. For example, the effect of changes in fish aggregating behaviour will in part be determined by fishers' access to appropriate gear and knowledge that enable them to continue fishing. Populations' needs and preferences will also determine the substitutability of different species in the fishery.	Reefs with moderate degradation in a matrix of reef habitats may continue to contribute to food security and local livelihoods (Robinson et al., 2019). Other sources of food and employment will be needed to meet the shortfall (Bell et al., 2013). Reefs that cannot support reef-associated species will be unable to sustain fisheries with health implications, including the loss of a vital source of micro-nutrients (Golden et al., 2016), and socio-economic consequences from the loss of livelihoods and associated knowledge.
Coastal protection (Regulating)	Structural complexity (Graham & Nash, 2013) Carbonate budgets (Januchowski-Hartley, Graham, Wilson, Jennings, & Perry, 2017) Reef height and depth (Ferrario et al., 2014) Socio-cultural importance of coastal areas (Hicks et al., 2014)	Coastal protection services from reefs are determined by the abiotic (e.g. wave height and geomorphic setting), biotic (e.g. reef growth rate and resulting structure), and socio-cultural context in which coastal areas are used. Importance of coastal areas can be ascribed in terms of population density or built assets, or in relation to the activities that take place there. For example, many beaches are used as places to clean fish and socialize.	Reefs with moderate degradation may continue to provide some protection to coastal areas, though there may be changes in shoreline positioning. Reefs could be used to inspire coastal protection solutions that help address issues of reef degradation and coastal protection (Reguero et al., 2018). A combination of severe weather events, sea level rise and reef degradation may result in reefs being unable to protect current shoreline configurations. Atolls may become un-inhabitable (Storlazzi et al., 2018), and there may be tensions in re-locating people and activities from the coast further in land.
Underwater recreation (Cultural)	Fish abundance, coral condition and reef colour (Uyarra, Watkinson, & Cote, 2009) Accessibility of reef sites (Yee, Dittmar, & Oliver, 2014) Presence and/or abundance of charismatic species (Giglio, Luiz, & Schiavetti, 2015)	There is large variation in the preferences and expectations of underwater tourists. Although certain general rules may apply (e.g. accessibility), the preferences of dive operators and tourists will determine the importance of different traits. For instance, less experienced divers tend to prefer charismatic species, whilst more experienced divers tend to prefer cryptic species.	Reefs with moderate degradation that retain some fish biomass may remain aesthetically pleasing (Uyarra et al., 2009), though some species specific tourism may decline. Reefs that are in relatively better condition may attract dive tourism because of their rarity. Reefs with high degradation may sustain low levels of tourism from inexperienced divers more interested in the excitement and experience of diving (Lucrezi, Saayman, & Merwe, 2013). Declines in water quality and sand production may affect beach aesthetics and other water-based activities.
Habitat (Supporting)	Species richness (Duffy, 2019) Structural complexity (Graham & Nash, 2013)	Different reef regimes are characterized by a variety of species assemblages and processes that co-exist at scales relevant for service provision. Identifying which reef regimes occur within a study area can help identify traits of service providers that reflect the natural variability of reef communities, that services come from a matrix of habitats, and that many reefs are already transitioning away from a dominance of hard coral cover.	Coral reefs with moderate degradation may be able to sustain some habitat. Different reef states support different species and processes. Specific adaptations (e.g. through behavioural plasticity) may also mitigate the effects of habitat loss (Karkarey, Alcoverro, Kumar, & Arthur, 2017). Reefs with no live coral cover and no structural complexity are unlikely to be able to provide habitat for reef-associated species. Herbivorous species may benefit from increases in algal growth but will be negatively affected if algal stands are too dense (Hoey & Bellwood, 2011).

hard corals are encroaching on temperate reefs at a rate of 14 km a year, Nakamura, Feary, Kanda, and Yamaoka (2013) suggest tropicalization may benefit local dive tourism and fisheries productivity (Figure 2). Of course, species incursions into temperate areas will alter ecosystem functioning of temperate habitats and potentially the pre-existing services they generated (Vergés et al., 2019).

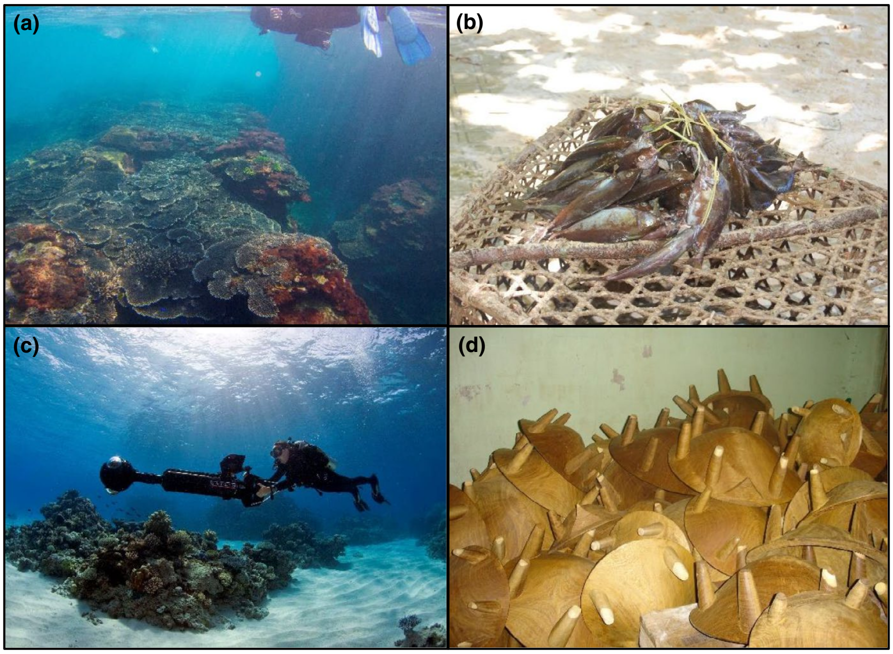

FIGURE 2 Novel ecosystem services from coral reefs. (a) Tourist diving on a tropicalized reef off Kochi, Japan. Tropicalised reefs provide a growing number of opportunities for tourism and education with local children (Y. Nakamura, *personal communications*.); (b) A packet of *Siganus sutor*, Praslin, Seychelles. Siganids are herbivorous and can sustain fishery yields on regime-shifted reefs (Robinson et al., 2019); (c) XL Catlin Seaview SVII camera and diver, the Coral Sea. This camera captures 360° panoramas of reefs allowing anyone to self-navigate on a virtual dive (XL Catlin Seaview Survey, 2015); (d) Tanoa bowls from Kabara, Southern Lau, Fiji. Tanoa bowl carving brings in a relatively high income in Kabara, which may decrease dependency on marine resources (Turner et al., 2007). (Photographs: (a) Takuma Mezaki; (b) and (d) Nick Graham; (c) The Ocean Agency/XL Caitlin Seaview Survey)

Reefs underpin services within a matrix of habitats (Guannel, Arkema, Ruggiero, & Verutes, 2016), which are also under pressure from climate change and local human activities (Unsworth, McKenzie, Nordlund, & Cullen-Unsworth, 2018). In addition, anthropogenic structural alterations are increasingly present in nearshore environments through artificial reefs, land reclamation, aquaculture and coastal defences. Dominance by altered benthic habitats may sustain services traditionally associated with hard coral-dominated reefs. For instance, naturally occurring areas of tropical macroalgae can support a diversity of fish and other organisms, including some of important fishery value (Fulton et al., 2019). Macroalgae on regime-shifted reefs can also support herbivores, which can sustain substantial fishery yields (Robinson et al., 2019; Figure 2). Further work is needed to understand the longevity of interactions that produce services on altered reefs (Rogers et al., 2018) and to understand what services could occur from structurally and functionally different reefs interacting with modified nearshore environments.

Novelty could also emerge from circumstances that mediate the interactions between reefs and people. In the western Indian Ocean, there is evidence to suggest that rights, knowledge, economic, and social and institutional processes combine in locally specific ways to determine the bundles of services that people perceive (Hicks & Cinner, 2014). Changes in any of these processes could therefore result in altered relationships in the co-production of services. Technological innovation has arguably changed how people perceive reefs, for example the use of underwater photography to document the world's reefs in 360°, making it possible for people to experience reef environments virtually (XL Catlin Seaview Survey, 2015) (Figure 2). These changes can connect reefs to much broader audiences, who are not traditionally considered as benefitting from reef ecosystems (Gurney et al., 2017).

Finally, novelty could come from changes in the well-being of people who benefit from reef ecosystems. Ecosystems and well-being are both multidimensional, and there is the possibility for mismatches between ecological and well-being outcomes (Abunge, Coulthard, & Daw, 2013). Though connected through ecosystem services, human well-being and the environment are both influenced by a range of processes external to that relationship. Independent of reef condition therefore, changes in the circumstances of individuals can result in a change in the interactions from which services are born. For example, the importance of fish as a provisioning service may decline when other income generating activities increase (Turner et al., 2007). This does not mean that other services, like cultural services, attached to fish and fishing are not maintained, but the interactions through which services occur may shift, with implications for how people engage and potentially shape their environment (Turner et al., 2007) (Figure 2).

5 | CONCLUSIONS

Research approaches that can incorporate the social–ecological dynamics of reefs are increasingly seen as essential for understanding reef futures in the Anthropocene (Williams et al., 2019). However, explicitly engaging with the reciprocal nature of coral reef ecosystem services remains a challenge (Bennett et al., 2015). To address this, we draw on conceptual advances in the field of ecosystem services research and tools from functional ecology to propose an approach that recognizes the co-production of services from interactions between social and ecological systems. Using this framework, we can begin to identify traits that are socially and ecologically relevant for service provision (Table 2), and to connect these traits to disturbances (Figure 1). Reflecting more broadly on the co-production of services incentivizes the need to also consider whether novelty in ecosystem services could occur (Figure 2).

It is unlikely that coral reef ecosystem services in the future will be the same as they are now (Table 2). Evidence suggests for example that coral reef fisheries in some tropical Pacific countries will be unable to meet local nutritional needs in the long term due to climate change, but in the short term due to the demand from growing human populations (Bell et al., 2013). Further work is needed to identify possible causal relationships between traits and perceived ecosystem services (Bellwood et al., 2019; Carturan et al., 2018), and these relationships are highly likely to be context dependent (Andersson et al., 2015). Filling these knowledge gaps will be useful for predicting changes in the mechanistic basis of services, but will not give an indication of who is accessing services. Understanding the implications of changing and novel ecosystem services should therefore be incorporated into wider research on who is perceiving these services (Fortnam et al., 2019), whilst cognizant of the fact that the relationships between people and the environment can change independent of reef condition (Turner et al., 2007). Nonetheless, embracing a broader understanding coral reef ecosystem services and a research agenda that links reef functional ecology to ecosystem service provision will be an important step in anticipating the challenges faced by people and reefs in the future.

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AUTHORS' CONTRIBUTIONS

All authors contributed equally to the conception and development of ideas. A.J.W. led the writing of the manuscript. All authors contributed critically to the drafts and editing of the manuscript and gave final approval for publication.

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